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THE VEGETATION ON BAUXITIC SOILS IN JAMAICA

RICHARD A. HOWARD AND GEORGE R. PROCTOR

With nine plates

THE OCCURRENCE of a red-colored, mineral-bearing soil in the Greater Antilles has been recorded in the literature of the area for nearly one hundred fifty years. In the past the principal mineral element has been considered to be iron and its occurrence has been recorded in quantities of commercial significance. It has also long been recognized that these red soils of Jamaica, Cuba, Haiti and the Dominican Republic, generally called "terra rossa" are not particularly fertile for agricultural purposes. The agricultural worker has recognized that terra rossa soils also possess peculiar physical properties relative to erosion, water absorption, slickness to traction and texture. The farmer has acknowledged that special techniques are necessary for even marginal crop production and the botanists have learned of often unusual and endemic plants occurring on these soils.

For Jamaica, the first significant mention of aluminum ores in the red soil appeared in the memoirs of the first official Geological Survey when C. Barrington Brown described a "red ferruginous earth" widely covering a limestone formation as "principally a mixture of iron and alumina" (Sawkins Mem. Geol. Survey (Jam.) 167–8, 1869). While several analyses were made for mineral and agricultural purposes in the succeeding years, it was not until 1939 during the course of a systematic chemical investigation of soil types in Jamaica that the red soils of Jamaica were discovered to contain sufficiently high alumina and low silica percentages to make the soil a satisfactory source of commercial aluminum. Similar deposits are also known from Haiti (Goldich, S. S. & Berquist, H. R., Aluminous lateritic soil of the Republic of Haiti, W.I., U.S. Geol. Sur. Bull. **954–C**: 1948) and from the Dominican Republic (Goldich, S. S. & Berquist, H. R., Aluminous lateritic soil of the Sierra de Bahoruco Area, Dominican Republic, W.I., U.S. Geol. Sur. Bull. **953–C**: 1947). The analytical work of the Agricultural Chemistry division of the Department of Agriculture in Kingston, Jamaica, was directed to a study for improvement of the red, infertile soils of the limestone districts. The first efforts of analysis and improvement were applied at Grove Place in the parish of Manchester and at Bull Savanna in the parish of St. Elizabeth. Similar soils in other parishes then came in for attention and it was in this way that Sir Alfred D'Costa, often incorrectly given credit for the discovery of alumina in Jamaica, secured the analysis of soils on his properties in the Lydford area near Claremont in St. Ann parish. An investigation directed towards commercial exploitation of these potential ore-producing areas was speeded by the war effort in the early 1940's. Post-war surveys later revealed ore in commercial quantities in other areas of Jamaica and between 1949 and the present time three industrial concerns have bought lands for the mining of aluminum-bearing ores. It is now recognized that a major portion of the land surface of the island of Jamaica contains aluminum-rich ore, a sizable percentage of this in commercial quantities, and that bauxite will constitute a major national resource of the island for many years to come. Bauxite and alumina together currently represent the second largest source of income for the island.

The commercial utility of the infertile "terra rossa" soils, however, does not remove the practical and scientific problems of the agricultural use of these soils, both now and in the future, and the botanical problems concerning the nature of the vegetation which occurs in such areas. In fact, commercial mining, using strip-mining techniques, poses other problems in the reclamation of the land and its proper use in the future. In this regard it is encouraging to note that the aluminum mining companies and the government of Jamaica, with its departments of mining, agriculture and forestry, are attempting a many-sided approach to the problems of adaptation and use of bauxite soils prior to and following mining, as well as independent of the mining processes. The legal position of mining operations in Jamaica is covered by The Bauxite and Alumina Industries (Encouragement) Law, Law 12 of 1950. The problems involved are clearly reflected in the Order made under the Law by the Governor in Executive Council on the 18th of September, 1950. This Order stated in part that "the recognized producer shall at all times maintain or cause to be maintained all lands . . . vested in or occupied by the recognized producer and which immediately before they became so vested or occupied were used for agricultural or pastoral purposes in as efficient a state of agricultural or pastoral productivity as such lands were immediately before they became so vested." The second condition of the order is that "so soon as may be after mining operations are concluded in any particular sector the recognized producer shall (a) restore every acre mined in such sector to the level of agricultural or pastoral productivity of such acre which existed immediately prior to the commencement of the mining thereof: or (b) if the Commissioner of Mines is satisfied that it is not economically practicable to comply with the provisions of sub-paragraph (a) of this paragraph as the Government of Jamaica may elect either (i) clear or reclaim one acre of land which immediately prior to such clearing or reclamation was not used for agricultural or pastoral purposes for each acre mined, in the relevant sector; or (ii) pay to the Government of Jamaica the sum of fifty pounds in respect of each acre so mined."

Thus legally the Government of Jamaica recognizes that arable land surfaces are limited in relation to an increasing population which basically has depended and will continue to depend upon its land for sustenance and profit. The law in the basic paragraph is an attempt to continue in useful condition lands temporarily withdrawn from the use of private citizens or small land-holders. The law recognizes that pastures or arable lands left idle in Jamaica, as elsewhere in the Caribbean, are soon reclaimed by noxious weeds, tenacious shrubs or forest growth, imposing on future owners tedious and expensive labor for land reclamation. The law specifies that once mining operations are concluded lands are to be restored to a level of production equal to that which existed prior to the mining process. A far-sighted law further recognizes that the mining of bauxite, being strip-mining in principle, may alter contours of the land in such a way that returning the area to its original condition relative to vegetation is impractical and the Commissioner of Mines, acting as the Government of Jamaica, may suggest either the reclamation of a comparable area of land in the vicinity or the payment of a fine. The goals of this legislation based on English law are to prevent the progressive development of large areas of waste land similar to the barren areas produced by strip-mining in many sections of the British Isles, as well as in the United States and other lands. The nature of the reclamation process has been left in the hands of the Commissioner of Mines who has worked with the cooperation and advice of specialists of the Departments of Agriculture and Forestry and with representatives of the mining companies. The representatives, individually and collectively, recognize the complexity of the problems involved. Thus there is in effect in Jamaica at the present time an honest effort, unique in the Caribbean and in the general history of strip-mining operations, to consider the problems and adapt the results for mutual benefit and for the present and ultimate well-being of Jamaica and its people.

The problems of revegetating mined-out bauxite areas are not simple. They involve acceptance of the fact that the soils are basically poor from the agricultural point of view and that in Jamaica, as in other heavily populated tropical areas, the lands have not received the attention and proper use deemed ideally desirable. The proper use of "terra rossa" soils has not been fully explored, but is currently receiving study and will necessitate continued study. The existing vegetation of bauxite soils is often unusual in habit, association and composition, as this study will show. Replacement of this vegetation by duplication may be difficult and may involve a series of carefully controlled steps. In fact, exact duplication of the existing vegetation may be undesirable and efforts are being made not only to revegetate the soil surface in mined-out bauxite areas, but to produce on these soils a vegetation of greater potential value than existed previously. In some cases this has meant the replacement of shrub-forest vegetation with pasture lands or the obverse replacement of pasture vegetation with forest trees following mining. Adjustments have to be considered relative to the contours developed during mining operations, for steep-sided pits negate the use of pasture grasses or require fencing, while practices of fill or land movements depend on the economics of such operations as well as the machinery required. The relationship between the mineral content of the soil and the nature and growth of the vegetation upon that soil is admittedly complex, and clearly so in the relationship of these plants to aluminum ions. Thus, there are many problems on which representatives of mining, agronomy, forestry, chemistry and botany must share their knowledge. These are problems which are being worked out in Jamaica.

The authors of this paper, working under the auspices of the Institute of Jamaica, have undertaken a survey of the existing vegetation on bauxite soils in Jamaica. The senior author can call upon field experience in the bauxite areas of Hispaniola for comparison, but recognizes that further work is necessary on that island, as well. We have worked with the cooperation of the Commissioner of Mines and the directors and staff members in the Departments of Agriculture and Forestry. Permission to study at will the vegetation of the lands being mined or planned for mining in the future has been granted by the Reynolds Jamaica Mines and the Kaiser Bauxite Company. Over the past three years we have visited each area of mining operation during various seasons of the year. For comparative purposes, similar studies have been made of the vegetation on limestone outcrops adjacent to the bauxite accumulations. Studies are also under way on areas of bauxite accumulations to be considered for mining in the future.

Our efforts, as will be indicated subsequently in this paper, have been to determine the nature and the composition of the vegetation on known accumulations of aluminum-rich bauxite soils. We have studied and recorded the species of plants found in these areas, as well as the relative abundance of economic and academically significant species. Transects and population counts have been made for significant areas. Data are preserved as herbarium specimens collected at various seasons to insure material in flowering and fruiting conditions. Herbarium specimens, suitably indicated as to origin, are on deposit at the Institute of Jamaica and are available at any time for reference or study. Duplicate collections have been placed in the Herbaria of Harvard University, the British Museum of Natural History and the New York Botanical Garden. Additional specimens are available for other interested botanical organizations.

We wish to acknowledge our appreciation to the many individuals and organizations who have assisted materially in the progress of this study. Their cooperation and interest, their financial and intellectual support have made this study a pleasure to us and of benefit in the study of botany in the West Indies. We mention particularly the assistance we have had from Mr. C. P. deFreitas, Commissioner of Lands and Mines; Mr. B. E. Frayling, Deputy Commissioner of Mines; Mr. J. R. Elliott, Deputy Commissioner of Lands; Mr. J. F. Hart, Mines Officer; Mr. E. J. Gregory, Deputy Director of Agriculture; Dr. R. M. Arnold, Superintendent of Livestock Services; Mr. M. S. Motta, Senior Agricultural Officer; Mr. E. M. Brown,

Conservator of Forests; Mr. H. S. Deans, Assistant Conservator of Forests; Mr. William S. Cole, Resident Manager of the Reynolds Jamaica Mines and his staff members, Mr. Alastair A. Keeling, Mr. Charles M. Baker and Mr. W. R. McDaniels; Mr. Donald C. Tretzel, Works Manager of the Kaiser Bauxite Company and his staff members, Mr. F. Miles, Mr. W. F. Jones and Mr. E. L. Mais; and finally to Mr. C. Bernard Lewis, Director of the Institute of Jamaica and Mr. Ronald P. Bengry of the Institute staff.

THE VEGETATION OF THE BAUXITE SOILS AND ADJACENT AREAS

Location of the Deposits

The survey conducted by the Geological Survey Department has been admirably summarized by Dr. V. A. Zans, senior geologist of the Geological Survey of Jamaica in a publication "Bauxite Resources of Jamaica and Their Development" (London 1954). Mr. Zans points out that through the efforts of the members of the Geological Survey and the geologists of the interested companies, commercial deposits of bauxite ore have been found in the parishes of Manchester, St. Elizabeth, St. Ann and Trelawny. Similar workable deposits are found in the parishes of St. Catherine, Clarendon, St. James and Portland. The other parishes either lack bauxite deposits completely or have only small accumulations of no commercial value. Currently, however, mining operations are limited to three areas in Jamaica. The Reynolds Jamaica Mines are operating on lands in St. Ann parish near Lydford Post Office. The Kaiser Bauxite Company operates areas of bauxitic soils in St. Elizabeth below Spur Tree Hill and south of the crossroads known as Gutters. These are the areas which have received our attention because of the diverse vegetation types represented and the different ecological conditions prevalent in the two areas. A third area of commercial operation is near Shooters Hill in the parish of Manchester, where the Alumina Jamaica Ltd. mines a more limited area similar in aspect to that operated by the Kaiser Company. We have given little attention to this area.

THE REYNOLDS AREA IN ST. ANN

The lands currently being mined by Reynolds Jamaica Mines are located chiefly among rocky wooded hills southeast of Lydford Post Office in the parish of St. Ann. The ore bodies occur primarily on a plateau in pocket-shaped hollows which range in elevation from 1100 to 1300 feet above sea level (Plate I, fig. 1). The surrounding limestone hills are heavily wooded with a rich array of hardwood tree species, an abundance of shrubs, numerous ferns and orchids occurring chiefly as epiphytes on trees on the limestone outcrops and a large number of weedy species of pantropical or Pan-Caribbean distribution occurring on lands once in agricultural or pastoral use.

This area north of Moneague has long been an area of extensive plantations and estates, the names of which, in use today, go back over one hundred fifty years. Patrick Browne's map associated with his "Natural and Civil History of Jamaica" showns no named properties in the Moneague area in 1749 and Hans Sloane ("Voyage to . . . Jamaica" Vol. 1, 1707) mentions only the Moneague Savanna as a feature of the road or tract over Mt. Diablo to St. Ann's Bay. Edward Long in the History of Jamaica published in 1774 (Vol. 2, page 90) describing St. Ann parish avers that "the hills contain very few sugar works. The mould here is extremely superficial; and underneath lies a deep vein of a white marle, or hard chalk. The pimento loves this kind of soil; and vast woods of it overspread the hills to a great distance from the coast. Behind this range of hills and mountains the land is diversified with open, level savannahs, environed by rocky eminences, or with little cock-pits. The soil of the latter is cultivated successfully with guiney-grass. The savannahs are covered with fern, and applied to no use. The road by Monte Diablo, in Sixteen mile-walk, leads into it on the south-east part, and is a mere avenue cut through the woods, there not being more than four or five settlements on the whole road. About five miles from Monte Diablo is the Rio Hoja, which, running about a mile and a half from its first spring, discharges itself into a large lake of immense depth." "The district of the parish intersected by these three avenues (Mt. Diablo, Pedro, Cave Valley roads) comprehends near one hundred and eighty thousand acres, as yet unsettled. In so vast a space, there must needs be a very great variety of soil, and numberless spots of very fine cultivated land. But, exclusive of a few fern savannahs, the whole of it is in its primitive forest, full of large cedar (*Cedrela*), mahogany and other valuable timber trees. The soil, over which the roads pass, is in general a reddish fat clay, intermixed with mould, or a black-shell mould."

Between Long's report of 1774 and 1811, when the first issue of "The New Jamaica Almanac and Register" to contain names of properties was published, the area attracted settlers and by 1810 such estates as Albion, Phoenix Park, Bellmont, Ramble, Grier Park and Crescent Park were evidently well established. Bel(l)mont and Crescent Park, two estate areas currently being mined for bauxite, were reported to have 51 and 99 slaves and 124 and 411 head of stock (including cattle), respectively. These lands have remained in large estates and in the hands of relatively few owners during the last century, and the land has been devoted to the raising of cattle with a few side exploits noted. The mention by Sloane and Long of savannahs and fern areas describes well the current situation with the limited fertile soils occurring as pastures and the shallower soils broken by small outcrops of limestone supporting the areas of fern (*Nephrolepis*). The wooded areas could not be regarded as of comparable productivity today, for while pimento is of scattered occurrence, cedar and mahogany have to a large extent been eliminated. Little information is available whether the depletion of these once richer forested areas came about through lumbering for purposes of construction, fuel for sugar mills closer to the coasts, or by generation after generation of slash cutting for fuel and buildings by residents of the area. All three probably played a role and the shallow soils, underlain by marl, controlled replacement forest growth on the flat lands as the blocks of limestone in the "rocky eminences" limited forest replacement on the hilltops.

A few attempts at diversified crop agriculture have been attempted in the bauxite areas of St. Ann as indicated by the few pimento groves and casual plantings existing as remnant trees of cola, citrus, jak fruit, coffee and cocoa.

The area being mined by Reynolds in St. Ann parish today consists of numerous small glades or depressions partially filled with bauxite soils and low-elevation hills of loose limestone blocks of varying sizes. In recent years the flat lands have been devoted to pastures for cattle raising (PLATE V, FIG. 1). The limits of these areas are clearly defined in the vegetation, for the pastures stop at the rocky outcrop and the forests do not occur on the deeper soils. The margin of these two vegetation types is marked by shrub growth, in part natural and in part created by the convenience of the area for fuel wood cutting. Often these areas are covered with extremely dense stands of fern (*Nephrolepis biserrata*) creating a tangle difficult to penetrate. We have been unable to find an area of deeper soil supporting a forest. We wonder if such areas ever did exist or whether the deeper bauxite soils have always had a savannah vegetation.

The Environment

Vegetation can be interpreted in terms of soil types and climatic conditions as well as the plants which comprise it. Asprey and Robbins in their recent paper on the Vegetation of Jamaica (Ecological Monographs 23: 359–412. 1953) accept a method of vegetation classification which they state is largely one of convenience, recognizing both environment and species composition. Without discussing the vegetation of terra rossa soils specifically, they refer to them as "residual" soils "developed from weathering of hard white limestone through solutions and being typically coarse and porous in nature." They report that "although under conditions of poor drainage degraded forms of these bauxitic soils occur, they are usually much leached, acid, well oxidized and dehydrated. The red color is due to ferric oxide and their depth over the limestone plateaus varies greatly. There is no distinctive profile, but the surface has a high content of organic matter on which the agricultural value of the land depends." These observations, in our minds, do not appear to apply well to the pasturelands in St. Ann which are subtended by bauxite in commercial quantity. Profiles dug through these areas show very slight penetration of the root systems and relatively little organic content. The root systems of herbaceous plants and woody shrubs rarely penetrate more than eight inches and rarely do tree roots go deeper than two feet. The response of the vegetation to programs of soil improvement indicate natural low nutritional values for plant growth. The soil seems to be a definite limiting factor in the development of better pasture areas or for the growth of forest trees. A soil analysis is available for the areas in St. Ann now being mined but none has been made for the mine area in St. Elizabeth. Samples of surface soil taken no deeper than six inches showed the following analysis which indicates the low level of essential elements:

pH	6.1
Organic matter	7.68 %
Phosphorous	0.019 — 0.036%
Nitrogen	0.48 — 0.53 %
Potassium	0.07 — 0.14 %
Calcium	0.14 %
Iron	0.84 — 1.63 %

The soil proved relatively rich in minor trace elements with no conspicuous deficiency noted.

The climatic factors are less restricting. Temperature records for the vicinity of Crescent Park and Lydford Post Office near the mines indicate a mild, even climate with a cloud cover on the hottest of days which aids in reducing transpiration and water loss. Rainfall in the Crescent Park area is favorable, being 66.2 inches per year with peaks in May and in October and November and distributed as follows:

January	3.9	July	2.7
February	3.6	August	5.1
March	4.1	September	4.9
April	4.2	October	8.8
May	9.9	November	10.2
June	3.3	December	5.5

Accepting the basic figure of four inches of rainfall per month as the minimum figure for optimum plant growth in the West Indies, the Crescent Park area had only four deficient months, distributed in pairs; January–February and June–July, and eight months over the minimum. These eight months are favorably distributed in growing periods of three and five consecutive months.

The Pastures

The pastures in the area of mining operations in St. Ann are relatively low grade. Without improvement, the average of these would currently support only one head of cattle for every five or six pasture acres. An examination of many of these prior to the mining operation revealed incipient invasion of woody shrubs and vines which could be kept under control only by constant effort (PLATE V, FIG. 1.) The forage plants were few in number and the unpalatable and therefore untouched grasses and herbs were numerous, if not dominant. The following list represents a fair sample of plants typical of pasture areas in the St. Ann area on bauxite soils prior to mining:

Andropogon glomeratus
Borreria laevis
Borreria verticillata
Cardiospermum grandiflorum
Cassia ligustrina
Cassia occidentalis
Cassia uniflora
Centrosema virginianum
Cissampelos pareira
Crotalaria incana
Desmodium axillare var. acutifolium
Desmodium canum
Dichromena ciliata
Drymaria cordata
Eleusine indica
Euphorbia heterophylla
Euphorbia hirta
Euphorbia hyssopifolia
Hydrocotyle asiatica
Mimosa pudica
Nephrolepis biserrata
Nephrolepis exaltata
Paspalum blodgettii
Paspalum conjugatum
Paspalum notatum
Paspalum paniculatum
Passiflora foetida var. hispida
Passiflora suberosa
Physalis pubescens
Phaseolus lathyroides
Polygala paniculata
Priva lappulacea
Pteris longifolia
Rubus jamaicensis
Setaria geniculata
Solanum nigrum
Stenotaphrum secundatum
Trimezia martinicensis

The following herbaceous invaders of over-grazed pastures in the St. Ann area which are to be distinguished from the noxious young shrubs capable of dominating pasture areas if untended. Of this list, *Ipomoea cathartica*, *I. tiliacea*, *Cissus sicyoides*, *C. microcarpa* and *Urechites lutea* are vines which become locally dominant through their habit of climbing over the forage grasses present. *Indigofera suffruticosa*, *Solanum mammosum*, *S. stellatum*, *S. torvum*, *S. verbascifolium*, *Rhytidophyllum tomentosum* and *Hyptis capitata* become stout plants dominant by size.

Ambrosia paniculata
Asclepias curassavica
Asclepias nivea
Bidens pilosa
Capsicum baccatum
Cissus microcarpa
Cissus sicyoides
Elephantopus mollis
Emilia sagittata
Emilia sonchifolia
Eryngium foetidum
Hyptis capitata
Indigofera suffruticosa
Ipomoea cathartica
Ipomoea tiliacea
Lobelia viridiflora
Mikania micrantha
Pavonia spinifex
Phyla nodiflora
Rhytidophyllum tomentosum
Salvia micrantha
Sida rhombifolia
Sida urens
Stachytarpheta jamaicensis
Thunbergia alata
Triumfetta hispida
Triumfetta lappula
Urechites lutea
Urena lobata
Verbesina alata
Wedelia gracilis

Untended pastures are invaded by seedlings of woody shrubs which develop extensively, shading or crowding out more desirable plants.

Casearia guianensis
Chrysophyllum cainito
Citharexylum spinosum
Cordia globosa
Eugenia axillaris
Eupatorium odoratum

Eupatorium villosum
Lantana camara
Lantana trifolia
Petitia domingensis
Psidium guajava
Psychotria nervosa
Psychotria pedunculata
Psychotria pubescens
Tournefortia hirsutissima

The stout woody vine *Tournefortia hirsutissima* reaches extreme lengths in pasture areas and its presence becomes a factor in limiting the pasture available to cattle and humans.

Programs of pasture improvement are under way on properties managed by the Reynolds Jamaica Mines. These programs include controlled grazing, the applications of natural and chemical fertilizers, weed control and reseeding. Such work is being conducted on areas planned for eventual mining, as well as on lands which lack sufficient ore bodies for commercial operation. The development and improvement of these pastures has achieved significant results in the few years of operation, allowing the grazing of cattle in larger numbers. Such a program certainly exceeds the spirit as well as the letter of the mining laws.

The Wooded Lands

The forest vegetation in St. Ann on lands operated by the Reynolds Jamaica Mines occurs on small limestone hills, outcrops of limestone rock and on the face of a small escarpment. (PLATE I, FIG. 1.) Asprey and Robbins' classification of "lowland type on limestone" would apply to the forests we have observed. As we have indicated, we have been unable to locate any forests on deep deposits of soil, although historical records indicate such forests might have occurred and subsequently been cleared of the trees. All the forests we have observed have been on limestone rock and have possessed only slight accumulations of soil. All have been cut over or severely culled and show the effects of human activity as well as that of nature's ravages of wind, especially hurricane damages, and time. The original forests in these areas must have been a rich mesophytic forest in which such trees as *Terminalia latifolia*, *Dipholis nigra*, *Ceiba pentandra*, *Cedrela odorata*, *Coccoloba swartzii* and *C. plumieri*, as well as other woody genera, occurred. *Swietenia* has not been seen as a natural component of these forests, although Long referred to the abundance of these plants in 1774. Likewise *Pimenta dioica* appears today to be residual plantation trees or occasional spontaneous plants from seed dispersal rather than a component of the mature forest. The forested areas studied are largely open, with relatively little herbaceous growth within the forest. Shrubs and herbs dominate the forest edges near the end of the limestone outcrop. Vines are infrequent except where fellings occurred and newer trees are developing. Epiphytes in abundance, including orchids, bromeliads and ferns reflect the ample rainfall. The dominant forest trees and those reaching the largest size are the following:

Adenanthera pavonina
Alchornea latifolia
Andira inermis
Casasia piricarpa
Cedrela odorata
Ceiba pentandra
Celtis swartzii
Coccoloba longifolia
Coccoloba plumieri
Coccoloba swartzii
Colubrina ferruginosa
Cupania glabra
Dendropanax arboreum
Dipholis nigra
Dipholis salicifolia
Esenbeckia pentaphylla
Ficus harrisii
Ficus ochroleuca
Ficus wilsoni
Guarea glabra
Hyperbaena laurifolia
Nectandra antillana
Nectandra patens
Ocotea staminea
Oreopanax capitatum
Peltophorum brasiliense
Petitia domingensis
Pimenta dioica
Pithecellobium arboreum
Pouteria multiflora
Simaruba glauca
Sloanea jamaicensis
Terminalia latifolia
Tetrazygia hispida
Tetrazygia pallens
Torrubia fragrans
Wallenia laurifolia
Xylopia muricata
Zanthoxylum elephantiasis
Zanthoxylum martinicense
Zizyphus chloroxylon

To the casual visitors to the forests of St. Ann the dominant plant of the lower stories in the forests may appear to be *Acidoton urens*, known locally as the "cowitch" or "scratch-bush." This plant possesses stinging hairs on most of the younger portions of the stems, on the leaves, flowers and fruits, and causes painful irritation when encountered. Equally abundant are the numerous species of *Psychotria* and *Salpixantha coccinea*. Other woody plants of small stature as well as diameters of less than commercial significance than the dominant trees are:

Allophylus cominia
Bauhinia divaricata
Calyptranthes chytraculia
Capparis cynophallophora
Casearia aculeata
Casearia guianensis
Casearia odorata
Colubrina ferruginosa
Daphnopsis americana
Drypetes lateriflora
Elaeodendron dioecum
Erithalis quadrangularis
Erythroxylum incrassatum
Eugenia disticha
Eugenia eperforata
Guettarda argentea
Hamelia ventricosa
Laetia thamnia
Maytenus jamaicensis
Palicourea domingensis
Phyllanthus coxianus
Phyllanthus inaequaliflorus
Picramnia antidesma
Rhamnus sphaerosperma
Rheedia sessiliflora
Viburnum villosum
Xylosma fawcettii

To determine the size and relative abundance of the forest trees in any given area of forest, we have made transect studies through forest areas selected for the purpose. Some areas were thought to be typical, others showed unusual elements in the flora. Our transects were made by marking off with cord an area 300 feet long and 60 feet wide, representing 18,000 square feet or approximately 41% of an acre. Because of the sharp inclines and the irregular footing in most of the areas studied, cross lines were run to allow counts to be accumulated from smaller areas and trees were marked to prevent chance recounting. The flora is well known to us, yet voucher specimens were collected in cases of doubt.

We recorded the occurrence of all woody species having a trunk diameter of four inches at breast height. Considering the density of the vegetation, even species of known economic potential have little chance of maturing if they are of lesser diameter. However, in several of the transects which follow, these species are indicated in separate listings. Diameters were recorded in categories of 4–6, 7–9, 10–12, 13–15, 15–20 and over 20 inches.

REYNOLDS AREA TRANSECT #1

North slope. Area from lower plain, level of drying kiln up sloping limestone face to level of plateau. Plot 300′ × 60′.

	Total	4–6	7–9	10–12	13–15	15–20	Over 20
Dipholis nigra	11	1	8	2			
Simaruba glauca	8	5	1	2			
Brunfelsia americana	6	4	2				
Nectandra antillana	6	2	3	1			
Torrubia fragrans	6	2	1	1	1	1	
Casearia guianensis	5	5					
Celtis swartzii	5	5					
Bunchosia jamaicensis	5	3	1		1		
Daphnopsis americana	5	5					
Bauhinia divaricata	4	3	1				
Zizyphus chloroxylon	4	2	1			1	
Zanthoxylum martinicense	4	3		1			
Casearia sylvestris	3	1		1	1		
Sloanea jamaicensis	3	2			1		
Pithecellobium arboreum	3		1		1	1	
Ocotea staminea	3	2		1			
Cupania glabra	3	2	1				
Comocladia pinnatifolia	2	2					
Capparis cynophallophora	2	2					
Urera baccifera	2	1	1				
Coccoloba swartzii	2	1	1				
Dendropanax arboreum	1				1		
Oreopanax capitatum	1				1		
Andira inermis	1				1		

The largest of the trees encountered in this transect was 36 inches in diameter at breast height. This was an old and battered specimen of *Pithecellobium arboreum* which would not have produced a log of any value. Three trees with a marketable log over 12 feet long and 2 feet in diameter were found, two of *Torrubia fragrans* and one of *Pithecellobium arboreum.*

The explanation for the greater number of useful trees and trees of larger size and greater frequency in this continuation of TRANSECT #1 can be found in the nature of the rocky substratum onto which TRANSECT #2 extended. This limestone hill consisted of large, irregular, loose blocks of stone. Climbing through the area of steep slopes necessitated the use of two hands. Lumbering in such an area, while not impossible, would be more difficult than cutting trees in the area of TRANSECT #1 where the logs would be dragged to an opening and a roadway with much greater ease.

REYNOLDS AREA TRANSECT #2

A continuation of TRANSECT #1 from the level of mining operation on the plateau to the top of the closest adjacent limestone hill. Plot 150′ × 60′.

	Total	4–6	7–9	10–12	13–15	15–20	Over 20
Nectandra antillana	30	17	9	4			
Pouteria multiflora	19	9	5	4	1		
Torrubia fragrans	14	2	2	8			2
Daphnopsis americana	10	9	1				
Coccoloba swartzii	8	6	2				
Alchornea latifolia	6	5	1				
Cupania glabra	5	4		1			
Xylopia muricata	4	3	1				
Wallenia laurifolia	4	2	1			1	
Guarea glabra	5	4		1			
Bauhinia divaricata	3	3					
Pithecellobium arboreum	3			1			2
Capparis cynophallophora	3	3					
Guettarda argentea	2	2					
Allophylus cominia	2	1	1				
Comocladia pinnatifolia	1	1					
Zanthoxylum martinicense	1	1					
Oreopanax capitatum	1	1					
Hyperbaena laurifolia	1	1					

Another hill in the plateau mine area was selected for a transect study because of the several unique species found in the woods in considerable quantity. One of these trees, *Euphorbia punicea*, was the largest specimen either of us had seen, and apparently the largest on record. The plant has showy bright red bracts 1–1.5 inches long and possesses numerous flower clusters similar to the poinsettia. A specimen of *Euphorbia punicea* nine inches in diameter at breast height and thirty feet high was selected as the corner of a transect of one hundred fifty feet by sixty feet from the top of the hill where the *Euphorbia* grew to the margin of the forest at the lower edges of the hill. This transect showed the following tabular composition:

REYNOLDS AREA TRANSECT #3

Limestone hilltop above mine area on plateau. Hill forest dominated at the peak by specimens of *Euphorbia punicea*. Plot 150′ × 60′.

	Total	4–6	7–9	10–12	13–15	15–20	Over 20
Pouteria multiflora	15	8	2	2		2	1
Nectandra antillana	9	1	8				
Omphalea triandra	6	4	1	1			
Alchornea latifolia	6	1	2	2	1		
Torrubia fragrans	5	1	2	2			
Casearia guianensis	4	2	1	1			
Oreopanax capitatum	4	1	2		1		
Comocladia pinnatifolia	4	4					
Exothea paniculata	3	3					
Andira inermis	3	2	1				
Rhamnus spherosperma	3	3					
Xylopia muricata	3	3					
Euphorbia punicea	2		2				
Coccoloba swartzii	2	2					
Pithecellobium arboreum	2			2			
Dipholis nigra	2	1		1			
Cupania glabra	2	1		1			
Zanthoxylum martinicense	1		1				
Capparis cynophallophora	1	1					
Terminalia latifolia	1				1		
Bauhinia divaricata	1	1					
Daphnopsis americana	1	1					
Zizyphus chloroxylon	1	1					

The "different" appearance of the forest vegetation on this hilltop was supported by the composition study of the transect above. This was accentuated when consideration was given to the shrubby growth and trees having a diameter of less than four inches.

The two hilltops represented in TRANSECTS #2 and #3 were small and the hills more or less conical in shape. Another hilltop in the same area had essentially the same degree of slope to the hilltop but the top was flat and of several acres in extent. This hill drew our closer attention because of the current and relic cultivation which had taken place on its slopes. The steep limestone slope had been cut and burned and crops of *Colocasia*, *Manihot*, *Musa* and *Cajanus* were under cultivation in some areas. Other areas once cultivated had grown up in a dense stand of *Solanum*, *Bocconia* and *Lantana* under trees of *Cecropia*. It appeared to be only a matter of time before cultivation practices would remove the woody vegetation on this hilltop.

The vegetation in this forest was largely undisturbed in the area of the transect. It was dominated, however, by the four very large trees with spreading and dense crowns. One of these, *Oreopanax capitatum*, had a diameter of thirty-six inches at breast height and a trunk extending approximately sixty feet to the first branch. The large specimen of *Pithocellobium arboreum*, with a diameter of twenty-six inches, covered a ground radius of approximately seventy feet and the forest floor was covered with myriad seedlings. A specimen of *Dipholis salicifolia* was a matriarch of the hilltop with a large spreading crown and dense foliage. Seedlings of this aged tree dominated the undergrowth throughout the transect area.

REYNOLDS AREA TRANSECT #4

Flat top of limestone hill above stand of *Cecropia palmata*. Plot 150′ × 60′.

	Total	4–6	7–9	10–12	13–15	15–20	Over 20
Nectandra antillana	14	5	3	5	1		
Dipholis salicifolia	11	5	3		1	1	1
Alchornea latifolia	11	4	3		2	1	1
Torrubia fragrans	9			7		2	
Oreopanax capitatum	8	1	1	4		1	1
Capparis cynophallophora	6	4	2				
Pouteria multiflora	6	3			2	1	
Wallenia laurifolia	6	3	2	1			
Dipholis nigra	6	1	4		1		
Coccoloba swartzii	4	4					
Comocladia pinnatifolia	4	4					
Pithecellobium arboreum	3			2			1
Zizyphus chloroxylon	3	3					
Terminalia latifolia	3		2			1	
Omphalea triandra	2		1		1		
Thrinax jamaicensis	1	1					
Cecropia peltata	1	1					

The density of young plants under the canopy of the forest trees recorded in the transect varied from the exposed margin to the interior. Variation was also seen relative to the exposure of the slope. A small quadrat twelve feet square was selected and studied in several of these transects and the number and height of the smaller woody plants recorded.

QUADRAT #1 was located in the margin of the forest and the open grassy pasture of the woods reported in TRANSECT #1. This transect contained seventy-one woody plants from one foot tall to over fifteen feet in height, but none of them exceeded two inches in diameter at breast height. Ten genera and species were found as recorded on the next page.

A second quadrat in a comparable area but with a southern exposure had a different composition with thirty-one species represented by sixty-eight individuals in an area twelve feet square. The plants encountered in this quadrat are recorded on the following page.

QUADRAT #1

Upper edge of TRANSECT #2. Western exposure. Plot 10′ × 12′.

	Total	1–3′	3–7′	7–15′	Over 15′
Acidoton urens	19	2		3	14
Piper jamaicense	10	1	1	8	
Malvaviscus arboreus	7			3	4
Capparis cynophyllophora	7	1	2	4	
Nectandra patens	7		4	3	
Guettarda argentea	6			4	2
Comocladia pinnatifolia	5	1			4
Coccoloba swartzii	5			5	
Rhytidophyllum tomentosum	3		2	1	
Bauhinia divaricata	2			2	
Total	71	5	9	33	24

In addition, a small portion of this quadrat contained a colony of *Polypodium polypodioides* growing on a rock and rotted log. The number of individual plants in this colony were too numerous to estimate.

QUADRAT #4

Nectandra antillana	20	*Capparis cynophyllophora*	1
Guzmania monostachya	13	*Pouteria multiflora*	1
Casearia guianensis	10	*Piscidia piscipula*	1
Cereus sp.	12	*Zizyphus chloroxylon*	1
Polypodium plumula	8	*Clusia* sp.	1
Eugenia sp.	6	*Dendropanax arboreum*	1
Hohenbergia sp.	4	*Ocotea floribunda*	1
Tillandsia valenzuelana	3	*Zanthoxylum martinicense*	1
Cupania glabra	3	*Ipomoea* sp.	1
Campyloneuron phyllitidis	3	*Cedrela odorata*	1
Comocladia pinnatifolia	2	*Rhipsalis cassytha*	1
Lonchocarpus sp.	2	*Anthurium grandifolium*	1
Chiococca parvifolia	2	*Campylocentron* sp.	1
Coccoloba swartzii	2	*Peperomia amplexicaulis*	1
Calyptranthes chytraculia	2	*Tillandsia tenuifolia*	1

The relationship between the sizable plants usually counted for a transect and the number of smaller plants of no economic, i.e., timber, value is frequently not taken into consideration. The development of any seedling into a mature plant is determined in nature, in Jamaican woodlands at least, by a number of factors including the presence or absence of competitors; the number of vines which may cause contortion or strangulation; the nature of the rock substratum on which the seedling obtains its start; the number of larger trees which may die or fall, limiting the growth of the younger plants, and the activity of termites in the area, to mention only a few.

One wooded area near the head of the conveyor belt at the Reynolds Jamaica Mines represented a mature forest area which, previous to mining operations, had been isolated by its location away from roads and bounded by rather difficult rocky slopes. During the course of our trips to this area this forest, now readily available to man on foot or in a car, has been attacked by machete and hoe. This forest proved to have a slightly different composition in its mature trees from the forests encountered and recorded in the transects just cited. The specimens were tabulated as follows:

Reynolds Area Transect #5

Northern exposure, summit of limestone hill. Plot 300′ × 60′.

	Total	4–6	7–9	10–12	13–15	15–20	Over 20
Nectandra antillana	7	3	1	3			
Rhamnus sphaerosperma	7	4	2	1			
Ocotea floribunda	6	1	5				
Torrubia fragrans	6	1		3		1	1
Cupania glabra	4	2	1	1			
Guarea glabra	4		3		1		
Allophylus cominia	4	3	1				
Andira inermis	4	2		2			
Daphnopsis americana	4	3	1				
Zanthoxylum martinicense	3		1		1		1
Alchornea latifolia	3		2		1		
Casearia guianensis	2		1	1			
Oreopanax capitatum	2			1			1
Annona jamaicensis	1				1		
Phyllanthus coxianus	1	1					

With this tabulation complete, a line was then placed through the center of the transect and all plants within a distance of 1.5 feet on either side of the line were recorded. A total of 451 plants, representing 40 genera and 45 species, were counted. Because of the smaller size of the plants in this sample, only four of the 451 plants had appeared in the transect tabulation, although no conscious effort to avoid them was made in laying out the line.

The great diversity of the vegetation is, of course, one of the attractions which the vegetation of Jamaica and the Caribbean area in general have for the botanist. The diversity in genera and species is clearly indicated in the transects and quadrats compiled for the forested areas in the parish of St. Ann. The variations between hilltops, not only in aspect but in actual composition, are shown. Species and genera present, often dominant in one mixed forest on one hilltop, will be fewer in number or absent on the adjacent hill.

From an economic point of view, these are not profitable forests. The plants which make up the wooded areas are small in size and few in number. Whether these areas ever contained what today would be considered marketable timber trees is a matter of conjecture. Even if Long's description of 1774 is accurate for the two species of commercial value which he mentions, *Cedrela* and *Swietenia*, some question must be raised as to whether these species could ever have dominated the area in view of the current mixed stands present. The trees which comprise the present forests are not important timber trees. Only a few, a dozen at most, of the species encountered in these areas are important trees and the majority of these are significant from the standpoint of cabinet woods alone. It is possible that in the past one hundred fifty years the marketable trees have been removed from the area either for lumber or for fuel. If that were so, one would expect a few gnarled old giants which, lacking good form or proximity to access roads, would have persisted. Such trees are rarely found and the "forest giants" are almost without exception trees of little commercial value and for that reason alone remain uncut.

QUADRAT #5

Top of hill near loading pit for conveyor belt. Plot 300′ × 3′.

Piper jamaicensis	51	*Cupania glabra*	6
Acidoton urens	45	*Coccoloba longifolia*	5
Pilea crassifolia	38	*Daphnopsis americana*	5
Eugenia disticha	35	*Blakea trinervia*	5
Rhytidophyllum tomentosum	27	*Chiococca parvifolia*	4
Psychotria sp.	21	*Hamelia patens*	4
Eupatorium macrophyllum	21	*Andira inermis*	4
Guettarda argentea	18	*Casearia odorata*	4
Eugenia axillaris	17	*Guarea glabra*	3
Nectandra antillana	15	*Casearia sylvestris*	3
Piper arboreum	14	*Wallenia laurifolia*	3
Calyptranthes chytraculia	14	*Paullinia jamaicensis*	3
Bauhinia divaricata	12	*Salpixantha coccinea*	3
Rhamnus sphaerosperma	9	*Zanthoxylum martinicense*	3
Casearia guianensis	9	*Xylosma fawcettii*	3
Coccoloba swartzii	9	*Cestrum diurnum*	3
Comocladia pinnatifolia	7	*Bunchosia swartziana*	3
Eupatorium villosum	7	*Allophylus cominia*	3
Torrubia fragrans	7	*Tetrazygia hispida*	2
Viburnum villosum	7	*Xylopia muricata*	2
Ocotea staminea	7	*Alchornea latifolia*	2
Miconia laevigata	7	*Pithecellobium arboreum*	1
		Annona jamaicensis	1

The question might be raised as to why the trees which we studied in the forests of the St. Ann parish are no larger. Reasons for this lack of size were sought in a careful study of the areas represented by TRANSECTS #1 and #2. Possible answers were numerous. The area of the forest consisted primarily of limestone hills and the hills were composed of large blocks of limestone more or less tumbled in position. Hill areas not of distinct blocks consisted of limestone deeply fissured, often in a checkerboard pattern. This substratum which did not possess an accumulation of soil or humus represented an inferior spot for seed germination or for tree growth. Numerous seedlings encountered appeared to grow only to the extent of the stored food present in the cotyledons. Root development was poor and, with little humus to hold water, it appeared that most of the seedlings died from lack of available moisture, even though the area received an average of sixty-six inches per year. Forest litter, where such occurred, could be exceedingly dry during many of the seasons of our visits.

In the two transect areas studied, only four large trees could be considered as rooting in sufficient soil and that generally accumulated in the fissures of boulders. The vast majority of the trees were rooted on blocks of limestone with the roots extending around and below the blocks, as well as penetrating into the porous limestone. The effect of such a rooting habit was particularly evident in this area which received the effects of the last two major hurricanes in 1944 and 1951. Some of the largest trees were prostrate and rotting and an examination of the bases of these plants revealed that the blocks holding the trees had given way. The roots remained securely fastened to a tilted block of stone. It is apparent that the hurricane felled trees in this area of the Caribbean not by uprooting trees or fracturing trunks but by an indirect factor; i.e., alteration of the substratum.

Another factor in the relationship of tree species persistence to size and age is present in the limestone which, while hard, is eroded by the heavy rainfall in combination with the natural acids produced by decaying vegetative matter. The erosion of these blocks into a type of dog-tooth limestone is all too evident to the botanist who traverses these forests.

The effects of the vines and lianas, alone and in combination with the other effects mentioned here, in such a forest is also a factor in tree growth. Vines were not abundant in the very dense forests, but where openings occurred through natural or man-made causes, the vines appeared to scramble, with the aid of the smaller shrubs and saplings, into the tops of the larger trees. The extent and mass of some of these vines were surprising and a calculation of the weight involved in some of the larger woody vines would be a most imposing sum. Huge woody epiphytes or vines in this area included *Blakea trinervia*, *Clusia* sp., *Ficus* spp., *Solandra grandiflora*, *Rourea paucifoliata*, *Schlegelia parasitica* and *Ipomoea grisebachii*. Lighter weight vines or scrambling plants included *Chiococca parvifolia*, *Vernonia acuminata* and *Vernonia cinerea*, *Eupatorium odoratum*, *Clematis dioica* and *Notoptera hirsuta*. The effects of these plants would be felt through the dead weight involved, the concerted pull of the vines in any wind-induced movement of the forest canopy and in the tension exerted by the vine through its growth in various directions. It seemed obvious, from several trees we felled and others we observed in a contorted fashion, that the death or destruction of one tree entangled in vines would be reflected on the others nearby and their growth pattern altered accordingly. In the younger plants the weight and pull of the young vines often contorted the sapling, removing completely the possibility of normal growth into a desirable timber tree. Strangulation of the host tree by the climbing vines was also apparent in the abnormal growth of the stems being squeezed.

A final effect was due to the activity of wood-eating termites in these forests. Termite tubes and termite nests were present on living and dead trees alike. Apparently any injury to a forest tree producing a break in the stem opened an avenue of attack from termites. Certainly the rapidity with which fallen timbers disappear is a tribute to the appetite and activity of the large termite population. These insects obviously play another role in the rapid destruction and alteration of potential timber trees in the tropics. The contrast is found in the temperate areas away from termite attacks where broken branches or trunk wounds would be healed over by callus tissue. Such self-repair is rarely encountered in the forests of the West Indies.

THE KAISER AREA IN ST. ELIZABETH

Location and Environment

The Kaiser Bauxite Company is currently mining bauxite soil in a dry, broad valley in the parish of St. Elizabeth (PLATE VI, FIG. 1 and PLATE VII, FIG. 1.) A view west from the company offices on Spur Tree Hill looking towards the Santa Cruz mountains and Malvern details the mining operation in the valley 1600 feet below. A road south from Gutters to Alligator Pond runs the length of this valley and the headquarters for the present mining operation is at a new location appropriately (but by coincidence) called New Buildings. In many aspects, from the techniques of mining to the vegetation involved, there are contrasts with the area in St. Ann operated by the Reynolds Mines. The same attention and techniques have been applied in our study to the pastures and forests associated with the bauxite deposits, but usually with less comfort. The entire mining area is lower in altitude, being only about 700 feet above sea level. Its location on the south coast of the island places it in the lesser southern rainfall division. The rainfall recorded during the year at New Buildings in contrast to Crescent Park totalled 44.75 inches, with lesser peaks in June and October–November.

The monthly rainfall has been recorded as follows:

January	2.42	July	0.72
February	1.82	August	4.80
March	0.94	September	4.23
April	3.37	October	6.35
May	3.75	November	10.31
June	5.19	December	0.85

The distribution of rainfall as recorded at New Buildings indicates that seven of the twelve months receive less than the four inches of rain considered necessary for optimum plant growth. Two additional months, August and September, receive only slightly in excess of the minimum. The number of consecutive months receiving above the minimum rainfall is also less in comparison with Crescent Park. These occur in August, September, October and November. The isolated month of June also receives above the minimum rainfall.

The temperatures in the valley also mount to greater heights and the evaporation rate is also high due to the extraordinary number of sunny days.

From the standpoint of climatic factors alone, the vegetation present in the Gutters valley exists under comparatively different conditions. As might be expected, the nature and composition of this vegetation is also different. Unfortunately, soil analyses are not currently available for these soils.

A map published in Patrick Browne's description of Jamaica of 1749 shows a "Pepper" plantation near Gutters and also a road south to Alligator Pond. Sloane apparently makes no mention of this area but Edward Long (The History of Jamaica 2: 185, 1774) reports that "about the foot of Mayday Hills the breadnut trees grow luxuriantly, and afford to the bordering settlements great abundance of nourishing fodder for their flocks." Long (l.c. 189) also refers to the area as "Labour-in-vain savannah" a term he states is "perfectly descriptive of its nature." He further comments that "In these parts there are but few sugar-plantations, though a great number of very fine penns for breeding horned cattle, horses, mules, sheep and goats, as well as poultry of all kinds."

Specific historical evidence for the properties now being mined is lacking. The New Jamaica Almanac citing statistics for the year 1810 apparently fails to list a single property in the immediate area of New Buildings. Plantations to the north toward Santa Cruz and the northwest foothills of the Santa Cruz Mountains supported 1529 and 1447 head of cattle, while plantations nearer by are cited as owning five and ten head of cattle. It seems obvious that high-quality pastures have never existed in the Gutters area.

Within the last few decades a special type of cultivation involving heavy mulching with quantities of guinea grass has developed and permitted the use of the land by small holders for the production of root crops, tobacco, pigeon peas and tomatoes. Large land holdings for the breeding and raising of cattle and other animals have largely disappeared. The lack of certain water supplies has reduced the emphasis on cattle raising with the result that few pasture areas comparable to those of the St. Ann area are to be seen. The lands now operated by the Kaiser Bauxite Company therefore involve fewer areas of pasture and more small crop fields now removed from cultivation.

The Pastures

A study of the areas to be mined which have been devoted to pastures revealed a very low grade forage present composed of a larger number of grasses than we encountered in St. Ann. A survey of these pastures revealed the following grasses:

Andropogon glomeratus
Andropogon virginicus
Axonopus compressus
Cenchrus echinatus
Cenchrus gracillimus
Chloris petraea
Digitaria sanguinalis
Eleusine indica
Panicum adspersum
Paspalum caespitosum
Paspalum fimbriatum
Paspalum propinquum
Pennisetum purpureum
Setaria geniculata
Sporobolus indicus
Trichachne insularis

Several of these species unpalatable to cattle had become dominant. While guinea grass, para grass and napier grass have been introduced in some areas and have remained as dominant stands when properly cared for, in adjacent areas they have given way to unpalatable species, reducing the value of the pasture. Weedy herbaceous invaders comprised essentially the same species as reported for pastures in St. Ann. Woody invaders of marginal pastures or pastures which have been neglected appear to grow faster and assume dominant roles much faster in this lowland area. One area under our observation for the years of this study changed so markedly that a quadrat study was made. This area was functional pasture in December, 1953. In January of 1956 (PLATE VI, FIG. 1) the shrubs had become so large and abundant that penetration was difficult and cattle tended to avoid the section. The area studied was located near a stand of logwood and the area selected for quadrat study was a hundred yards from the margin of this thicket. The following woody species were encountered in this effectively abandoned pasture:

QUADRAT #6

Kaiser property near New Buildings — area 101. Plot 40′ × 40′.
The number of individuals of all woody species over 12″ tall are recorded in the table.

Haematoxylon campechianum	350	*Cordia globosa*	5
Lantana camara	44	*Urechites lutea*	4
Colubrina ferruginosa	42	*Ayenia pusilla*	3
Casearia guianensis	36	*Wissadula amplissima*	2
Eupatorium odoratum	26	*Hyptis pectinata*	2
Waltheria americana	23	*Crescentia cujete*	2
Melochia pyramidata	19	*Zanthoxylum martinicensis*	2
Triumfetta lappula	17	*Solanum verbascifolium*	2
Cordia jamaicensis	17	*Indigofera suffruticosa*	1
Croton lucidus	16	*Abutilon crispum*	1
Guazuma ulmifolia	9	*Psidium guajava*	1
Calliandra portoricensis	7		

The number and size of the plants which had invaded this pasture and developed to maturity in a period of two years is indicative of the problems of maintaining high quality pastures in Jamaica. While seedlings were present at the time of our first observation, cattle roamed and grazed in this area freely. Two years later the woody plants, especially the thorny *Haematoxylon,* constituted a real barrier. A total of 631 individuals over 12 inches tall in an area of 1600 square feet of pasture were counted. The largest plants encountered were a specimen of *Haematoxylon* 12 feet tall and 1.5 inches in diameter at the base; plants of *Lantana camara* (also spiny) and *Eupatorium odoratum* seven feet tall; specimens of *Hyptis pectinata* reached seven feet, as did spreading plants of *Solanum verbascifolium.* These latter two species spread prolifically once established in a pasture. The basic forage species of *Paspalum* and *Panicum* had given way to a dominance of *Andropogon* which cattle are reluctant to eat.

The sample represented by the QUADRAT #6 is not an exception to the general invasion and replacement affecting pastures in the valley of Gutters. Maintenance of pastures in this area requires constant care and prudent grazing practices.

The planting practices instituted by the Kaiser Bauxite Company on mined-out pits will be considered later. Within the first few years of operation, however, it appears as though limited pasture areas planted to good forage grasses carefully managed may persist as economical forage lands. (PLATE VII, FIG. 2.)

The Wooded Lands

The broad, flat valley around New Buildings contains low limestone outcrops rarely 100 feet high which support forests. (PLATE VI, FIG. 1 and PLÂTE VII, FIG. 2.) In general the limestone here is not in loose blocks, but exists as a solid, though checked, outcrop. Humus or soil is scarcely more abundant than in St. Ann, but is thick enough in places to allow tree growth upon the soil layer. The majority of these forests are secondary growth, having been cut continuously and now have few large trees other than specimens of *Bursera simaruba.* We were fortunate to find in one area of the Kaiser property a forest on a limestone outcrop which apparently has been well protected. No evidence of cutting was found on our first visit, although cutting has occurred subsequently. A transect study was made of this area and showed a composition as follows:

TRANSECT #6

Kaiser property, area 101. Forest on low limestone outcrop of 25 feet relief apparently protected and undisturbed. Plot 300′ × 60′.

	Total	4–6	7–9	10–12	13–15	15–20	Over 20
Dipholis salicifolia	67	20	4	23	8	10	2
Ocotea staminea	8	6	1	1			
Hyperbaena domingensis	6	4		2			
Calyptranthes chytraculia	5	4		1			
Thrinax sp.	5	5					
Casasia longipes	4	2	1	1			
Guarea glabra	4	2	1	1			
Coccoloba proctori	4	1	1				2
Zanthoxylum insularis	4	1	2	1			
Coccoloba swartzii	3	3					
Wallenia laurifolia	2	2					
Omphalea triandra	2	2					
Lonchocarpus domingensis	1		1				
Comocladia pinnatifolia	1	1					
Bursera simaruba	1					1	
Sarcomphalus laurinus	1		1				
Piscidia piscipula	1		1				
Bauhinia divaricata	1	1					

The largest trees on this limestone forest represent some of the largest of their species known to us to exist in Jamaica. *Coccoloba proctori*, a new species, certainly fits that category but exceeds in two trees (36 and 24 inches in diameter at breast height) the largest specimens of this important timber genus known in the West Indies. The large number of *Dipholis* specimens, known locally as "bullet" would represent a significant forest resource if the pattern of distribution observed in this forest were repeated in the vicinity. Unfortunately this is not true and the occurrence of "bullet" here can only be taken as indication that the species does well in this area and should be considered as one of the species to be replanted on the mined-out pits.

The succession from pasture to forest land in the Gutters area is clearly marked in a number of woodlands. The shrubby growth described above which invades a misused pasture may assume control and is soon dominated by the logwood (*Haematoxylon*) in this dry area (PLATE VI, FIG. 1.) Apparently the only exceptions we have seen to this first step was a thicket of *Leucaena glauca*. In the majority of instances observed, however, the logwood was prevalent. In flat areas with a bauxite base, the logwood remained as the dominant tree and several of the old stands are being exploited today with logs collected for commercial use as a source of dye (PLATE IX, FIG. 1). On limestone, however, the logwood thicket soon becomes host to smaller plants of other tree species. In several logwood thickets we observed the development of specimens of *Nectandra coriacea*, *Wallenia laurifolia*, *Casasia longipes*, *Cupania glabra*, *Piscidia* *piscipula, Metopium brownei, Coccoloba swartzii, Zanthoxylum insularis, Zanthoxylum flavum, Dipholis salicifolia,* and *Diospyros tetrasperma.* In time these simple or broader leafed species assume dominance over the compound leaves of *Haematoxylon* and apparently crowd out the latter. Dead and dying mature trees of logwood are common in limestone-based secondary forest thickets. These secondary forests are more diverse in their composition than the undisturbed forest previously described.

One limestone outcrop now supporting a secondary forest was distinguished as a former old field by the presence of stone walls traversing it. A transect in this area showed the following composition.

TRANSECT #7

Secondary forest on limestone. Kaiser property, area #18. Plot 300′ × 60′.

	Total	4–6	7–9	10–12	13–15	15–20
Metopium brownei	31	24	6	1		
Bursera simaruba	12	6	5	1		
Haematoxylon campechianum	12	11		1		
Diospyros tetrasperma	10	10				
Lonchocarpus domingensis	7	7				
Dipholis salicifolia	6	6				
Simaruba glauca	5	4		1		
Tabebuia riparia	5	3		2		
Piscidia piscipula	5	5				
Zanthoxylum flavum	4	4				
Coccoloba swartzii	4	4				
Exothea paniculata	3	3				
Clusia sp.	3	2		1		
Gymnanthes lucida	2	2				
Allophylus cominia	2	2				
Picramnia antidesma	1	1				
Krugiodendron ferreum	1	1				
Bauhinia divaricata	1	1				

Consideration in the transect was limited to trees having a diameter of four inches or more at breast height. In addition to these established trees, representatives of the following genera and species were found in the same area.

Acidoton urens
Bunchosia swartziana
Casearia sylvestris
Celtis swartzii
Chiococca parvifolia
Clusia flava
Cordia globosa
Cordia jamaicensis
Croton linearis
Cupania glabra
Erythroxylon confusum
Eugenia sp.
Hamelia chrysantha
Phyllanthus nutans
Pisonia aculeata
Portlandia grandiflora
Psychotria myrstiphyllum
Schaefferia frutescens
Spathelia sorbifolia
Tabebuia angustata
Thrinax sp.
Xylosma sp.

One limestone outcrop was found supporting a secondary forest which extended into a pasture currently in use. A transect was made of this forest area beginning immediately behind the young shrub and tree area which could be distinguished as the pasture.

TRANSECT #8

Secondary woodland invading current pasture. Area 101 Kaiser property. Plot 300′ × 60′.

	Total	4–6	7–9	10–12	13–15	15–20	Over 20
Dipholis salicifolia	14	8	3	2			1
Diospyros tetrasperma	14	10	3	1			
Bauhinia divaricata	12	9	1	2			
Haematoxylon campechianum	9	8		1			
Coccoloba swartzii	9	7			2		
Ocotea staminea	7	6		1			
Gymnanthes lucida	6	5	1				
Bursera simaruba	4		1	2	1		
Amyris elemifera	3	2	1				
Wallenia laurifolia	3	3					
Simaruba glauca	3	1	1		1		
Calyptranthes chytraculia	2	2					
Piscidia piscipula	2	1	1				
Casasia longipes	2	1			1		
Picramnia antidesmia	2	1			1		
Esenbeckia pentaphylla	2		1			1	
Zanthoxylum flavum	2	2					
Oreopanax capitatum	2		1	1			
Metopium brownei	2			2			
Exothea paniculata	2	1	1				
Sarcomphalus laurinus	1	1					
Casearia guianensis	1	1					
Cupania glabra	1	1					
Capparis cynophallophora	1	1					
Coccoloba diversifolia	1	1					

The dry land forests of the Gutters area are more open in aspect than the forests of St. Ann. In spite of the relative abundance of light reaching the forest floor, herbaceous growth is scanty and consists primarily of a few species of ferns and *Peperomia*. No orchids have been seen in the areas examined. Epiphytes are numerous in local areas, but consist primarily of *Tillandsia recurvata* and *Tillandsia balbisiana*. *Syngonium auritum* occurs on the exposed limestone. The composition of these forests, primary or secondary, consists of a larger number of genera and species than were found in the forests of the wetter areas of St. Ann. The forests likewise appeared to have suffered greater ravages from man by being cut for fuel and building purposes. The economic value of the limestone forests for lumber purposes is low.

A complete listing of the species found on lands to be mined, as invaders of mined-out pits and as occupants of the adjacent limestone outcrops to bauxite deposits is given in the second part of this paper for both the locations in St. Ann and St. Elizabeth.

THE RELATION OF THE VEGETATION TO ALUMINUM IN THE SOIL

The relationship of the plant to the soil has formed the basis for most agricultural research since man first cultivated plants. From such studies over a period of time has come our knowledge of root growth, structure and function, of mineral relationships to plant metabolism and growth involving major and minor elements, including trace elements and plant tolerances, preferences and responses to mineral elements, whether as deficiencies or in toxic abundance. As a companion study the botanist has often sought in the plant or the soil evidences of controlling factors in mineral-plant relationships. The recognition of plants as indicators of mineral components has attracted research and guided exploration for gold, iron and more recently for uranium. It is not unnatural, then, that we looked for plants as indicators of aluminum concentrations in our study of bauxite soils. The senior author, on previous field trips in Hispaniola, encountered several species of plants which are known only from depressions rich in bauxite and which are currently the site of mining operations. More recent collecting has not shown these plants on other than aluminum-rich soils. Whether such plants should be considered as indicators of aluminum soil or only plants tolerant of aluminum ions in the soil, in contrast to other species, remains to be established. Agricultural research dealing primarily with crop plants has shown that two considerations are possible for plants to be grown on soils rich in aluminum ions. These can be: A. plants susceptible to aluminum damage (i.e., non-tolerant species); or B. plants resistant to aluminum damage or tolerant of varying concentrations of aluminum in the soil.

It is known that certain plants will not tolerate any concentration of aluminum ions and are killed if grown on soils containing even small quantities of aluminum. Seedlings grown in soils or solutions containing aluminum ions show characteristic effects proved attributable to the concentration of aluminum. Slow growth and contortion of the shoot system comprise the obvious symptoms, but an examination of the plants shows root damage due to the "browning" of the roots or root hairs (Hoffert, G.N. & Carr, R.H. Accumulations of iron and aluminum compounds in some plants and its probable relation to root rot. Jour. Agr. Res. 23: 801. 1923). Continued deterioration of the root system results in starvation and eventual death of the plants. Previously much of this damage was attributed to the high acidity of the soil.

Information in this category is best known concerning the cultivated and crop plants of the temperate regions rather than the natural vegetation of the tropics where aluminum ore is mined. Gilbert and Pember (Tolerance of certain weeds and grasses to toxic aluminum, Soil Sci. **39**: 425. 1935) reported that aluminum in the soil served to regulate competition between certain weeds and grasses. They concluded that grass seeds and seedlings were less affected by aluminum than dicotyledonous plants and so pasture areas under their observation developed pure stands of grasses, weed-free. (See also Shorland, F.B. The estimation of aluminum in pastures with special reference to soil contamination. Proc. Roy. Soc. N. Zeal. **64:** 35. 1934).

We observed the growth of pastures on areas of known bauxite concentration and the invasion and replanting of mined-out bauxite areas for these plant reactions. Although we are dealing with different genera and species, the results do not support the observations of Gilbert and Pember and of Shorland that aluminum itself in greater concentration limits the selection of species which invade or which could be planted.

It appears to be possible to establish three categories for plants which will grow on aluminum-rich soils. These are: 1. Plants requiring aluminum ions in their metabolism; 2. Plants known as "aluminum accumulators" which concentrate aluminum ions in plant tissues with visible but non-lethal effects; and 3. Plants which are tolerant of aluminum but collect little or only small percentages of aluminum in their tissues.

The role of aluminum as an essential element for plant growth has been investigated for a few areas and a few crop plants. Of particular interest is the fact that members of the Ericaceae, Moraceae and a great many ferns and Lycopodiaceae are considered now to require aluminum for proper development (Shorland, L.C. and Sommers, A.L. Studies concerning the essential nature of aluminum and silicon for plant growth. Univ. Calif. Pub. Agr. Sci. **5** (2): 57. 1926).

Vaccinium and *Rhododendron*, according to these reports, will not grow on control solution culture unless aluminum is added to the solution. Field work on the distribution of these two genera in Java supports the idea that aluminum is present where these plants occur and is absent where the species are absent (von Faber, F.C. Die Kraterpflanzen Javas in physiologisch-ökologisches Beziehung. Arb. Treub-Lab., Weltevreden 1. 1927). The distribution of *Vaccinium* species in the Antilles does not seem to follow the pattern described for the Far East. *Vaccinium* species do not occur on the deep bauxite soils in Jamaica but are montane plants, while *Rhododendron* is not native to the Antilles but species are cultivated at higher altitudes where temperature is more a factor than the absence of aluminum in the soil.

Several species of *Ficus* also require aluminum for normal development, according to the work of von Faber (l.c.). Many species of *Ficus* are present in Jamaica and the other islands of the Antilles, but occur apparently without special relationship to the concentration of aluminum ions. They are, however, a conspicuous feature of bauxitic pastures in Jamaica and clearly thrive in this environment.

The most detailed work on plants requiring aluminum has been done on ferns and club-mosses. Yoshii (Yoshii, Y. Aluminum requirements of solfatara plants. Bot. Mag. Tokyo **51**: 262. 1939) found that ferns in the Asiatic area grew most luxuriantly on soils rich in aluminum and that species of *Alsophila*, *"Aspidium"* and *Polypodium* failed to develop normally in the absence of aluminum.

The specific role of aluminum as an essential element is not completely understood. It appears to be associated with maturation, particularly of the fruiting portions of the plant and the setting of seed. Thus corn plants grown on aluminum-rich soils or solutions showed earlier flowering, earlier fruiting and heavier fruit production when compared with control plants (Sommers, l.c.). It is also suggested by literature of the field as reviewed by Hutchinson (Hutchinson, G.E. The Biogeochemistry of aluminum and of certain related elements. Quart. Rev. Biol. **18**: 1, 128, 242, 331. 1943) that aluminum may play a role in the uptake of water by plants. This factor alone may account for the heavier fruit production.

Aluminum may also have a catalytic effect on plant growth as shown in the case of citrus crops. *Citrus*, normally susceptible to damage by copper, is more highly resistant to copper injury when grown on soils rich in aluminum.

More attention has been paid to the ability of certain plants to accumulate aluminum ions as compounds, e.g., aluminum succinate within the tissues of the plants (Smith, H.G. Proc. Roy. Soc. N. S. W. **37**: 107–20. 1903). Such plants are called accumulators and are considered such when the concentration of aluminum ions equals or surpasses 0.01% of the dry weight of the plant. Accumulations as high as 8.5% have been reported in species of *Carpinus*.

The most comprehensive survey of the plant kingdom to determine the frequency of aluminum-accumulating plants in all groups has been completed and reported by Chenery in a series of papers (Chenery, E.W. Aluminum in the plant world. Kew Bull. **1948**: 173; **1949**: 433, 466). The original impetus for such a survey came when it was determined that the historic use of certain plants as mordants for dye work was due to the concentration of aluminum in the tissues. Further study of these mordant plants showed visible characteristics applicable to other aluminum-accumulating plants. In addition to the mordant properties, the presence of a characteristic yellowish green color in the leaves, the presence of pH sensitive anthocyanin pigments which respond to concentrations of aluminum by changing color (as in *Hydrangea*) and the presence of a characteristic bright blue-colored fruit, would indicate an accumulator species.

In his survey Chenery used a test reagent of ammonium aurine tricarboxylate in ammonium acetate, gum acacia and hydrochloric acid. Small fragments of leaf material when boiled in this solution caused a change in the orange reagent to scarlet, crimson or to opaque crimson, depending on the concentration of aluminum in the leaf tissue. It has been shown by other workers that the concentrations of aluminum within the plant are greatest in the roots, becoming less in the stem and leaves. A few plants accumulated aluminum in the roots and failed to transport the ions beyond the root system. L. J. Webb (Aluminum Accumulation in the Australian-New Guinea Flora, Austral. Jour. Bot. 2 (2): 176–196. 1954) has recently reported that "variation in results occurred when samples of the same species were tested from different localities, or when different parts of the tree were tested." In various species Webb reported positive accumulator reactions from one locality when negative from another, or a positive reaction from the bark but negative from the leaf. In *Quintinia sieberi* plants which establish themselves as epiphytes, reactions were negative in young plants, but older ones exhibited a positive test. A second species lacking the epiphytic habit was positive in reaction. Webb concluded that "these variations suggest that aluminum accumulation is not always obligatory among individuals of some species."

The results of Chenery's extensive survey and Webb's comprehensive coverage of a local flora must be considered as being on the conservative side as much of the work was done with dried and herbarium materials, involving only fragments of single plants.

In neither Chenery's nor Webb's work is any evidence given of the presence of aluminum in the soil where these plants were growing. We regret that we have not had the opportunity of applying Chenery's techniques to a survey of the plants growing on bauxite areas of known concentration in Jamaica. Such tests would demonstrate either accumulator or tolerant species.

Webb has listed the families which are known to contain species which accumulate aluminum based on the reports of his own research and that of Hutchinson and Chenery. These are Monimiaceae, Lauraceae, Violaceae, Polygalaceae, Vochysiaceae, Crypteroniaceae, Geissolomaceae, Proteaceae, Theaceae, Myrtaceae, Melastomaceae, Rhizophoraceae, Scytopetalaceae, Euphorbiaceae, Cunoniaceae, Escalloniaceae, Hydrangeaceae, Celastraceae, Icacinaceae, Octoknemataceae, Juglandaceae, Diapensiaceae, Symplocaceae, Diclidantheraceae, Loganiaceae, Apocynaceae, Rubiaceae, Gentianaceae and Lentibulariaceae. Webb considers the data compiled and discusses it along biochemical ecological and taxonomic lines. He suggests as cited in his summary that "A high aluminum content of the organs of accumulating plants appears to be associated with normal metabolism." Further, that "obligate accumulators are confined to leached acid soils from a variety of parent materials, in comparatively high-rainfall areas."

Few of the families which contain accumulator species occur in Jamaica and fewer still on bauxite soils. Chenery points out that the greatest *number* of accumulator species have been found in the Rubiaceae and the Melastomaceae, both families represented in Jamaica, and that the greatest *percentage* of accumulator species belong to the Diapensiaceae and the Symplocaceae. In the latter two families all species tested proved to be accumulators, and for the Symplocaceae Webb found eight species as accumulators of the eight species tested. *Symplocos* occurs in the West Indies and three species have been reported from Jamaica but are not associated with bauxite soils. Such genera containing known accumulating species as *Morinda, Oldenlandia, Lasianthus, Psychotria, Miconia, Ternstroemia, Cyathea, Dicranopteris* (*Gleichenia*) and *Lycopodium*, do occur in Jamaica. A few of these genera have been found on bauxite soils but in no case are they limited to bauxite soils. They are, in fact, much more abundant elsewhere, indicating that aluminum in bauxitic concentrations is not necessary for their growth, and that other factors control their distribution in Jamaica. No species of these accumulator genera are restricted to bauxite soils. Certainly the observations of Chenery and Webb that acid soils and high rainfall are required for high accumulator species cannot with ease be applied to the composition and distribution of the vegetation found on bauxite soils in Jamaica.

Webb uses the data regarding accumulator species for practical taxonomic considerations. He reports that the "recorded accumulators are mainly restricted to what are usually regarded as the more primitive groups in dicotyledons and filicales, suggesting that accumulation is a physiological relic in these groups." He points out that "with the exception of the Rubiales, all the well-developed accumulating orders are confined to the Archichlamydeae or the primitive sections of Metachlamydeae. Accumulation is erratically developed in *Rubiales* and only slightly in other Metachlamydeae." If it can be assumed that aluminum accumulation is associated with normal metabolism and therefore characteristic of those species, then until further tests are made, the vegetation which occurs on bauxite soils in Jamaica must be considered as species which are neither accumulators nor non-tolerant of aluminum concentrations. Instead, it appears that the bauxite flora of Jamaica consists of plants which are unaffected by aluminum and tolerant of its presence.

Webb also suggests that accumulation of aluminum seems to be a useful character to supplement other data in the clarification of some taxonomic problems. He cites examples of *Helicia* and *Finschia* where the proper affinities of the species are suggested by the accumulation of aluminum. Manske and Marion (Manske, R.H.F. & Marion, L. The alkaloids of Lycopodium species. Canad. Jour. Res. B. **20**: 87, 153. 1942; **21**: 92. 1943; **22**: 1. 1944) found that in *Lycopodium*, where the color of the plant is often used as a supplementary character for dividing the genus, the color was a direct indication of the percentage of aluminum in the tissues.

We have looked in vain for an application of Chenery's suggestion of blue fruit, yellow-green color to the foliage and pH-sensitive anthocyanin pigments in the vegetation on the bauxite soils. Such plants occur in Jamaica, but without correlation to bauxite. As we have indicated, in the course of our work to the present we have been unable to find undisturbed forests or savannah vegetation on the deposits of bauxite of known concentrations. Explorations by the bauxite companies continue in more remote parts of the island, such as the John Crow Mountains and the Cockpit country where future expansion of the mining operation will take place. In such areas we still hope to encounter a vegetation which will demonstrate the existence of endemic species related to bauxite soils or counter effectively the slight evidence on hand from the deposits in the Dominican Republic and Haiti. To the present we have found no species characteristic of bauxite soils, nor have we demonstrated that the vegetation of adjacent areas currently not found on the bauxite deposits will not grow on the bauxite soils. To the contrary, the invasion of plants from adjacent areas on barren, mined-out pits and the plantations established in these pits indicate that factors other than the concentration of aluminum will control the success or failure of these species on bauxite.

MINING TECHNIQUES IN JAMAICA REGARDING BAUXITE ORE

Strip-mining techniques for the extraction of bauxite ore in Jamaica are relatively simple in contrast to those used in areas of greater amounts of overburden. The deposits in Jamaica encountered to the present are all superficial, the bauxite having been deposited in pits on a hard limestone base. The nature of these deposits is well described and illustrated by Zans (l.c. 318, plates III, IV and VI), who reports that bauxite deposits are "confined either to circular or oval declines (cockpits) and large elongated 'glades' (bowl or catchment deposits), or to larger, uneven depressions in limestone plateaux blanketed by undulating sheets or lenses of bauxite. Smaller deposits occur in pockets, pipes, and irregular solution cavities on the hillsides of the honeycombed limestone and also filling the fissures and brecciation zones." "All the deposits are surface accumulations, covered only by a thin layer of soil and sparse vegetation." "The deepest pocket drilled in Jamaica is 114 feet deep in a deposit near Williamsfield in the parish of Manchester. Deposits less than five feet in thickness are not considered workable, and the average minable thickness is of the order of ten to thirty feet. The tonnage of the individual commercial ore-bodies varies from a few thousand to several million tons."

In opening the deposits for mining the top soil ("overburden") is removed by bulldozer or dragline scraper and set aside for replacement once mining operations are completed (PLATE VI, FIG. 2.) The removal of the overburden is in part a practical operation and in part a consideration for the future reclamation of the mined-out pit. The overburden contains remnants of the plant life, the root systems and the accumulation of organic material, but consists of the same chemical, i.e., aluminum composition as the lower deposits. Processing of the overburden would require ashing of the organic material. Removing and stockpiling the overburden avoids the necessity for this complicated operation.

With the overburden set aside for future use, the ore is removed by mechanical excavators, power shovels, drag lines or scrapers (PLATE I, FIG. 2 and PLATE VI, FIG. 2.) The ore is then hauled to transportation centers by bottom- and rear-dump trucks. Equipment used and methods of transportation vary with the companies; however, both Kaiser and Reynolds dry the ore, removing eighty to eighty-six percent of the moisture contained. The dried ore is then exported for further processing to alumina and metallic aluminum.

The nature of the depression that remains following removal of the bauxite ore varies with the size of the ore body and with the contour of the hard limestone base. Minable deposits average ten to thirty feet in depth, but a few located in small limestone "cockpits" were deeper, the resulting depressions being steep-sided. The larger the ore body, the less precipitous were the borders of the depression and the easier could be the early steps of pit reclamation. In general, the practice of the companies appears to be to alter steep-sided depressions where possible by blasting or by using tractors to ease material into the hole. Contours of the larger depressions are smoothed with tractors and bulldozers. (PLATE V, FIG. 2 and PLATE VII, FIG. 1.) Overhangs are removed and dangerous slopes fenced off. Once the contour has been adjusted, the overburden is replaced and leveled. Distribution of the overburden is made as uniform as possible and the overburden is contoured with the greatest possible agricultural utilization in mind. The soil surface is then processed, generally using sheepsfoot rollers but occasionally by discing, harrowing or ploughing. Contours are established and attempts at erosion checks are made. (PLATE II, FIG. 2 and PLATE VII, FIG. 1.) The problems of re-establishing vegetation on these naked mined-out pits are evident. Soil samples from the bottom of several pits have been analyzed and show an organic content of 0.10% to 0.15% and a nitrogen count from 0.00% to 0.033%. The pH of these soils varied from 5.9 to 6.1. Potassium counts averaged 0.7% and phosphorous 0.41%. Even with the replacement of the overburden, the organic content remained very low. Without the proper surface preparation the soil is very compact.

SUCCESSION ON THE EXPOSED MINED-OUT PITS

We have been fortunate in having the cooperation of the managers and the agricultural specialists of both the Reynolds Jamaica Mines and the Kaiser Bauxite Company in the course of our investigations. At our suggestion and with the approval of the Commissioner of Mines, control areas have been established in the mine areas. Mined-out pits have been allowed to stand fallow to permit our observations concerning the natural invasion and succession in mined-out bauxite pits. (PLATE II, FIG. 1).

A complete list of the plants which have appeared as invaders of the mined-out pits appears as a tabulation in the second part of this paper. Within six months from the cessation of mining operations in the control pit at the Reynolds Mines sixty-one species of plants were recorded as established within the pit. A definite zonation was evident with vines, primarily *Cissus sicyoides*, *Mikania micrantha*, *Ipomoea cathartica* and *I. tiliacea* on the slopes and the abundance of herbaceous and woody species in the silted-in center depression. The greater number of invaders appeared on the area where the overburden had been replaced, indicating both the comparatively greater fertility of this soil and the possible presence of weed seeds in the overburden. Additional species which have not been seen in the control pit were found in other pits which received special plantings. It was of interest to note that several species of plants not recorded elsewhere in the area appeared in the mined-out pits. These were *Aster exilis, Lactuca jamaicensis*, *Crepis japonica*, all herbs, and *Ochroma pyramidale*. Woody plants which were among the early invaders were *Ficus suffocans, Bocconia frutescens*, *Zanthoxylum martinicense*, *Cordia globosa*, *Petitia domingensis* and several species of *Solanum*. *Zanthoxylum martinicense* and *Petitia domingensis* were given special significance as the woods of both species are used for light construction work on the island. During the first year of observation, changes were recorded in the relative composition and the size of the plants. Many species disappeared after one seed generation, but plants known elsewhere as persistent pan-Caribbean weeds remained and often increased in number. Species of *Sida*, *Solanum*, *Stachytarpheta*, *Eupatorium*, *Lantana*, *Borreria* and *Cassia* flourished. *Ambrosia* became locally abundant. The vines, especially *Cissus sicyoides* and *Ipomoea cathartica*, fruited heavily and spread rapidly for most of three years, forming a tangle over the ground which impeded travel but seemed to have little effect on the erosion rate of the area. Natural decline of these two species has already set in as other plants have appeared on the slopes of the control pit.

The growth of *Petitia domingensis*, a useful timber tree, has been very slow. *Zanthoxylum martinicense*, however, grew rapidly and has continued that rate. (PLATE III, FIG. 1.) Additional specimens of this species have been recorded since the original observations, and several of these plants increased in height by nine feet between two of our visits, nine months apart. *Ochroma pyramidale*, which was not present in our original observations, appeared subsequently and now towers over the vegetation in the control pit (PLATE III, FIG. 2). Specimens of *Terminalia latifolia* also appeared in the course of our observations and have grown prolifically since. Ferns, particularly *Pteris longifolia*, have appeared in quantity but grasses are scarce, the most abundant plants being *Stenotaphrum secundatum* and *Andropogon glomeratus*. *Stenotaphrum*, like *Cissus* and *Ipomoea*, appears to dominate areas by the long, sprawling habit developed, but these plants have not rooted naturally along the runners and hence are of slight value in retaining the soil.

No attempts at following succession were made on pits which had been planted, since cultivation practices in these areas altered the invading vegetation. One of the goals of the succession study on a controlled pit was to locate if possible a naturally established, ground-covering plant which would reduce erosion. Three plants which were prominent in pits other than our control pit appear to serve this purpose. They are *Mimosa pudica*, a legume capable of enriching the soil, *Borreria laevis* and *Wedelia fragilis*. Both *Mimosa pudica* and *Borreria laevis* seem well suited for the purpose, being low, prostrate plants which seed abundantly and cover well. The latter is eaten by cattle and could be considered low forage.

However, it has been suspected of producing toxic effects and should be encouraged only with this caution in mind.

As might be suspected in the drier area of the Kaiser operations in St. Elizabeth, the rate of invasion was slower than at Reynolds and the number of species at a given time was fewer. Thus, in six months following the cessation of mining operations, a control area on the Kaiser property had only forty-one species of plants. These were fewer in individual representatives and much more scattered in distribution. Subsequent changes at Kaiser have not shown the same loss of species and in our last visit all the species encountered in previous visits were still to be found. Additional invaders have been few. Grasses such as *Setaria, Andropogon, Digitaria, Cenchrus* and *Stenotaphrum* are more numerous and specimens of *Haematoxylon* and *Lantana* appear to be the most conspicuous elements. *Haematoxylon* is probably the most abundant plant in the valley near the mining operations and with its samara-like fruits is obviously distributed widely. The logwood, therefore, must be considered in any attempts to maintain pastures or woody plantings in the mined-out pits. No plants of potential economic value have appeared spontaneously in the Kaiser pits.

The relative fertility of the overburden when stockpiled adjacent to the mining operations has drawn the attention of visitors to the mine area. It must be pointed out that the overburden contains not only the organic matter and the roots, but the fruits and seeds of the area. Thus the rapid covering of relatively luxuriant vegetation on the stockpile of overburden is mostly indicative of the presence of plant life and propagating material in the soil. At the Reynolds Mine area we have been able to watch the development on stockpiles of overburden of twenty-three species of plants which in four years of observation have not appeared spontaneously in the mined-out pits. These plants include five pasture grasses as well as the following potentially valuable economic plants: *Musa sapientum*, *Cecropia palmata, Ricinus communis, Hibiscus elatus, Ceiba pentandra* and *Pimenta dioica*. In the Kaiser area none of the plants recorded from stockpiles of overburden is different from those appearing as natural invaders of the mined-out pits. Of the natural invaders, only *Haematoxylon campechianum,* the logwood could be considered of any economic value.

REPLANTING THE MINED-OUT PITS

The majority of mined-out pits on the Kaiser properties have been of such contours to allow development as pasture areas. In these plantings a variety of pasture grasses have been attempted by seed and rhizome propagation. Most have been established as pure stands. Guinea grass (*Panicum maximum*) has proved the most successful and controlled grazing has already been permitted on several of these reclaimed pits. (Plate VII, fig. 2.) Pangola grass (*Digitaria decumbens*) is now being tried both for forage and erosion control and looks promising. Para grass (*Panicum purpurascens*) and Wynne grass (*Melinis minutiflora*) have not, to our view, been so successful. In all pasture areas there has been an invasion of weed herbs and woody species and these have necessitated manual labor to maintain the pastures.

The Kaiser Company has also devoted some of its reclaimed pits, generally those of steeper contours less suitable for cattle, to reforestation. In general these have received mixed plantings, although some nearly pure stands have been set out. The seedlings are obtained from the Forestry Department, usually from their nurseries at Spanish Town on the south coast, to supply plants which have been started and grown under comparable conditions of temperature, exposure and rainfall. Forest tree plantings have been primarily of *Swietenia mahogani* (mahogany), *Cassia siamea*, *Hibiscus elatus* (mahoe), *Cedrela odorata* (cedar), *Tectona grandis* (teak) and a very few specimens of *Melia composita*. *Swietenia*, well adapted to the environmental conditions of the area, has done well. Plantings two years old average six feet in height and about an inch in diameter at breast height. Some infestation of tip borers has been experienced. The habit of these plants is normal and little pruning appears necessary. The few specimens of *Melia composita* have shown the most rapid growth rates, with specimens two years old reaching now to over twenty-seven feet. In all cases, these have been planted in the lower portions of the depressions. *Cassia siamea* is little grown as a timber tree in the New World, but is often planted as a source of building poles, fuel and lumber in Asia. When interplanted with *Hibiscus elatus* or *Swietenia* these trees have done well and since they will mature more rapidly, will be cut as a source of fuel and as a means of thinning the plantings. (PLATE IX, FIG. 2.) Some trees of *Cassia siamea*, three years after planting, are now twenty-five feet tall with diameters of eight inches and are in flower.

A few plantings of economic or agricultural crop plants have been attempted without outstanding success. Lime and other citrus plants have not adapted themselves to the area and survivors have tended to branch from the base to produce dense and crowded crowns. The pigeon pea, *Cajanus cajan,* has been grown on the mined-out pits but has not fruited so heavily as control plants on undisturbed soils.

More recent plantings have been on deeper soils in mined-out pits and greater attention has been given to soil preparation. One mined-out pit has been devoted to test plantings of peanuts, cassava, sweet potatoes and a variety of garden vegetables. Commercial fertilizer has been used and the crops appear to flourish vegetatively, although a complete crop cycle has not elapsed. On well-tilled soil the peanuts have flowered and produced small fruits which at the time of our last visit had not matured. A variety of fruit trees including breadfruit and mangoes have also been planted in this area.

The development of plantings of *Hibiscus elatus* from the foresters' viewpoint has been most disappointing in the St. Elizabeth area. Originally our observations indicated a high percentage of loss following transplanting and of the survivors a majority suffered die-back. (PLATE VIII, FIG. 1.) Such a response has been attributed to the toxic effects of aluminum ions in the soil. Our initial reaction was that this significant timber species in

Jamaica was not adaptable to reforestation of mined-out pits. However, in subsequent visits it has been apparent that not all the plants suffering from die-back necessarily died. In fact, a majority of these sprouted from the base and presented a problem of a different nature. Additional observations have shown that if mahoe seedlings are given proper care between digging and replanting, losses can be reduced. Furthermore, while watering of transplanted trees is impractical, planting times can be adjusted to rainy periods and survival percentages thus further increased. Mulching would also be helpful. The problem of managing large plantations of trees which have suffered die-back and have branched from the base is, however, an imposing one. Obviously several trunks cannot be permitted. (Plate VIII, fig. 2.) Laborers must be trained in proper pruning practices regarding these plants. In general the mahoe growing in mined-out pits in St. Elizabeth, in contrast to those planted in St. Ann, have not grown in height at the expected rate. Instead the average plant has developed a much more dense crown and has branched freely from the lower region of the trunk. Crown development in width and density has dominated trunk development. Again the question is raised of the economic feasibility of pruning branches for trunk development.

Hibiscus elatus as a timber tree has not proved as satisfactory on the mined-out bauxite pits in St. Elizabeth as it has on comparable pits in St. Ann and on other terrain elsewhere in Jamaica. From information so far obtained, the climate of the valley near Gutters is not ideally suited for the growth of the mahoe as a timber tree.

Maintenance problems of young forest plantations in St. Elizabeth seem slight in comparison with those encountered in St. Ann. Most evident is the lack of vines which strangle or contort the saplings and the cleaning of forest plantations in St. Elizabeth can be regarded as a minor expenditure.

In the operational area of Reynolds Jamaica Mines in St. Ann (as in St. Elizabeth) both pasture development and forest planting has been carried out. Only a few of the mined-out pits have been considered of suitable shape for the development of new pastures. In these either guinea grass (*Panicum maximum*) or para grass (*Panicum purpurascens*) have been planted primarily by rhizome propagation. One area is documented in photographs which show the contours of the valley prior to and during mining operations and after reclamation. (Plate V, figs. 1 and 2.) A survey was made of this area before mining operations began to record the quality of the pasture in terms of the plants present. Comparatively, the area which would carry at most one cow for every five acres before mining operations began, will be expected to supply forage for at least one cow for each acre now that the pasture is well established. Reclamation in this area has increased the available pasture, improved its quality and definitely improved the contour of the area by an increase in the level acreage.

More recently, para and guinea grass clumps have been planted in steeper contoured pits along with forest trees. It has been demonstrated that the clumps of grass serve effectively as checks to the erosion which was destroying many of the forest tree plantings. (Plate II, fig. 2 and

PLATE IV, FIG. 1.) Pangola grass (*Digitaria decumbens*) is also being tried in the vicinity to rebuild overgrazed pastures and as an erosion control.

In the mined-out pits of steeper contours, where pasture establishment is not possible, forest trees have been planted. The nature of the environment in these areas has been deemed most suitable for mahoe (*Hibiscus elatus*) and fruit trees. *Cassia siamea* and *Swietenia mahogani* have not been tried in the area. It is hoped that future planting plans will include prickly yellow (*Zanthoxylum* spp.), fiddlewood (*Petitia domingensis*), broadleaf (*Terminalia latifolia*) and balsa (*Ochroma pyramidale*), which have proved in the control pits to be adaptable to the area. As these timber trees are valued in local industry, plantations of these will find a ready market when mature.

By contrast with the plantings in St. Elizabeth, the mahoe in the Reynolds Area of St. Ann adopts an upright although slender habit and has, in all cases observed, produced a fine trunk branching at normal, i.e., higher levels. Larger plants now two years old are twenty feet high with trunk diameters of five inches and are in flower. (PLATE IV, FIG. 2). Die-back was originally evident in the early plantings of mahoe and the avocado in the St. Ann area, but such die-back seems more readily controlled by giving greater care to transplanting practices and to the time of planting in relation to the rainy months.

Plantings of avocadoes (*Persea americana*) called "pear" in Jamaica have proved successful on the reclaimed pits. (PLATE II, FIG. 2 and PLATE IV, FIG. 1.) With the selection of the best strains or by budding the trees once the root system is established, an important economic crop can be assured.

In the moist climate of the Reynolds operations, *Pinus caribaea* shows signs of promise as a timber tree. Small experimental plantings two years old show excellent growth to five feet.

The workers of the mines have added materially to the experimental selection of plants for the mined-out bauxite pits through surreptitious planting of a variety of vegetable crops. We have followed the illegitimate gardens with interest and have observed that corn (*Zea mays*), cabbage and beans have done well. Less successful have been plantings of yams (*Dioscorea*), taro or "coco" (*Colocasia*) and cassava (*Manihot*). Pumpkin vines produced an abundant crop.

The problem of erosion control has been a major one in this area of sixty-six-inch rainfall. A test planting was made of kudzu (*Pueraria lobata*), but these plants failed to thrive, though a few have survived. Mulching of the forest trees has been found successful in reducing the loss of these seedlings due to erosion. Mulching materials are scarce in the area and burlap sacks weighted down with rocks proved less successful than sizable tangles of vines surrounding the trees and weighted with logs or rocks. (PLATE II, FIG. 2). Scattered plantings of grass tufts within the forest tree plantings have also helped to reduce erosion. Application of chicken manure or commercial fertilizer has hastened the establishment of the grass. Experience has shown, however, that until a complete ground cover is established, sizable accumulations of silt can be expected in the bottoms of the mined-out pits. If saplings are planted in the bottom areas, silting causes the death of a high percentage of these young trees. Planting practices have been adjusted accordingly in recent operations.

Weed control, especially control of vines, remains a major problem in plantation management in the Reynolds area. Only constant attention in the first few years of growth will prevent the vines from either strangling or contorting the young trees. *Ipomoea cathartica* and *Ipomoea tiliacea* are the major pests, along with several others of lesser importance. Hand labor originally was directed at cutting these vines away from the young trees, but this technique had little lasting effect. More recently, grubbing all the plants from the area at the base of the tree with a broad-bladed hoe has been more effective. Clearing the area of vines has also supplied the mulching material to be applied in newer forest plantings where a ground cover of vegetation has not been established.

These initial years of mining operations in Jamaica have been marked with admirable cooperation between the government of Jamaica, through its various departments, and the mining companies. The strip-mining technique and its implications are new to the islands of the West Indies. Certainly the program of land reclamation following mining operations is new to the tropics of the Western Hemisphere. Much has been learned in the past four years and although not all problems are solved, the direction of cooperation and intent is encouraging. The improvement of existing agricultural lands, the rehabilitation of mined-out pits, the introduction of new capital and additional employment, the added source of local and governmental income and the demonstrations of new techniques along with the exchange of knowledge have been the subject of mutual concern and mutual welfare to the government, the people and the mining companies. Agriculture and forestry have taken steps forward in meeting the problems presented and it is hoped the information gained will be shared in furthering the knowledge and the welfare of the West Indies.

(*To be continued*)

ARNOLD ARBORETUM
and
THE INSTITUTE OF JAMAICA

EXPLANATION OF PLATES *

PLATE I, FIGURE 1. View of the escarpment and area of mining operations of Reynolds Jamaica Mines near Lydford P. O. in St. Ann Parish. Pasture area in foreground is on a limestone outcrop. The intermediate area represents a deeper body of ore. Areas in view between wooded limestone outcrops have been mined out and replanted. Arrows indicate areas of transects. Lower arrow shows forest of TRANSECT #1 and upper arrow, forest of TRANSECT #2.

* PLATES I–V: Reynolds Jamaica Mines area in St. Ann. PLATES VI–IX: Kaiser Bauxite Company in St. Elizabeth.

PLATE I, FIGURE 2. Mining operations in St. Elizabeth. A cockpit-type depression between two limestone hills containing accumulations of bauxite ore being mined by power shovel.

PLATE II, FIGURE 1. A mined-out ore body now preserved as a control area. Six months after mining operation ceased only herbaceous plants and young shrubs were present. Two and one-half years later, at the time of this picture, shrubs dominate the herbaceous invaders and five species of trees, starting from seed, have grown into conspicuous plants.

PLATE II, FIGURE 2. A mined-out ore body adjacent to control pit. The need for a covering vegetation to control erosion is evident. Young avocado plants are mulched with vines and debris cut from adjacent fields. For a comparison showing the growth one year later, see PLATE IV, FIGURE 1.

PLATE III, FIGURE 1. *Zanthoxylum martinicense* in control pit. This specimen first recorded as a six-inch spontaneous seedling and then as a sapling three feet tall nine months prior to the date of this picture.

PLATE III, FIGURE 2. Woody plants in the control pit representing spontaneous invaders grown from seed. *Ochroma pyramidale*, *Zanthoxylum martinicense*, *Cecropia palmata*, *Terminalia latifolia* and *Petitia domingensis* are all represented in this group. Growth to heights of twelve (*Zanthoxylum*) and fifteen feet (*Ochroma*) occurred in the period of two years' observation.

PLATE IV, FIGURE 1. An avocado tree which bore several fruits two years after being planted as a sapling (see PLATE II, FIGURE 2) on a mined-out bauxite pit. Para grass and wynne grass have been planted on the slopes of this pit and were fertilized with an initial application of chicken manure. The grasses now appear to have become established and are effectively checking the erosion on the slopes.

PLATE IV, FIGURE 2. Mahoe (*Hibiscus elatus*) planted on a mined-out pit. The largest specimens shown were planted as saplings about three feet tall two years previously. The plants died back to six inches in height (see PLATE VIII, FIGURE 1) before the root system became established. The plants were pruned to a single stem and the trees illustrated developed to a height of eighteen feet with trunk diameters of six inches in two years. The smaller trees shown in the picture indicate that growth is slow until a vigorous root development is made. Several trees show trunks covered with herbaceous and semi-woody vines. The ground cover is natural weed vegetation dominated by *Borreria verticillata* and *Wedelia gracilis*, with *Mimosa pudica*, *Desmodium canum* and *Bidens cynapifolia* also abundant.

PLATE V, FIGURE 1. Pasture area in St. Ann prior to mining. Shrub invasion of one section of this pasture is conspicuous in the foreground.

PLATE V, FIGURE 2. The same area two years later. Bauxite ore has been removed. The pit surfaces were contoured and the overburden replaced. The rehabilitated pit was then planted to para grass and fertilized with chicken manure to establish the grass. The relative productivity of the area has been increased about five times in terms of quality pasture with a slight increase in pasture acreage in this tract.

PLATE VI, FIGURE 1. Area of Kaiser Bauxite Company mining operation in St. Elizabeth parish. Photograph shows the dominance of shrubby vegetation on a pasture area. Two years earlier this pasture had been open and was easily grazed by cattle. Shrubs are *Solanum* spp., *Haematoxylon campechianum* and

Latana camara. Two forested limestone outcrops are visible in the background. The area between the forests of broad-leaved species comprises a dense stand of logwood (*Haematoxylon campechianum*) on limestone with recent development of broad-leaved species not evident in the photograph. TRANSECT #8 was made in the forested hill on the right. QUADRAT #6 was made in the overgrown pasture beyond the right-hand side of the picture.

PLATE VI, FIGURE 2. An area near New Buildings in St. Elizabeth being prepared for mining. The overburden has been removed by bulldozers and is piled at the left of the picture. A dragline shovel in the center at the rear is used to remove the ore.

PLATE VII, FIGURE 1. An area comparable to that of PLATE VI, FIGURE 2 following planting of forage grasses. Mining has been completed. The deeper pits have been partially filled and the slopes eased. Contours have been established on the slopes and pangola grass has been planted.

PLATE VII, FIGURE 2. A mined-out pit replanted to guinea grass. This stand is one year old. Commercial fertilizer was used to establish the grass.

PLATE VIII, FIGURE 1. An example of "die-back" in young mahoe plants. A three-foot sapling has died back to six inches and three lateral buds have started to develop into shoots. Die-back has been reduced by better soil preparation and by more careful attention to planting during the rainy periods.

PLATE VIII, FIGURE 2. The type of mahoe plant which develops from saplings having suffered from die-back. Such a tree is of no commercial value. Proper pruning is essential for plants which suffer die-back if a single-trunked, marketable timber tree is to be produced.

PLATE IX, FIGURE 1. A mature stand of logwood (*Haematoxylon campechianum*) on bauxite soils in St. Elizabeth. The commercial market for logwood has been small in the last decade, but limited supplies can still be sold. Few broad-leaved species are found in logwood forests on bauxite soils in contrast with the dominance of broad-leaved species over logwood on limestone outcrops.

PLATE IX, FIGURE 2. Forest planting on a mined-out pit in St. Elizabeth. The photograph was taken three years after planting saplings in the area. Plants of *Cassia siamea* on either side of Mr. Proctor are twenty feet tall with trunk diameters of five inches at breast height. The mahoe shown at the sides were fifteen feet tall and were in flower. The mahogany trees in this mixed planting were seven feet tall and one is shown at the right side of the picture. Proper pruning practices have been essential in this area where both *Cassia siamea* and *Hibiscus elatus* plants tended to branch freely near the base. The plants illustrated are the best specimens in this rehabilitated pit area and cannot be regarded as average for the area.

HOWARD & PROCTOR, VEGETATION ON BAUXITIC SOILS

Howard & Proctor, Vegetation on Bauxitic Soils

Howard & Proctor, Vegetation on Bauxitic Soils

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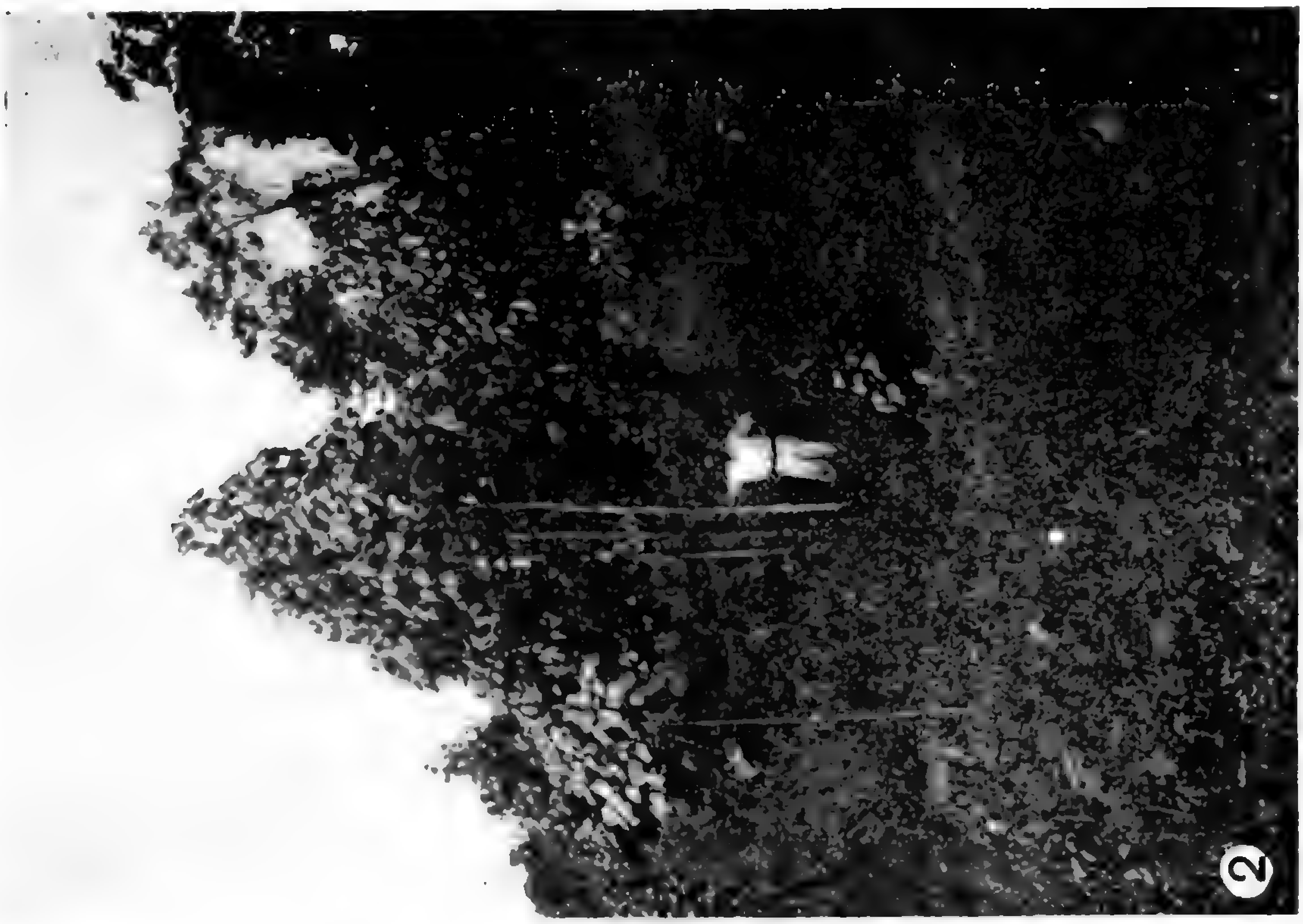

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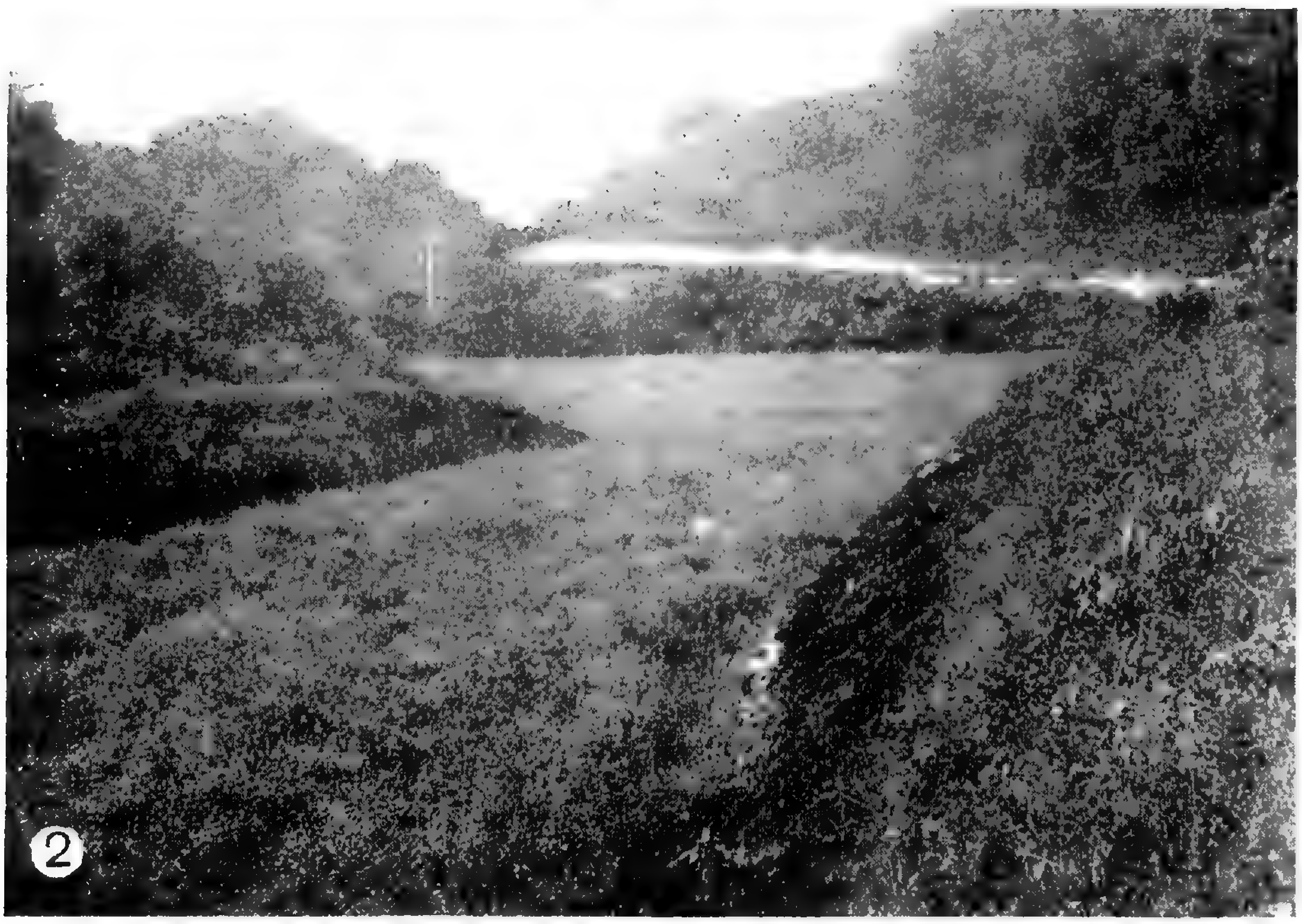

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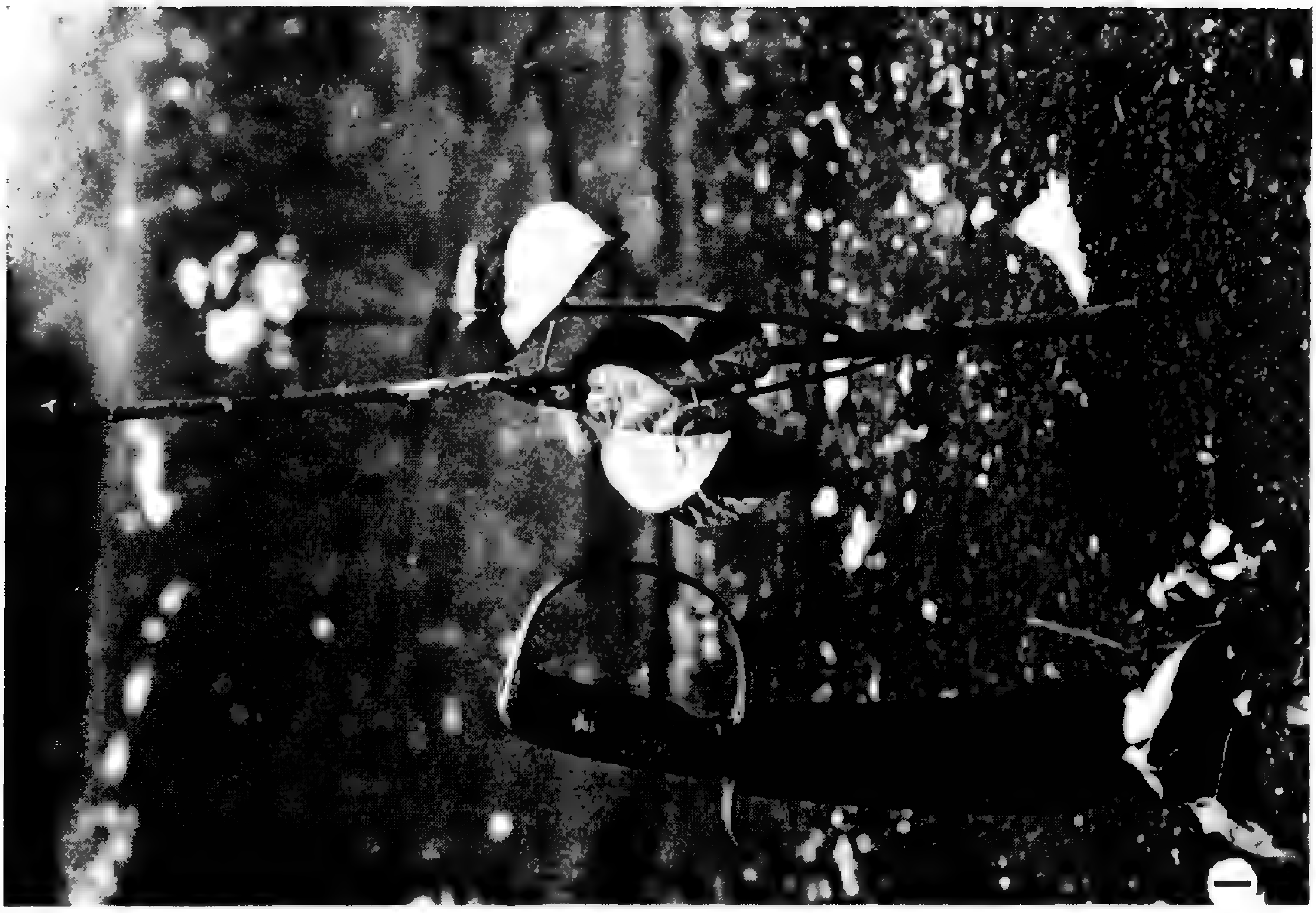
HOWARD & PROCTOR, VEGETATION ON BAUXITIC SOILS

HOWARD & PROCTOR, VEGETATION ON BAUXITIC SOILS

HOWARD & PROCTOR, VEGETATION ON BAUXITIC SOILS

PLATE VIII



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HOWARD & PROCTOR, VEGETATION ON BAUXITIC SOILS

Howard & Proctor, Vegetation on Bauxitic Soils

A MONOGRAPHIC STUDY OF THE WEST INDIAN SPECIES OF PHYLLANTHUS *

Grady L. Webster

With one plate

Subgenus II. **Kirganelia** (Juss.) Webster, Jour. Arnold Arb. 37: 344. 1956.

Kirganelia Juss. Gen. Pl. 387. 1789.
Phyllanthus sect. *Kirganelia* (Juss.) Muell. Arg. Linnaea 32: 11. 1863; DC. Prodr. 15(2): 341. 1866.

Trees, shrubs, or herbs with phyllanthoid branching; monoecious or dioecious. Male flower: calyx-lobes 5 or 6; disk of 5 or 6 segments; stamens 5 or 6, free or rarely united by the filaments; anthers dehiscing vertically or horizontally; pollen grains more or less globose, colporate. Female flower: calyx-lobes 5 or 6; disk usually as in male; ovary of 3–12 carpels; styles mostly bifid, sometimes entire, often thickened and fleshy. Fruit capsular or baccate; seeds trigonous.

This subgenus, typified by sect. *Anisonema*, comprises about 35 species in several closely related sections. None is native to the New World, and most of the species are restricted to Africa and the Mascarene islands, although they also occur in India, China, Japan, Malaysia, and Australia. Subgenus *Kirganelia* includes not only some of the most primitive of the species with phyllanthoid branching but also a number of highly specialized herbaceous species (in sect. *Floribundi*) which form a transition to the herbaceous representatives of sect. *Phyllanthus*. A significant indication of the relative primitiveness of this subgenus is the great floral variability. In the West Indies subgenus *Kirganelia* is represented by two very different species belonging to two different sections.

KEY TO THE SECTIONS

Fruit capsular; stamens 5, filaments free	2. **Floribundi**
Fruit baccate; filaments connate in two groups	3. **Anisonema**

Sect. 2. **Floribundi** Pax & Hoffm. Pflanzenw. Afr. 3(2): 22. 1921.

Trees, shrubs, or herbs with phyllanthoid branching; leaves (in ours) membranous, not over 2 cm. long. Monoecious or dioecious, flowers in abbreviated unisexual or bisexual axillary cymules. Male flower: calyx-lobes 5, small, uninerved; disk of 5 discrete segments; stamens 5, filaments free; anthers dehiscing vertically or horizontally; pollen grains subglobose, 4-colporate (in *P. tenellus*), finely reticulate. Female flower: pedicel long

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* Continued from volume XXXVII, p. 359.

and capillary; disk cupulate; ovary of 3 carpels, smooth; styles free or united beneath, bifid, the style-branches slender or dilated. Capsule oblate, the valves membranous and veiny; seeds trigonous, smooth or rugulose.

TYPE SPECIES: *Phyllanthus floribundus* Muell. Arg. [= *P. muelleranus* Exell].

This exclusively Old World section of perhaps 10 to 15 species is best developed in Africa; only one species, *P. tenellus* Roxb., has become naturalized in America. The group as here defined has a different circumscription from that of Pax and Hoffmann. They included in sect. *Floribundi* those species previously classified in sect. *Menarda* which had fascicles of inflorescences at the nodes. Consequently, they retained *P. tenellus* and its relatives, which lack fascicled inflorescences, in sect. *Menarda*. Unfortunately, however, even the emended sect. *Menarda* of Pax and Hoffmann contains discordant elements. The type species, *P. cryptophilus* (A. Juss.) Muell. Arg., contrasts with all of the other species by virtue of its non-phyllanthoid branching and opposite leaves of peculiar texture. In the present circumscription, therefore, sect. *Menarda* is restricted to *P. cryptophilus* and a few other species of Madagascar, while all of the other species placed in the group by Mueller and by Pax are removed to sect. *Floribundi*. The latter, as thus constituted, is polymorphic and perhaps could be further divided, but any additional change in its definition must await careful study of the African species.

The description of the section is based primarily on the single species in the West Indies, *P. tenellus*, and therefore cannot be regarded as authoritative for the entire section. The relationships of sect. *Floribundi* are perhaps closest to sect. *Chorisandra* (Wight) Muell. Arg. The type species of the latter group, *P. pinnatus*,[11] agrees in having a crustaceous capsule, slender bifid styles, and free stamens (though 6 in number instead of 5). However, the seeds of *P. pinnatus* are very different, being hollowed out at the hilum. It is possible that further study may result in the merging of the two sections. On the other hand, sect. *Floribundi* is doubtless rather closely related to sect. *Anisonema*. Although the West Indian representatives of both groups are very easy to distinguish, there are species in Africa and Madagascar which seem to defy sectional limits; and future revision in the boundaries of these two groups may perhaps be required, although they are so distinctive on the whole that there would appear to be little advantage in merging them.

4. **Phyllanthus tenellus** Roxb. Fl. Ind. [ed. 2] 3: 668. 1832; Muell. Arg. in DC. Prodr. **15**(2): 337. 1866; Hook. f. in Hook. Icon. 1569. 1887. (TEXT-FIG. 6; PLATE I, *fig.* 3).

Phyllanthus corcovadensis Muell. Arg. Fl. Bras. **11**(2): 30, *pl. 6, fig. 2.* 1873.
Diasperus tenellus (Roxb. "em.") O. Ktze. Rev. Gen. **2**: 601. 1891.

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[11] **Phyllanthus pinnatus** (Wight) comb. nov.; *Chorisandra pinnata* Wight, Icon. Pl. Ind. Or. **6**: 13, *pl. 1994.* 1853; *Phyllanthus wightianus* Muell. Arg.

Phyllanthus minor Fawc. & Rend. Jour. Bot. **57**: 65–66. 1919.
Phyllanthus nummulariaefolius sensu Croizat, Torreya **42**: 14. 1942; non *P. nummulariaefolius* Poir.

Erect annual herb, typically with a single main (primary) stem c. 2 — 5 dm. high, 1.5 — 2 mm. thick, olivaceous or stramineous, smooth, terete or roundly angled, sometimes channelled; internodes mostly 10 — 35 mm. long. Cataphylls: stipules lanceolate, 0.7 — 1 mm. long, 0.2 — 0.3 mm. broad, acuminate, not auriculate, entire, olivaceous or reddish with rather narrow scarious margins; blade linear-lanceolate, 0.6 — 0.9 mm. long, attenuate-acuminate, similarly colored. Penultimate branches well developed in vigorous individuals (becoming up to 2 dm. long) or quite suppressed in smaller plants. Deciduous branchlets ascending, mostly 5 — 15 cm. long, 0.25 — 0.5 mm. thick, olivaceous, smooth or scabridulous, somewhat angled, with mostly 10 — 25 leaves; first internode (5–) 8 — 15 (–25) mm. long, median internodes c. 3 — 6 mm. long. Leaves: stipules lanceolate, 0.7 — 1.1 mm. long, acuminate, not auriculate, entire, olivaceous or reddish with white scarious margins. Petiole 0.5 — 0.8 mm. long. Leaf-blades membranous, smooth on both sides, mostly broadly elliptic to obovate, (6–) 10 — 20 (–24) mm. long, (4–) 5 — 9 (–11) mm. broad, acute or obtuse at the tip, acute to rounded at the base; above bright or dark green with the midrib and arching laterals (5 — 8 on a side) slightly raised; beneath pallid, the midrib raised, the laterals forming with the tertiary veinlets a fine reticulum; margins smooth.

Monoecious; all axils of deciduous branchlets usually floriferous. Proximal axils bisexual, the 1 or 2 female flowers beneath, the 2 or 3 male flowers above; distalmost cymules usually reduced to a single female flower.

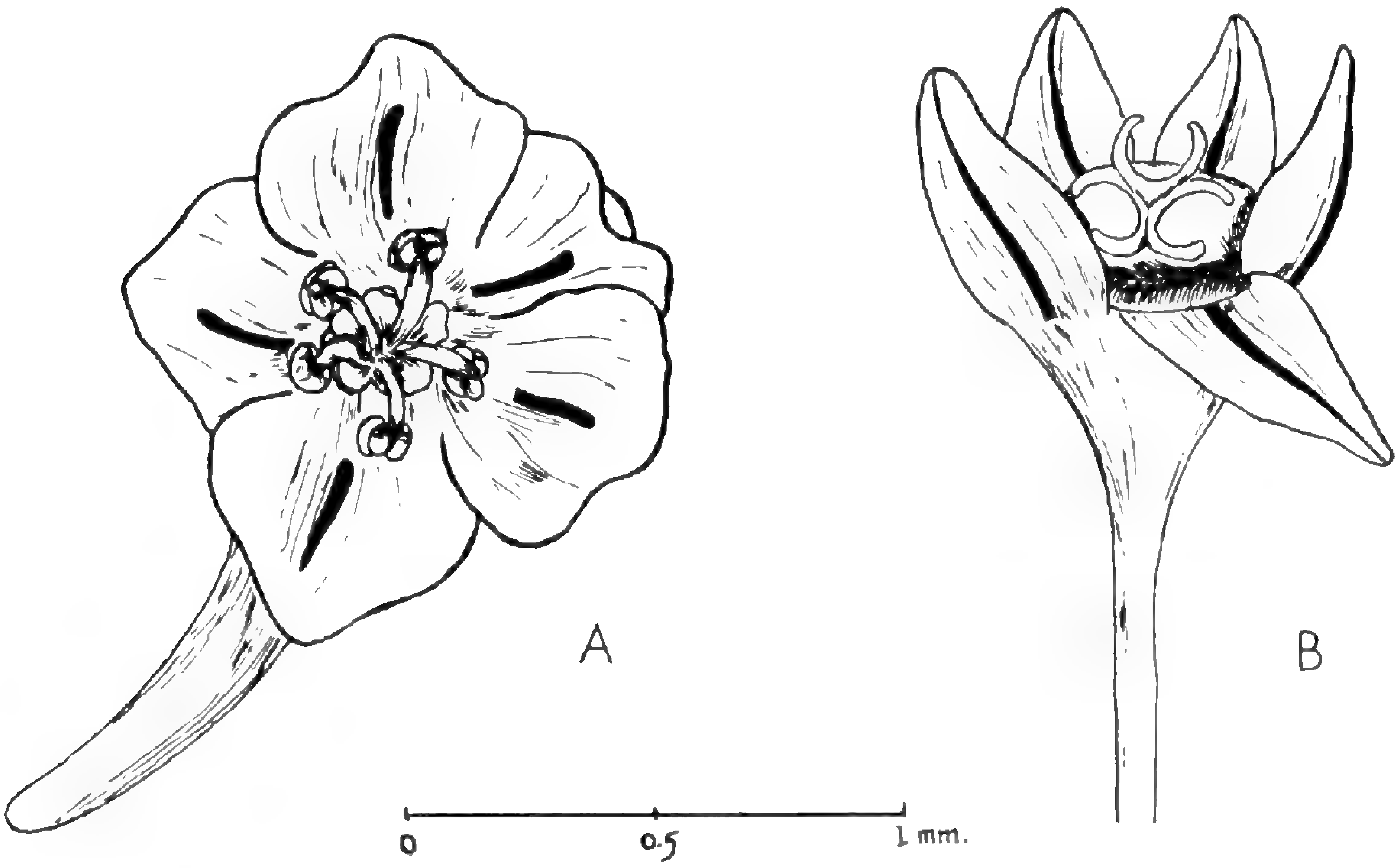
Male flower: Pedicel filiform, 0.5 — 1.5 mm. long. Calyx-lobes 5, imbricate at anthesis, subequal, broadly elliptic or obovate, c. 0.4 — 0.6 (–0.7) mm. long, 0.5 — 0.7 (–0.8) mm. broad, acute to rounded at the tip, entire, membranous, whitish except for the narrow green unbranched midrib. Disk-segments 5, broadly cuneate, thin, entire, c. 0.2 mm. across. Stamens 5, alternate with the disk-segments; filaments free, filiform, c. 0.2 — 0.3 mm. long, bent near the top; anthers reniform, 0.15 — 0.25 mm. broad, the long axis almost or quite horizontal; anther-sacs divergent, the slits confluent near the apex of the anther; pollen grains 17.5 — 19 μ in diameter, 4-colporate, the colpi not meeting at the poles.

Female flower: Pedicel capillary and flexuous, (2.5–) 3 — 5 (–7) mm. long, olivaceous (or reddish below), smooth and terete, dilated into a cylindrical pulvinus at the base and often bent at the pulvinar apex. Calyx-lobes 5, spreading at anthesis, triangular-ovate, 0.6 — 0.8 mm. long, 0.3 — 0.5 mm. broad, narrowed to an acute tip (in fruit reflexed, elliptic or oblong, and obtuse), entire, membranous, whitish except for the narrow green unbranched midrib. Disk patelliform, fleshy but thin, the margins undulate. Styles free, horizontally appressed, spreading, c. 0.25

mm. long, very slender, bifid to ⅔ parted, the branches divaricately spreading, the tips subcapitate.

Capsule oblate, rounded-trigonous, c. 1 mm. high, 1.7 — 1.9 mm. in diameter, greenish, obscurely reticulate-veiny. Seeds trigonous, c. 0.9 mm. long, 0.7 — 0.75 mm. radially and tangentially, light brown, densely pebbled on all sides with rounded processes; hilum linear-oblong.

Collected May through December, but perhaps flowering throughout the year where conditions are favorable.



TEXT-FIG. 6. *Phyllanthus tenellus* Roxb. (*Harris 12204*[GH]). A, male flower; B, female flower.

TYPE: Botanic Gardens, Calcutta, *Wallich 7892A ex p.* (K, HOLOTYPE). According to Roxburgh, the species was introduced from Mauritius in 1802 by Captain Tennant. However, Baker (Fl. Maur. 310. 1873) was unable to find a single Mauritian specimen of the plant. Since it appears improbable that so aggressive a weed as *P. tenellus* could have been overlooked by visitors to that island, the species was most likely collected in one of the other Mascarene islands. De Cordemoy (Fl. Reunion 346. 1895), for instance, has recorded it as very common everywhere in Reunion.

DISTRIBUTION: the typical var. *tenellus* (var. *roxburghii* of Mueller), native to the Mascarene islands, has been introduced into the southeastern United States, the West Indies, Brazil, and doubtless other areas of the New World.

JAMAICA. ST. ANN: Mt. Diablo, road to Hollymount, *Webster & Wilson 5016* (A, JAM, MICH). CLARENDON: 0.5 mile NW of Kupuis, *Proctor 10331* (GH). ST. ANDREW: Hope Grounds, in shady places, alt. 700 ft., *Harris 12123* (GH, NY, US), *12157* (NY, US), *12208* (GH, JAM, MT, NY, US; *P. minor* based on all three Harris collections).

LESSER ANTILLES. GUADELOUPE: Camp-Jacob, Choisy, Bagatelle, *Duss 2442, 3557* (NY); Montebello, *Questel 440* (US); between Goyave and Petit Bourg, Bailly, *Rodriguez 4390, 3935bis* (P). DOMINICA: Sylvania Estate, cleared forest land, *Hodge 573* (NY). MARTINIQUE: Morne-Rouge, Carbet, Fonds St. Denis, *Duss 47a* (NY, US); 1847, *Hahn 374* (A, P); environs St. Pierre, *Hahn 585* (G); St. Pierre, *Steinheil 24 ex p.* (P, mixed with *P. amarus*). GRENADA: under nutmegs, Grenville Vale, St. George Parish, *Hunnewell 19476* (GH).

Croizat (loc. cit.) has followed the example of Leandri (Not. Syst. 7: 168–169. 1939) in reducing *P. tenellus* to a synonym of *P. nummulariaefolius* Poir. As Leandri remarks, leaf size and pedicel length are excessively variable in this species-group, and the distinguishing characters proposed by Mueller are not convincing. Nevertheless, after examination of the holotype of *P. nummulariaefolius* (Herb. Lam., P) and of some Madagascar specimens cited by Leandri (*Humbert 5848, 6122*; A), I believe that these specimens represent a species closely allied to but distinct from *P. tenellus.* The calyx-lobes of the male flower of *P. nummulariaefolius* are about 1 mm. long, or almost twice the length of those of *P. tenellus;* and the pedicel of the male flower is about 3 — 6 mm. long in the former species, while in our West Indian plants it is never over 1.5 mm. in length. The leaf-shape also appears to be somewhat different in the two species, the blade of *P. nummulariaefolius* being rhombic- or suborbicular-obovate and rather abruptly contracted to a point, while that of *P. tenellus* is obovate and smoothly obtuse or rounded at the tip. Fawcett and Rendle were correct in noting the differences between the Jamaican plant and *P. nummulariaefolius*, but did not realize that the former was conspecific with *P. tenellus.*

As Leandri has observed (in lit.), the species of the complex to which *P. nummulariaefolius* and *P. tenellus* belong are at present so poorly defined that a careful monographic revision of them will be necessary before there can be any confidence with regard to species delimitation. The status of the six additional varieties of *P. tenellus* described by Mueller, as well as such closely allied species as *P. capillaris* Schum., must therefore be regarded as provisional.

The earliest record of *P. tenellus* from the West Indies is apparently the collection made on Martinique in 1839 by Steinheil. Judging from its rapid spread over Florida and Georgia within about twenty years of its introduction into the United States, it probably dispersed rapidly over the Lesser Antilles once given a foothold there. Its present naturalized area in the West Indies is strikingly parallel to that of another Old World congener, *P. urinaria*; both are widespread in Jamaica and the Lesser Antilles but have failed to become established on Cuba, Hispaniola, or Puerto Rico. The reasons for this are not entirely clear, for there are plenty of mesophytic habitats in the latter group of islands which would be attractive to the two species. The absence of *P. tenellus* from these islands is particularly surprising in view of the aggressively weedy nature of the plant; as Croizat remarks, it will quickly overrun a greenhouse if given a chance.

This "aggressive" nature of *P. tenellus* is largely due to the rapidity of growth and reproductive maturation of the plant. A seedling when only a few centimeters high is already producing explosively dehiscent capsules, and deciduous branchlets which have only two or three leaves unrolled will already have a completely developed fruit.

Phylogenetically *P. tenellus* is of considerable interest, because it and its allies appear to represent the link connecting the shrubby species of sect. *Floribundi* with the herbaceous species of sect. *Phyllanthus*. In its usual growth habit it agrees with some of the latter so closely that it can easily be confused with them. However, when grown in the greenhouse *P. tenellus* betrays its less specialized nature, for it may persist three years or more, become definitely shrubby at the base, and branch many times above. Indeed, Roxburgh reported that his original plant in the gardens at Calcutta grew to be a shrub 3.5 feet high. In contrast, the annual herbaceous species of sect. *Phyllanthus* such as *P. amarus* live only about a year or less even when pampered in the greenhouse.

Although the general aspect of *P. tenellus* is that of many species of sect. *Phyllanthus*, there is no reason why it should be confused with them. The long pendent capillary fruiting pedicels of *P. tenellus* are diagnostic, and of course no other herbaceous West Indian species has male flowers with five free stamens.

Sect. 3. **Anisonema** (A. Juss.) Griseb. Fl. Br. W. Ind. 34. 1859.

Kirganelia Juss. Gen. Pl. 387. 1789.
Anisonema A. Juss. Euphorb. Tent. 19, *pl. 4, fig. 11.* 1824.
Kirganelia sect. *Anisonema* (A. Juss.) Baill. Etud. Gen. Euphorb. 613–614. 1858.
Kirganelia sect. *Anisonemopsis* Baill. op. cit. 614.
Kirganelia sect. *Eukirganelia* Baill. ibid.
Phyllanthus sect. *Kirganelia* (Juss.) Muell. Arg. Linnaea 32: 11, 1863; DC. Prodr. **15**(2): 341. 1866.
Phyllanthus sect. *Typophyllanthus* subsect. *Kirganelia* (Juss.) O. Ktze. in Post & Kuntze, Lexicon 434. 1904.

Shrubs or small trees with the habit of *Breynia;* leaves chartaceous with rather conspicuous venation. Monoecious; flowers long-pedicelled, in bisexual cymules, the female flowers one or few, the males more numerous. Male flower: Calyx-lobes 5 or 6, unequal, entire; disk of discrete segments; stamens 5, unequal, in two sets: the inner connate with long filaments, the outer discrete with shorter filaments, filaments all free in some extralimital species fide Mueller; anthers extrorse, dehiscing longitudinally, the anther-sacs not confluent; pollen grains globose, tricolporate, finely reticulate. Female flower: Calyx-lobes 5 or 6, unequal, entire; disk of discrete or paired contiguous segments; ovary smooth, of 3 — 12 carpels; styles more or less bifid, often thickened and fleshy, more or less connivent. Fruit capsular or baccate; seeds trigonous.

TYPE SPECIES: *Phyllanthus reticulatus* Poir.

This section of about 10 Old World species is best distinguished by the curious androecium of five stamens unequally united into two sets. *Anisonema* and *Kirganelia* were distinguished by A. Jussieu (as genera) and by Baillon (as sections) on the basis of the number of locules in the ovary. However, the type species of the two groups, *P. reticulatus* Poir. and *P. casticum* Willem., agree in having the characteristic androecium, and Mueller was quite justified in combining them. Possibly he did not go far enough, for some of the species he included in his sect. *Kirganelia*, such as *P. physocarpus*, could as easily be placed in his sect. *Menarda* (i.e., sect. *Floribundi*).

The taxonomic difficulties attendant with sectional limits here are aggravated by the nomenclatural vagaries of typification. Mueller (DC. Prodr. 15(2): 341. 1866) and Pax and Hoffmann (Naturl. Pflanzenfam. **19c**: 62. 1931) applied the epithet *Kirganelia* to the present section. It is true that *Kirganelia* is the oldest generic name, but as a sectional name in *Phyllanthus* it must yield priority to *Anisonema*. This, as it turns out, is fortunate, because the type species of *Kirganelia* (*P. casticum*) has such a broad latitude of variation that among its own subspecies it nearly bridges the gap with sect. *Flueggeopsis*. All these nomenclatural difficulties are symptoms of an unstable taxonomy. When a monographic study can be made of subg. *Kirganelia*, it is likely that several of these closely related sections will be combined.

In the West Indies sect. *Anisonema* is represented only by a single introduced species.

5. **Phyllanthus reticulatus** Poir. Enc. Method. **5**: 298. 1804 (as *P. reticulata*); Muell. Arg. in DC. Prodr. **15(2)**: 345. 1866. (TEXT-FIG. 7).

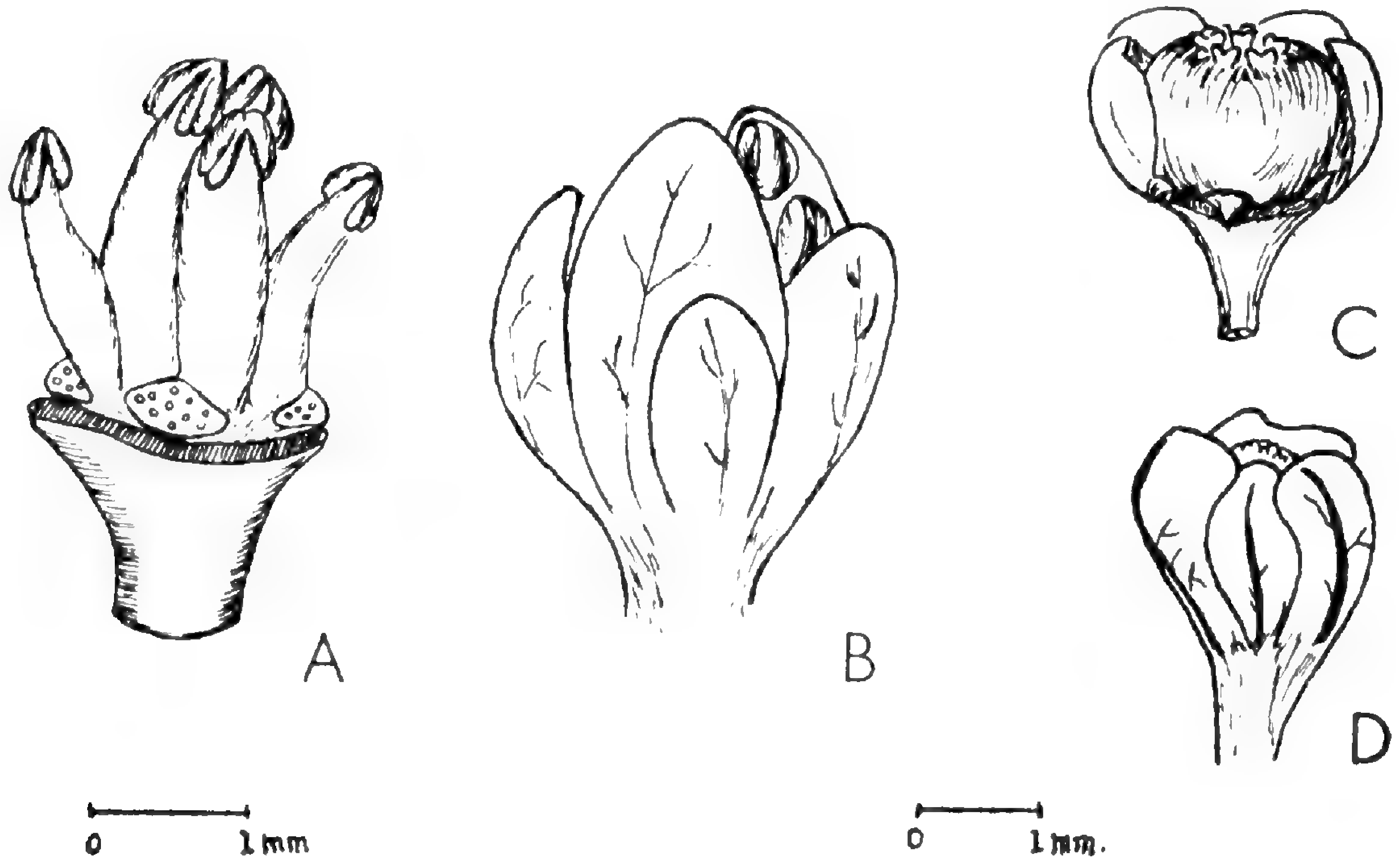
Phyllanthus jamaicensis Griseb. Fl. Br. W. Ind. 34. 1859 (for the remainder of the complicated synonymy see Mueller loc. cit.).

A much-branching shrub or small bushy tree up to 4 m. high; branches of current year smooth and glabrous, somewhat angled, dark brown, 2 — 3 mm. thick, with internodes mostly 1 — 2 cm. long. Cataphylls: stipules triangular, (1.2–) 1.5 — 1.7 mm. long, mostly 1 — 1.4 mm. broad, acuminate, truncate at the base, subcarnose, dark blackish brown, margins ciliate; blade lanceolate, (1.1–) 1.3 — 1.7 mm. long, 0.4 — 0.9 mm. broad, acuminate, similar in texture, ciliate. Deciduous branchlets steeply ascending, (8.5–) 10 — 20 (–25) cm. long, 0.5 — 1 mm. thick, dark brown, somewhat angled, quite smooth, with (10–) 13 — 16 (–25) leaves; internodes mostly 7 — 13 mm. long. Leaves: stipules lanceolate, (0.8–) 1 — 1.4 (–1.6) mm. long, 0.5 — 0.7 mm. broad, acuminate, truncate at the base, margins ciliate, olivaceous turning more or less dark brownish, rather scarious. Petioles smooth, plano-convex, 1.5 — 2.5 mm. long. Leaf-blades chartaceous, smooth on both surfaces, elliptic, (13–) 15 — 25 (–32) mm. long, (9–) 10 — 15 mm. broad, obtuse or rounded at the tip, cuneate at the base; midrib and laterals (5 — 7 on a side) raised and conspicuous particularly beneath, where they form with the tertiaries a conspicuous reticulum; margins not thickened, more or less plane.

Monoecious; most deciduous branchlets floriferous; first 1 or 2 (rarely more) proximal nodes barren, succeeding ones with bisexual cymules; female flower solitary or sometimes paired in each cymule, male flowers up to 8.

Male flower: pedicel capillary, 5 — 10 mm. long. Calyx-lobes 5 or 6, unequal, imbricate in 2 or 3 series, c. 2 — 2.5 mm. long, the outer oblong or obovate, rounded at the tip and c. 0.7 — 1.2 mm. broad, the inner nearly orbicular, subtruncate at the tip and c. 1.3 — 1.8 mm. broad; lobes of both series entire, with simple or sparsely branched midrib, somewhat thickened adaxially at the base; margins thin and scarious. Disk-segments 5, broadly ovate or reniform, thin, subcarnose, erect, entire, foveolate, 0.35 — 0.5 mm. across. Stamens 5, erect, in two sets: three with longer filaments (0.7 — 1.3 mm. long) coherent in a central column, two with shorter filaments (0.3 — 0.8 mm. long) free and displaced to the sides — or vice versa (i.e., two stamens central and coherent with three shorter ones peripheral and more or less free); filaments fusiform, often conspicuously thicker than the anthers, 0.25 — 0.5 (–0.6) mm. broad. Anthers erect, triangular, c. 0.3 — 0.5 mm. long and broad; anther-sacs divergent, dehiscing longitudinally, discrete, the slits apically contiguous but not confluent; pollen grains c. 14 — 17 μ in diameter, tricolporate, colpi conspicuously bordered and meeting at the poles, reticulum rather coarse.

Female flower: pedicel subterete, slender, (4–) 5 — 8 mm. long. Calyx-



TEXT-FIG. 7. *Phyllanthus reticulatus* Poir. (*Webster & Wilson 5237*[A]). A male flower with calyx-lobes removed to show androecium and disk; B, male flower entire; C, female flower with two calyx-lobes removed to show ovary and styles; D, female flower entire (B, C, and D to the same scale).

lobes 5 or 6, erect and closely investing the ovary, unequal, in 2 or 3 series (the innermost segment completely overlapped by the others); the outer oblong-elliptic, c. 1.6 — 1.8 mm. long and 0.9 — 1.2 mm. broad, strongly carinate, midrib simple or sparsely branched; the inner nearly orbicular, c. 1.4 — 1.7 mm. long, 1.2 — 1.5 mm. broad, carinate or plane, the midrib sparingly branched. Disk-segments 5 or 6, often subpaired, oblong or cuneate, somewhat thickened and fleshy, c. 0.3 — 0.4 mm. broad, obscurely foveolate. Ovary oblate-spheroidal, smooth, not perceptibly sulcate; carpels mostly 9 or 10 (in West Indian material); styles c. 0.25 mm. long, bifid, thickened and fleshy, free but inflexing and connivent over the top of the ovary as an irregular furrowed mass of stigmatic tissue.

Mature fruit baccate, globose or oblate, c. 4 — 6 mm. in diameter, shiny black with dark purplish pulp. Seeds trigonous (when in pairs), c. 1.6 — 2 mm. long, blackish, colliculose; hilum shallow, less than 0.5 mm. across.

Flowering and fruiting March to July, and probably later in the year as well.

Type: Herb. Lamarck (P, holotype). The type sheet contains a mixture of *P. reticulatus* and a species of *Breynia.*

Distribution: Widespread in the Old World from West Africa to India, Ceylon, China, Indonesia, the Philippines, and Queensland; introduced into the West Indies.

JAMAICA. common, Oct. 1857, *Wilson* (GOET, holotype of *P. jamaicensis*); donne par Sir W. Hooker, 1845 (P); center and east Jamaica, thickets and river banks, *Velez 3781* (US). St. Thomas: shores of Plantain Garden River, *Harris & Britton 10677* (NY, US), *Webster & Wilson 5237* (A, JAM, MICH); Bath, *Orcutt 2013* (US); fields, Holland Bay, *Britton 4067* (NY).

LESSER ANTILLES. St. Vincent: *Caley* (P); Liberty Lodge, alt. 500 ft., *Eggers 6769* (GOET, P, US); thickets near houses, hills near Kingstown, alt. 800 ft., *H. H. & G. W. Smith 872* (NY).

This introduced Old World plant is readily recognizable by virtue of its peculiar androecium and baccate fruit, and cannot be mistaken for any native West Indian species. Although in its native range *P. reticulatus* is extremely variable, the specimens from the West Indian populations all represent the glabrous form, var. *glaber* of Mueller. Poiret's type specimen is definitely pubescent, but since — as pointed out by J. D. Hooker (Fl. Br. Ind. 5: 288. 1887) — the pubescent and glabrous forms occur indiscriminately together, it does not seem worthwhile to designate the form in the West Indies with a varietal name. *Phyllanthus jamaicensis* Griseb. was described under the mistaken impression that the plant was endemic to Jamaica. However, the specimen collected by Wilson and now in the Herbarium Grisebachianum (GOET) can be matched by many sheets from the Old World, and shows no significant differences.

The only striking peculiarity of the West Indian specimens of *P. reticulatus* appears to be their infertility. Only two fruits were observed on a copiously flowering plant seen in the field at the Plantain Garden River, Jamaica (*Webster & Wilson 5237*), and each of these contained but a single well-developed seed. In contrast, many specimens from the Old World — e.g., *Merrill Species Blancoanae 674* (A) — have numbers of fruits, each of which have 12 — 16 mature seeds.

J. J. Smith (Add. Fl. Arb. Jav. 12: 67. 1910) describes the seeds of a living plant of *P. reticulatus* as greenish, with "testae strato exteriore succoso, strato interiore duro." If the seed-coat of *P. reticulatus* is actually fleshy, this would be an extremely interesting indication of a close relationship between this plant and species of *Glochidion* and *Breynia*. However, judging from the seeds of *Webster & Wilson 5237* and *Merrill 674*, the seed-coat could at most be called slightly fleshy. The outer seed-coat is scarcely thicker than the inner and certainly appears no different from that of many typical species of *Phyllanthus*. Furthermore, since there is no hilar indentation in *P. reticulatus* and the embryo is straight, it does not appear that this species represents a very close approach to the seed structure of *Glochidion*.

Subgenus III. **Cicca** (L.) Webster, Jour. Arnold Arb. 37: 344. 1956.

Cicca L. Mant. 17. 1767.

Trees or rarely shrubs with phyllanthoid branching. Monoecious or dioecious, inflorescences commonly fascicled or cauliflorous. Male flower: calyx-lobes 4 — 6; disk of 4 — 6 segments or absent; stamens 3 or 4 (rarely 2 or 5), filaments free; anthers dehiscing more or less vertically; pollen grains 3-colporate. Female flower: calyx-lobes 4 — 6; disk cupuliform or absent; ovary of 2 — 4 carpels; styles bifid, free or shortly connate at the base. Fruit indehiscent, woody or drupaceous; seeds 1 or 2 in each fertile locule.

This subgenus contains some of the most distinctive groups in the genus, and it is not surprising that at times sects. *Cicca*, *Aporosella*, and *Emblica* have been recognized as generically distinct from *Phyllanthus*. The accumulation of further evidence from such fields as wood anatomy and cytology may possibly justify the maintenance of one or more of these groups as an independent genus. However, at the present time they seem best regarded as divergent sections of *Phyllanthus*, especially since sect. *Ciccopsis* would appear to at least partially bridge the gap between sect. *Cicca* and typical representatives of sect. *Kirganelia*. It should also be pointed out here that the inclusion of sect. *Emblica* in the present subgenus is quite possibly contrary to natural relationship, and is justified in this West Indian study on the grounds of convenience.[12] With the exception of sect. *Emblica*, the species of subg. *Cicca* are all native to the New World.

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[12] The description of the subgenus applies only to the American representatives and does not refer to the special features of sect. *Emblica*.

KEY TO THE SECTIONS

1. Calyx-lobes 6; male flower with 3 stamens, the filaments free; leaves elliptic, obtuse or rounded at the tip. .... 4. **Ciccopsis**
1. Calyx-lobes 4 or if 6 then filaments of stamens united; leaves otherwise.
    2. Fruit indehiscent; calyx-lobes usually 4; leaves elliptic to ovate; female disk small or absent.
        3. Fruit drupaceous; monoecious (in West Indies); disk present; staminodes often present .... 5. **Cicca**
        3. Fruit pithy; dioecious; disk and staminodes absent. .... 6. **Aporosella**
    2. Fruit fleshy but at length dehiscent; calyx-lobes 6; leaves linear-oblong; female disk urceolate. .... 7. **Emblica**

Sect. 4. **Ciccopsis** Webster, Contr. Gray Herb. **176**: 57. 1955.

Shrubs or trees with phyllanthoid branching; cataphylls persistent; branchlets compressed, angled, often borne on spur-shoots; leaves with persistent stipules, corrugate petioles, chartaceous blades; monoecious, inflorescence semi-cauliflorous, the floriferous branchlets more or less fascicled on short spurs. Male flower: calyx-lobes 6, reflexed; disk-segments 6; stamens 3, free, the filaments erect; anthers deflexed at connective; pollen grains tricolporate, angular-aperturate. Female flower: calyx-lobes 6; disk 3-angled; ovary of 3 carpels; styles free, horizontal, bifid. Fruit and seeds unknown.

TYPE SPECIES: *Phyllanthus pseudocicca* Griseb.

This monotypic section is represented only by the type species, which is endemic to a relatively small area in eastern Cuba. Its relationships are somewhat dubious at present because of the doubt as to the nature of the fruit. However, there is little doubt that it is fairly closely related to sect. *Cicca*, if indeed that group is not its nearest ally. The pollen grains of *Cicca* are rather similar, and its cauliflorous condition could be rather easily derived from the semi-cauliflorous behavior of *Ciccopsis*. On the other hand, various African species in subg. *Kirganelia* — in particular *P. physocarpus* Muell. Arg. — have a suggestive general resemblance to *P. pseudocicca* in both floral and vegetative morphology. It is quite possible that sect. *Ciccopsis*, when better understood, may prove to represent the closest approach to a connecting link between subg. *Kirganelia* and subg. *Cicca*.

Section *Ciccopsis* is of further phylogenetic interest because of its apparent relationship to sect. *Omphacodes* (subg. *Xylophylla*). Indeed *P. pseudocicca* and the type species of that section, *P. subcarnosus*, are so strikingly similar in leaf venation and details of floral morphology that a fairly close degree of affinity between them appears highly probable, even though they are widely separated in the linear arrangement of taxa. The somewhat fleshy fruit and the ecological requirements of *P. subcarnosus* further suggest a general relationship to subg. *Cicca*. In fact, if it were not for their areolate pollen grains, the two species of sect. *Omphacodes* could just as well be put adjacent to sect. *Ciccopsis* in the present arrangement.

6. **Phyllanthus pseudocicca** Griseb. Goett. Nachr. **1865**(7): 166. 1865; Muell. Arg. in DC. Prodr. **15**(2): 384. 1866.
(PLATE XV, *figs. A–C*).

Diasperus pseudocicca (Griseb.) O. Ktze. Rev. Gen. **2:** 600. 1891.
Phyllanthus brevistipulus Urb. Symb. Ant. **9:** 183. 1924.
Phyllanthus punctulatus Urb. ibid. 184.

A glabrous shrub (Ekman) or slender tree to c. 10 m. high (Wright); branches of previous year 3 — 4 mm. thick, with smooth or furrowed greyish bark, old nodes with spur-shoots c. 0.5 — 2 cm. long, 1.5 — 2 mm. thick, smooth or in age roughened with the cataphyll bases. Cataphylls dark brown, indurate, persistent, not reflexed: stipules broadly triangular, c. 1 mm. long and broad, blunt, typically entire, fused at the base into a massive scale; blades lanceolate, inconspicuous, c. 0.5 mm. long or less. Branchlets in part scattered along branches of current year, in part clustered on spur-like branches from the axils of nodes on old wood (i.e., on branches of previous years), 3 — 10 cm. long, 0.5 – 1 mm. thick, somewhat compressed, angled, stramineous, slightly shiny, with 5 — 9 leaves; first internode (5–) 10 — 17 mm. long, median internodes (5–) 7 — 10 (–15) mm. long. Leaves: stipules appressed, persistent, triangular, 0.5 — 1 mm. long and about as broad, blunt-tipped, dark reddish-brown, entire. Petiole (2.5–) 3 — 4 mm. long, stramineous, flattened adaxially, transversely corrugate-lamellate. Leaf blades chartaceous, plane, elliptic or ovate, 2.5 — 5 (–6.5) cm. long, 1.5 — 3 (–4) cm. broad, obtuse or rounded at the tip, mostly obtuse at the base; above olivaceous or brownish (when dried), somewhat shiny, midrib plane or incised, laterals slightly raised, subconspicuous; beneath greyish-green (puncticulate with whitish waxy atoms) or yellowish, the midrib and laterals (4 or 5 on a side) conspicuously raised, anastomosing to form a prominent reticulum; margins thickened, plane or reflexed.

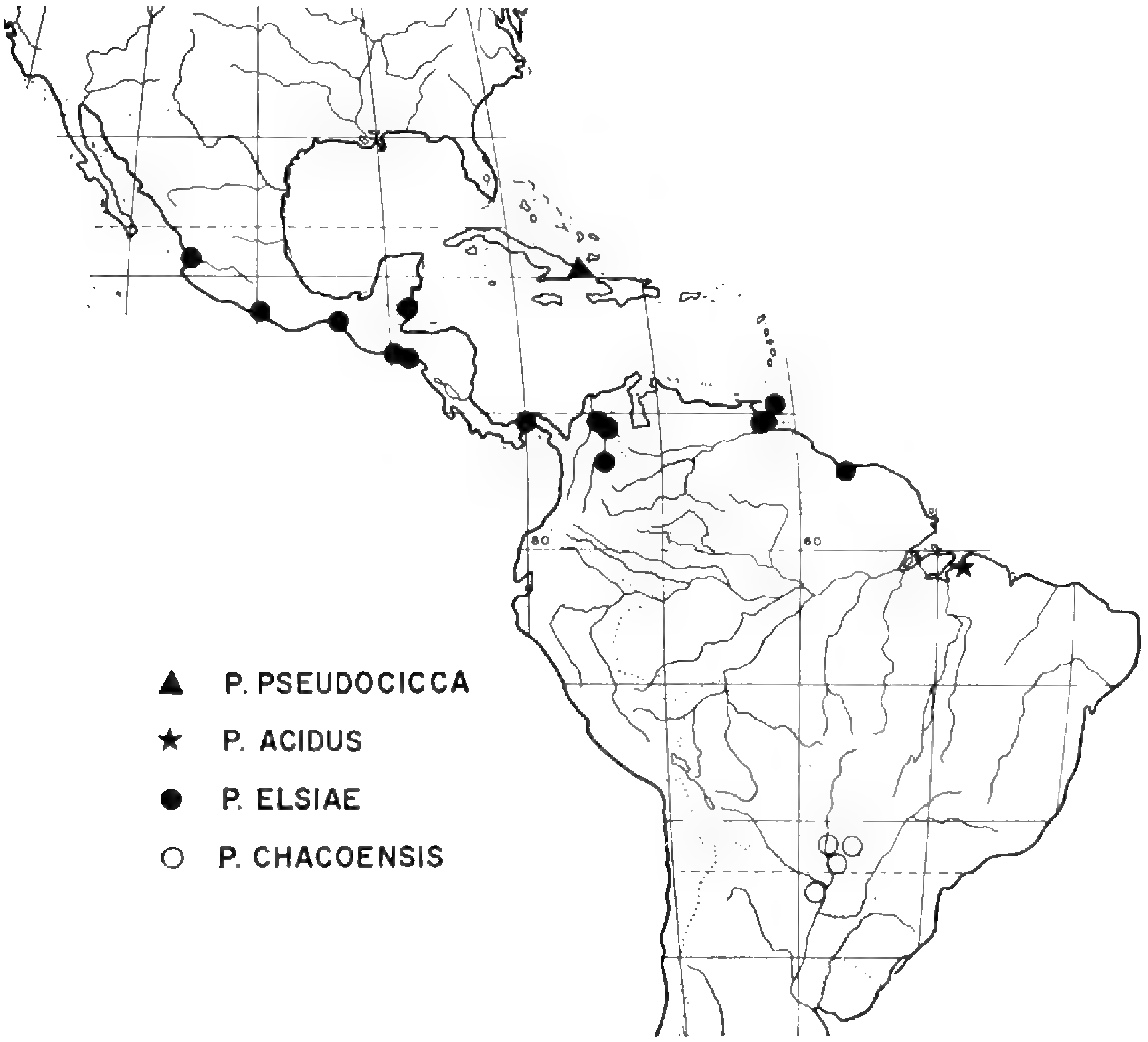
Monoecious (rarely dioecious?); floriferous branchlets sometimes nearly or quite aphyllous (the leaves reduced to cataphylls) but usually with only the proximal 2 — 4 leaves reduced and subtending male cymules, the distal leaves typical and subtending bisexual cymules of one female and several male flowers; occasional branchlets producing only male flowers.

Male flower: pedicel c. 2 mm. long, stramineous, smooth, definitely enlarged above the middle, the enlarged portion often with a few reddish-brown cells. Calyx-lobes 6, biseriate, subequal, bent and reflexed or flaring from above the middle at anthesis, oblong-obovate, c. 0.75 — 0.9 mm. long, 0.45 — 0.6 mm. broad, rounded at the tip, entire, the midrib unbranched, the midrib area somewhat thickened and fleshy, the margins thin, scarious, subhyaline. Disk-segments 6, erect and substipitate, quadrate, c. 0.2 mm. in diameter, crenulate, pitted. Stamens 3, free except at the very base (rarely 2 of them united), the filaments terete, erect, 0.4 — 0.5 mm. long; anthers sharply deflexed at the connectives, strongly flattened dorsiventrally, c. 0.2 mm. long, 0.3 mm. broad; anther-sacs strongly divergent, convergent at the apex but the slits not confluent; pollen grains tricolporate, c. 18 μ in diameter, angular-aperturate, the colpi narrowly bordered, not quite confluent at the poles.

Female flower: pedicel c. 10 mm. long, somewhat thickened distally. Calyx-lobes 6, subequal, oblong, c. 0.6 — 0.8 mm. long, 0.4 — 0.5 mm. broad, obtuse or acute, entire, somewhat spreading but not flaring as in the male, rather thicker and fleshier than the male, the scarious margin not so pronounced. Disk 3-angled, as of 6 segments fused in pairs, flat, thin, entire, not pitted. Ovary depressed-globose, sessile, smooth, trigonous, 6-sulcate; styles free, horizontally appressed to the ovary, 0.35 — 0.4 mm. long, bifid or ⅓-parted, the branches divergent or divaricate, the blunt tips spreading or slightly recurved.

Mature fruit and seeds not examined (ex Alain, a capsule 3 — 4 mm. in diameter).

Collected in flower in June and July.



Map III. Distribution of the American species of subg. *Cicca*.

TYPE: Cuba, Oriente, Cuchillas de Baracoa, a slender tree about 40 ft. high, flowers whitish, June 21, *Wright 1940* (GOET, holotype; G, GH, MO, isotypes; data ex GH).

DISTRIBUTION: endemic to the mountains of the Sagua-Baracoa range, Oriente Province, Cuba (Map III).

CUBA. ORIENTE: Sierra de Nipe, prope Rio Piedra, 4 Oct. 1919, *Ekman 9825* (S, HOLOTYPE of *P. punctulatus*); Moa region, Mina Cromita, Cayoguan, west of Punta Gorda, 24 July 1944, *Clemente & Alain 4079* (MICH); pineland barrens, Charrascos de Pena Prieta, Toa, alt. 600 m., 30 July 1953, *Alain 3484* (GH); same locality, 30 Dec. 1953, *Alain 3662* (GH); Baracoa, in the valley of the Rio Macaguanigua, 19 Jan. 1915, *Ekman 4323* (S, ISOTYPE of *P. brevistipulus*); Cuchillas de Baracoa, *Wright 1940* (G, GH, GOET, MO).

This extremely interesting species, although a phylogenetic relict and apparently rather rare, is not geographically narrowly confined, since its known range in the Sagua-Baracoa massif of Oriente Province is about 100 miles east to west. Its ecological requirements are not well known, the habit of pineland barrens as recorded by Alain being our only sure information. Judging from the data of Alain and others, however, it is evident that *P. pseudocicca* definitely does not occupy swamp woods or sublittoral forest habitats as do its relatives *P. acidus* and *P. elsiae*.

It is especially unfortunate that no mature fruits have been available for examination, since fruit structure is particularly significant in assessing relationships in subg. *Cicca*. The statement by Alain (Flora de Cuba 3: 53. 1953) that the fruit is a "capsula de 3 — 4 mm." may well be correct, for the ovary wall in *P. pseudocicca* at anthesis does not appear to be as thick as it is in *P. acidus;* however, the dehiscence of the fruit of *P. pseudocicca* may still not be typical for the genus. The lack of available fruits for examination is perhaps related to some peculiarity in the flowering habits of the species. Of the seven collections examined, five were completely sterile, and one of these, *Alain 3484,* was made only six days later in the year than the copiously fertile collection *Clemente & Alain 4079*.

The two species proposed by Urban, *P. brevistipulus* and *P. punctulatus*, were both founded on sterile Ekman collections. Urban compared the former to *P. nutans*, a completely different plant, and apparently was unaware that Grisebach had proposed the name *P. pseudocicca* for the same plant. Alain (loc. cit.) has already reduced *P. brevistipulus* to synonymy, and I feel certain that *P. punctulatus* merits the same treatment Urban merely compared its habit to that of *P. discolor* and *P. nutans* and added "sine dubio longe diversus." His comment was correct as far as it went, for the plant in question is indeed quite different from those two species. But Urban failed to realize that the type specimen of his *P. punctulatus* merely represents a large-leaved form of *P. pseudocicca*. The pale, slender branchlets c. 1 mm. thick, which indicate that the Ekman specimen belongs to *P. pseudocicca*, incidentally serve to distinguish this species from another vegetatively similar Oriente species, *P. leonis*, which is often found in the sterile condition. In *P. leonis* the branchlets are mostly 1.5 — 2 mm. thick and are definitely angled.

Sect. 5. **Cicca** (L.) Muell. Arg. Linnaea **32**: 50. 1863; emend.

Cicca L. Mant. 124. 1767.
Tricarium Lour. Fl. Cochin. 557. 1790.
Staurothylax Griff. Notul. **4**: 476. 1854.
Phyllanthus sect. *Cicca* subsect. *Eucicca* Muell. Arg. loc. cit.; DC. Prodr. **15**(2): 413. 1866.
Phyllanthus sect. *Typophyllanthus* subsect. *Cheramela* O. Ktze. Lex. Gen. Phaner. 434. 1904.

Trees with phyllanthoid branching, the flowers more or less cauliflorous. Monoecious or rarely dioecious. Male flower: calyx-lobes 4; disk of 4 segments; stamens mostly 4, filaments free, anthers dehiscing vertically; pollen grains globose, tricolporate, the colpi meeting at the poles. Female flower: calyx-lobes 4; disk lobed or separated into 4 segments; staminodes often present; carpels 3 or 4; styles free except at base, deeply bifid, spreading. Fruit drupaceous, endocarp bony; seeds 1 or less commonly 2 per fertile locule.

TYPE SPECIES: *Phyllanthus acidus* (L.) Skeels

The single species which comprises this monotypic section is so closely related to the representatives of sect. *Aporosella* that — despite the strong morphological discontinuity — it could almost as logically be associated with them in a single section. The production of staminodes in the female flower and the truly drupaceous nature of the fruit are the strongest distinguishing characters of sect. *Cicca*.

Robinson (Phil. Jour. Sci. Bot. **4**: 87. 1909; **6**: 323. 1911) has advocated generic status for *Cicca*, largely on the basis of the fruit, and has been followed by Merrill and other workers. There is of course no doubt that *Cicca* is a distinctive group, so that the question of its generic vs. infrageneric rank is to some extent a matter of judgment. In my opinion its close alliance with sects. *Ciccopsis* and *Aporosella* makes the inclusion of *Cicca* within *Phyllanthus* the most logical treatment.

It should be noted that the circumscription of sect. *Cicca* is here drastically altered from Mueller's concept so as to include only his subsect. *Eucicca* and to exclude his subsects. *Margaritaria*, *Prosorus*, and *Ciccoides*. Mueller's erroneous description of the fruit of *P. acidus* as capsular suggests that he had seen no good fruiting specimens and was extrapolating from the more or less dehiscent fruit of the other subsections. These latter, however, differ from *P. acidus* not only in their fruits but also in their non-phyllanthoid branching, annular floral disk, and fleshy seed-coat; indeed they scarcely have more in common with *P. acidus* than superficially rather similar tetramerous flowers. The species in these three subsections should all be removed from *Phyllanthus* and placed together in the genus *Margaritaria.*

The following West Indian species which have been included in *Phyllanthus* sect. *Cicca* are therefore to be transferred from the genus:

1. *Phyllanthus nobilis* (L.f.) Muell. Arg. = *Margaritaria nobilis* L. f.
2. *Phyllanthus virens* (Griseb.) Muell. Arg. = **Margaritaria tetracocca** (Baill.) comb. nov. (*Wurtzia tetracocca* Baill. Adansonia 1: 187. 1860–61).
3. *Phyllanthus scandens* (Wr. ex Griseb.) Muell. Arg. = **Margaritaria scandens** Wr. ex Griseb.) comb. nov. (*Cicca scandens* Wr. ex Griseb. Goett. Nachr. **1865**: 165–166. 1865).
4. *Phyllanthus hotteanus* Urb. & Ekm. (Ark. Bot. [Stockholm] **22A** [8]: 61. 1929) = **Margaritaria hotteana** (Urb. & Ekm.) comb. nov.

7. **Phyllanthus acidus** (L.) Skeels, U.S.D.A. Bur. Pl. Ind. Bull. **148**: 17. 1909. (PLATE XV, *figs. D–F*).

Neli-pouli Rheede, Hort. Malabar. 3: 57, *pls. 47, 48.* 1682.
Malus indica, fructu parvo rotundo acido striato Burm. Thes. Zeyl. 148. 1737.
Averrhoa ramis nudis fructificantibus, pomis subrotundis L. Fl. Zeyl. 80. 1747.
Cheramela Rumph. Herb. Amb. 7: 34, *pl. 17, fig. 2.* 1750.
Averrhoa acida L. Sp. Pl. 428. 1753.
Cicca disticha L. Mant. 1: 124. 1767.
Cicca nodiflora Lam. Encycl. 2: 1. 1786.
Cicca racemosa Lour. Fl. Cochin. 556. 1790.
Phyllanthus longifolius Jacq. Hort. Schoenbr. 2: 36, *pl. 194.* 1797.
Cicca acidissima Blanco, Fl. Filip. ed. 1, 700. 1837.
Phyllanthus cicca Muell. Arg. Linnaea 32: 50. 1863.
Phyllanthus cicca β bracteosus **Muell. Arg. ibid.**
Phyllanthus distichus (L.) Muell. Arg. in DC. Prodr. 15(2): 413. 1866.
Phyllanthus distichus f. *nodiflorus* (Lam.) Muell. Arg. op. cit. 414.
Phyllanthus acidissimus (Blanco) Muell. Arg. op. cit. 417.
Diasperus distichus (L.) O. Ktze. Rev. Gen. 2: 599. 1891.
Cicca acida (L.) Merr. Interpr. Rumph. Herb. 17. 1917.

A small or medium-sized glabrous tree up to 10 m. high, with rough grey bark; older branches subterete, up to c. 1.5 cm. thick, greyish brown, with rather prominent lenticels; terminal branches of current year dark brown, smooth, remaining spur-like or elongating up to c. 8 cm., 3 — 5 mm. thick, producing usually seven or eight leafy branchlets; inflorescences mostly borne on lateral spur-shoots (less than 1 cm. long) on older wood. Cataphylls blackish brown, rather firm but breaking away and not persisting, the stipules triangular-ovate, c. 1.5 mm. long, with entire to fimbriate margins; blade similar but narrower, acuminate, up to 2 mm. long. Deciduous branchlets ascending, (20–) 25 — 52 cm. long, c. 1.5 — 3 mm. thick, pale brown, terete (somewhat flattened or subangled toward apex), smooth, with 25 — 40 leaves; first internode 1 — 5 cm. long, median internodes c. 0.5 — 1 cm. long. Leaves: stipules appressed, the bases more or less persistent, triangular-acuminate, c. 0.8 — 1.2 mm. long and (0.3–) 0.5 — 0.8 mm. broad (the proximal ones somewhat larger), not auriculate, dark brown, scarious, entire or denticulate-fimbriate. Petiole 2.5 — 4 mm. long, yellowish brown, more or less rugose, with two blunt ridges and a low median ridge on the adaxial side. Leaf blade chartaceous, broadly ovate to ovate-lanceolate, (4–) 5 — 9 cm. long, (2–) 2.5 — 4.5 cm. broad, acute (sometimes abruptly so) at the tip, obtuse or rounded at the base; above olivaceous, sublucid, the proximally impressed midrib running to the tip, laterals ascending, reticulum of tertiary branches evident to conspicuous; beneath pale greyish brown, the midrib prominently raised, the laterals (c. 5 — 7 on a side) ascending, raised, anastomosing within the margins, forming with the tertiaries a fine subprominent slightly raised reticulum; margins undifferentiated, plane.

Monoecious (in West Indian material); flowers borne in dense pulviniform cymules at the nodes of "naked" branchlets on older wood, and usually also on the proximal branchlets of the current year's growth (at the tip of the branch). Cymules of cauline inflorescence axes (which are merely modified deciduous branchlets) bisexual, each with 1 — 9 female flowers accompanied by c. 25 — 40 males. First branchlets of the current year's growth often bearing bisexual cymules with 1 — 2 female flowers and a dozen (or less) males; succeeding ones with male cymules; distalmost branchlets quite sterile (sometimes no branchlets with bisexual cymules, or occasionally all branchlets sterile). Bracts of cymules blackish brown with reddish brown scarious fimbriate margins, less than 1 mm. long.

Male flower: pedicel slender, c. 1.5 — 3 mm. long. Calyx-lobes 4, subequal (the inner pair rather broader), elliptic to suborbicular, 1.1 — 1.4 (–1.5) mm. long, 0.8 — 1.3 (–1.4) mm. broad, rounded or obtuse at the tip, entire, the midrib unbranched. Disk-segments 4, more or less orbicular, c. 0.2 — 0.3 mm. across, not massive, entire. Stamens 4 (rarely 3), filaments free (at most slightly coherent at base), slender (c. 0.1 mm. thick), erect, 0.4 — 0.5 (–0.6) mm. long; anthers more or less deflexed at the connectives, emarginate or occasionally minutely apiculate, broadly elliptic to suborbicular, c. 0.25 — 0.3 mm. long, 0.3 — 0.35 mm. broad; anther-sacs parallel, dehiscing longitudinally, the slits not confluent; pollen grains 16 — 19 μ in diameter, tricolporate, not angular-aperturate, the colpi conspicuously bordered, confluent at the poles.

Female flower: pedicel straight, terete and rather stout (in fresh material; often becoming wrinkled or sharply ridged on drying), increasing in length from c. 1.2 — 1.5 mm. at anthesis up to c. 2.3 — 5 (–6) mm. in fruit, c. 0.3 — 0.5 mm. thick. Calyx-lobes 4, at first erect, later spreading, subequal, triangular-ovate or elliptic, (1–) 1.2 — 1.4 mm. long, (0.9–) 1 — 1.25 mm. broad, obtuse or rounded at the tip, thickened at the base, entire, the midrib unbranched. Disk c. 1 — 1.2 mm. across, mostly deeply lobed or separated into 4 quadrate or reniform segments, these c. 0.2 — 0.3 mm. across. Ovary at first more or less pyriform, c. 0.8 — 1.1 mm. high, 0.8 — 1.2 mm. in diameter, smooth, brownish, shallowly 3- or 4-lobed, usually definitely stipitate, the broad gynophore c. 0.2 — 0.25 mm. high;

styles very shortly connate into a column 0.2 — 0.25 mm. high, recurving, deeply bifid to the column, the slender tapering branches c. 0.8 — 1 mm. long. Staminodia 0, 1, or 2 (rarely to 4, ex Mueller) per flower, resembling the stamens but filaments much shorter.

Fruit drupaceous, oblate, of 3 or less commonly 4 carpels shallowly 6- or 8-lobed, the flesh (exocarp) firm, greenish yellow to creamy white, acid in taste, quite variable in size: when fresh, c. 1 — 1.5 cm. high, (1.2–) 1.5 — 2 (–2.5) cm. in diameter. Endocarp very hard and bony, the carpels firmly united and never separating on drying of the fruit, subglobose or oblate, deeply but obtusely ridged, c. (4.8–) 5 — 7 (–9) mm. high and 6 — 9 (–16.5) mm. in diameter. All carpels of a fruit rarely fertile, usually only 1 or 2 (–3) cells each developing 1 or less commonly 2 seeds. Seeds (when single) adaxially concave, c. 3.3 — 3.5 mm. long, 2.5 — 3 mm. broad; seed-coat thin (except around the hilum), brittle, light brown, smooth; hilum broad, circular, on the adaxial face.

Flowering (in the West Indies) mostly January through July; most flowering collections made January through March; sometimes flowering in the leafless condition, according to collectors.

TYPE: Linnaean Herbarium, sheet 592–3 (LINN). This specimen is here designated as the holotype, although ordinarily species first described by Linnaeus in the "Flora Zeylanica" would be based on specimens in the Hermann Herbarium (BM). As pointed out, however, by Trimen (Handb. Fl. Ceylon **4**: 26. 1898), there is no specimen of the plant in Hermann's herbarium, and the drawing cannot be identified with certainty. Rheede's figures are good (except that the leaves are shown as opposite!), and following the strictest priority one could make one of his two plates the type; but in view of the doubt connected with Linnaeus's original treatment, it seems preferable to typify the basionym *Averrhoa acida* by a particular specimen.

DISTRIBUTION: native probably to South America (MAP III); cultivated on all of the larger islands of the West Indies. Only representative specimens are cited.

BAHAMAS: Andros, Fresh Creek, *J. I. & A. R. Northrop 653* (F). CUBA: Las Villas, La Sierra, *Jack 7851* (A, S, US). JAMAICA: *R. C. Alexander* (GOET). PUERTO RICO: Isabon, *Sintenis 6487* (F, G). ST. CROIX: Bassin, *A. E. Ricksecker 268* (F, US). ST. THOMAS: Canaan, *Eggers 372* (G, M). ANTIGUA: *Wullschlaegel 496* (GOET). GUADELOUPE: Basse-Terre, *Duss 2929* (US). MARTINIQUE: *Duss 955* (US). ST. VINCENT: *Caley* (G, W). ISLA DE PROVIDENCIA: *Proctor 3462* (US).

Carl Linné the younger was the first to observe that *Averrhoa acida* and *Cicca disticha* were synonymous (Suppl. Pl. 416. 1781); and he also questioned the distinctiveness of *Cicca* as a genus distinct from *Phyllanthus*. The rather variable inflorescence in this species, together with the confusion introduced by Linnaeus when he redescribed it (twenty years after the "Flora Zeylanica") as *Cicca disticha*, has resulted in a rather complicated synonymy for the plant. Lamarck's *Cicca nodiflora* was based on a specimen in which the flowers were borne on leafy branchlets rather than on naked axes on older wood; but since both conditions may normally occur on the same plant, his name does not merit retention for a taxon of any rank. Jacquin's magnificent folded colored plate in the "Hortus Schoenbrunnensis" is the best illustration yet published of this species, and clearly shows both the hermaphrodite and unisexual flower forms.

The female flowers of *P. acidus* are unique in the presence of staminodes which at times apparently act as functional stamens. The number of staminodes per flower, however, is variable even in the same inflorescence and fluctuates on the same plant from 0 to 4. No flowering herbarium specimens were seen in which there was not at least one staminode in some of the flowers. Consequently, this feature could be used in support of the claim of *Cicca* to generic status; but the evidently close relationship of the present species to the two following more than outweighs the staminodial character, which after all appears to be a sort of "teratological" reversion and not a primitive character.

The number of fertile sporophylls is variable in both the male and female flowers of *P. acidus*. However, whereas there are regularly 4-carpelled flowers mixed among the predominantly 3-carpelled ones, fluctuations in the number of stamens are less common. Some trees appear to produce regularly male flowers with four stamens, while in others (represented by the herbarium specimens *Karsten s.n.* from Merida, Venezuela (W), and *Schwanecke 12* from Puerto Rico (W)), all flowers have only two or three stamens. In the *Schwanecke* collection, there are furthermore many flowers in which a pistillode-like structure occurs. However, it appears that this "pistillode" is actually a modified stamen, for in *P. acidus* it has not been observed in normal flowers with four stamens. It might be thought that these floral irregularities in *P. acidus* are related to its cultivated state; but if one may judge from the numerical fluctuations of the floral parts of *P. elsiae*, it seems more likely that there is simply an inherent tendency toward meristic variation in the flowers of *P. acidus*.

Phylogenetically, *P. acidus* is of great interest in that it forms a connecting link between sect. *Ciccopsis* and sect. *Aporosella*. Its androecium of stamens with elongated filaments and reflexed anthers, and its well-developed floral disk, agree with sect. *Ciccopsis;* but its massive ovary developing into an indehiscent fruit, its cauliflorous inflorescence, and its leaf form are more like sect. *Aporosella*. Sect. *Cicca* further agrees with sect. *Aporosella* in its tendency toward dioeciousness; although all West Indian specimens examined are monoecious, those from the Philippines are dioecious, as pointed out by Robinson (Phil. Jour. Sci. Bot. **4**: 87. 1909). On the other hand, its pollen grains appear to be somewhat less specialized than those of either *Ciccopsis* or *Aporosella*. If we conceive of the four American species of subg. *Cicca* as relict populations surviving from an anciently widespread ancestor, these cross-relationships and differential evolutions of organs can be mostly clearly and easily explained.

Heretofore, the relationships between *P. acidus* and the other American representatives of subg. *Cicca* have not been recognized, partly because of taxonomic confusion but perhaps mostly because of the prevalent misconception of the indigenous range of *P. acidus*. In common with many widely cultivated tropical plants, *P. acidus* has been regarded as of rather uncertain nativity. Nevertheless, all authors have credited the species to the Old World, and indeed most commonly to Madagascar and the Malay Islands. Trimen (Handb. Fl. Ceylon **4**: 26. 1898), for instance, observes that it is "much grown in native gardens for its acid fruit . . . and no doubt an ancient cultivation." It is recorded by Merrill (Enum. Phil. Fl. Pl. **2**: 397. 1923) as "of prehistoric introduction from Malaya." Numerous other authors could be cited in support of the "Malayan" origin of the plant, but on the other hand, there are some significant disclaimers. Thus Ridley (Fl. Malay Pen. **3**: 216. 1924) cites it only from gardens, and Burkill (Dict. Econ. Prod. Malay Pen. **1**: 537. 1935) classifies it as of "uncertain origin." J. J. Smith (Add. Fl. Arb. Jav. **12**: 82–83. 1910), a usually careful observer, notes that the species, to the best of his knowledge, has never been encountered wild in Java, although it is much cultivated there. Leandri (Not. Syst. **7**: 186. 1939) found no specimens of the species (even of cultivated trees) from Madagascar. The final impression given by a perusal of the literature is thus that of a "probably Malayan" plant which has never been discovered wild there!

In view of this nearly universal ascription of the homeland of *P. acidus* to the Indonesian region, it was a distinct surprise to find in the course of the present study that the closest congeners of the species are the two representatives of the New World sect. *Aporosella*, while on the other hand it has no close relatives in the Old World. In fact, specimens of *P. elsiae* have so often been misidentified as *P. acidus* that it is quite impossible to determine from published reports whether or not *P. acidus* is growing wild at a specific locality. Thus far attempts to discover the native habitat of *P. acidus* have been largely unsuccessful. The collections of Martius from Minas Geraes, cited by Mueller (Fl. Brasil. **11**[2]: 68. 1873), have unfortunately not been examined; but another collection from the same state (*Wawra & Maly* [W]) appears definitely to represent a cultivated plant, as do two collections made by Karsten at Merida, Venezuela, and Bucaramanga, Colombia (both at W). Only one herbarium specimen has been examined which would appear to represent *P. acidus* in its native habitat; it was collected by Poeppig in 1832 on the island of Colares in the Pará River delta, northeastern Brazil (W). Poeppig's notation that the habitat of the plant was in littoral woods ("sylvis littoreis") suggests very strongly that he was dealing with the native plant; for one would expect that *P. acidus* might have ecological requirements similar to those of *P. elsiae*.

A search through the floristic publications of Huber and Ducke on the Amazon delta region has failed to turn up any record of *P. acidus*, under its accepted or any synonymous name. This, however, would not appear to cast any doubt on the authenticity of the Poeppig collection. The coastal Amazonian region contains so many large stretches which because of the uninviting and inaccessible nature of the terrain are little-known botanically, that the existence of *P. acidus* in considerable abundance there is by no means excluded. If it inhabits the infra-mangrove forest zone, which is relatively narrow, it may have gone undetected, just as *P. elsiae* was until the studies of Lindeman in Surinam.

It is at the very least a remarkable and interesting coincidence that there is a similar uncertainty as to the origin of the oxalidaceous mimic of *P. acidus*, *Averrhoa bilimbi* L. The superficial resemblance of the two species is so arresting that it is not surprising that Linnaeus was misled into classifying both of them as species of *Averrhoa*. The geographical problem with regard to *Averrhoa bilimbi* is made even more puzzling by the fact that there is an equal uncertainty regarding the origin of the only other species in the genus, *A. carambola*. All three of these similar plants, which Burman grouped together as species of "Malus indica" are cultivated at present in tropical gardens throughout much of America and Asia; but the two species of *Averrhoa* show a much greater tendency to become naturalized. Knuth (Pflanzenf. ed. 2, **19a**: 39. 1931) has in fact ascribed the origin of the genus to *Averrhoa* to Malaysia on the basis of the report by Koorders (Exkursionsfl. Java 2: 413. 1912) that both species are found wild in Java.

Many authors have remarked that the species of *Averrhoa* are "obviously of ancient cultivation" in the Indian and Malaysian regions. However, in view of our sure knowledge of the rapid diffusion of corn throughout the Old World (cf. Mangelsdorf & Oliver, Bot. Mus. Leafl. Harvard Univ. **14**: 263–291. 1951), the possibility of a post-Columbian introduction from the New World must be admitted for *Averrhoa* as well as for *P. acidus*. Trimen (Handb. Fl. Ceyl. 1: 200. 1893) has already suggested that the two averrhoas were originally introduced into Ceylon from the New World by the Portuguese, and Merrill (Chron. Bot. **14**: 301. 1954) states positively that this was the case, though without adducing any specific evidence. The investigation of *Averrhoa* from the phytogeographic point of view is of especial interest since it appears to be the only genus of more than one species which is unknown in the indigenous state.

When all the evidence is considered, it appears that *P. acidus* certainly, and both species of *Averrhoa* probably, are indigenous to the New World and have been introduced into the Old World in post-Columbian times. Although the exact natural range of *P. acidus* is still unknown, it definitely is native to the Pará River delta, and will probably be discovered in a number of localities in the Amazon delta region. By analogy with the documented evidence for *P. acidus*, it appears most likely that both species of *Averrhoa* are also originally American plants which have had a similar history. The great superficial resemblance between these three species may not be entirely coincidence, for it is possible that all three are members of the sub-littoral forests of the South American coastline; and their similarity in life form may have a selective basis. Probably, as suggested by Merrill and Trimen, these plants were first encountered by the Portuguese on the Brazilian coast and from there carried to India and other parts of the Old World. The fascinating problems in ethnobotany posed by such species as *P. acidus* cannot be resolved with certainty until a more thorough knowledge of the coastal flora of northeastern Brazil can be correlated with an analysis of the earliest Portuguese explorations there. When this is accomplished, a definitive evaluation can be made of the hypotheses presented here.

Sect. 6. **Aporosella** (Chodat) stat. nov.

Aporosella Chodat, Bull. Herb. Boiss. 2 ser. **5**: 488–489. 1905.

Trees with completely cauliflorous inflorescences, flowering with the appearance of the leaves. Dioecious; flowers in aphyllous thyrsi (the leaves reduced to bracts). Male flower: calyx-lobes usually 4; disk absent; stamens usually 4, filaments free, anthers dehiscing vertically; pollen grains globose, tricolporate. Female flower: calyx-lobes 4; disk absent; staminodes absent; carpels 2 or 3; styles connate at the base, bifid or lacerate. Fruit indehiscent and woody, the endocarp bony, with 2 or 3 cells; fertile locules 1 or 2 per fruit, seeds solitary.

TYPE SPECIES: *Phyllanthus chacoensis* Morong [*Aporosella hassleriana* Chodat].

This small section of two American species is so divergent from the great majority of the species of *Phyllanthus* that on the basis of morphological characters alone it could be maintained as a distinct genus. The combination of arboreal habit, dioecious completely cauliflorous inflorescence, woody indehiscent fruit, and absence of a floral disk is unique, and indeed defines the group much more sharply from the typical species of *Phyllanthus* than do the characters which distinguish such genera as *Glochidion*, *Sauropus*, and *Breynia*. However, there can be no doubt that the two species of *Aporosella* are closely related to *P. acidus*, and through that species, perhaps via *P. pseudocicca*, to more "typical" species of *Phyllanthus* in subgenus *Kirganelia*. It would thus be manifestly contrary to natural relationship to recognize *Aporosella* as a distinct genus and at the same time leave sects. *Cicca* and *Ciccopsis* within *Phyllanthus*. A segregate genus comprising sects. *Ciccopsis*, *Cicca*, and *Aporosella* would be more satisfactory except that it would be nearly impossible to distinguish it from *Phyllanthus*. Consequently, it does not appear practicable at the present time to recognize any part or all of subg. *Cicca* as an independent genus.

Pax and Hoffmann (Pflanzenr. IV. 147. XV: 105–107. 1922) seriously erred in placing *Aporosella* in the subtribe Antidesminae between *Aporosa* and *Antidesma*. The resemblance between these three genera is confined to a superficial similarity in inflorescence and fruit; but the phyllanthoid branching of *Aporosella* clearly precludes its belonging to the Antidesminae. The original ascription of the type species to *Phyllanthus* by Morong (Ann. N. Y. Acad. Sci. 7: 218. 1892) after all comes closest to the mark.

8. **Phyllanthus elsiae** Urb. Repert. Sp. Nov. 15: 405–406. 1919. (PLATE XV, *figs. G–I*).

Glabrous small or medium-sized tree c. 7 — 15 m. high with a dense crown, the habit similar to that of *P. acidus;* older branches terete, c. 0.5 — 1.5 cm. broad, sometimes with conspicuous lenticels; branches of current year with up to 10 leafy branchlets. Cataphylls blackish brown, indurate, more or less deciduous; stipules triangular-ovate, c. 1.5 mm. long, with fimbriate margins; blade similar but narrower. Deciduous branchlets ascending, (10–) 15 — 30 cm. long, c. 1.3 — 1.8 mm. thick, pale to dark brown, obscurely angled or terete, smooth, with c. 10 — 20 leaves; first internode (0.3–) 1 — 2.5 (–4) cm. long, median internodes c. 1 — 1.5 cm. long. Leaves: stipules appressed, triangular-lanceolate, c. 0.8 — 1.2 mm. long, 0.5 — 0.7 mm. broad, acute, blackish-brown, scarious, subentire, not auriculate at the base. Petiole 2.5 — 3.5 mm. long, subterete, often corrugated, the edges of the blade decurrent on the adaxial face as two straight rather inconspicuous flanges. Leaf-blade chartaceous (sometimes stiffly so) mostly broadly elliptic to suborbicular and rather abruptly contracted to a short acumen, mostly 3 — 5 (–7) cm. long, 2 — 4 (–5) cm. broad, obtuse or rounded at the base; above olivaceous to plumbeous, the proximally impressed midrib running to the tip, laterals ascending, reticulum of tertiary veinlets obscure to subprominent; beneath greenish or greyish to reddish brown, the midrib prominently raised, the laterals (usually 4 or 5 on a side) ascending, raised, anastomosing within the margins, forming with the tertiaries a fine subprominent slightly raised reticulum; margins plane or often more or less undulate or crisp.

Dioecious; flowers borne only on naked branchlets (thyrsi) on older wood of the stem (these clustered on spur-shoots in the axils of old leaf-scars), never on leafy branchlets of the current year's growth. Bracts indurate, blackish brown; stipules broadly triangular, umbonate, margins lacerate-fimbriate, c. 1 — 1.5 mm. long and 1.2 — 1.4 mm. broad, the blade c. 0.7 — 1.5 mm. long. Male inflorescence axes (1–) 1.5 — 7 cm. long, with 5 — 13 (–19) nodes; cymules with c. 10 — 20 flowers. Female inflorescence axes (2–) 3 — 6 (–9) cm. long, with 7 — 13 (–19) nodes; cymules with 1 — 3 (rarely 4) flowers.

Male flower: pedicel (1.2–) 1.5 — 3 (–5) mm. long. Calyx-lobes 4, subequal, obovate, 1 — 1.7 mm. long, 0.7 — 1 mm. broad, obtuse or rounded at the tip, entire to minutely fimbriate, the hyaline margins narrow to rather broad, midrib unbranched. Disk absent. Stamens 4 (rarely 3 or 5); filaments free, slender, erect, only 0.1 — 0.25 mm. long; anther-sacs parallel, dehiscing vertically, the slits not confluent; pollen grains 17–21 μ in diameter, slightly angular-aperturate, colpi very narrow and not meeting at the poles.

Female flower: pedicel terete or subangular, straight or curved, smooth, (1–) 1.5 — 2 (–3) mm. long. Calyx-lobes 4, subequal (the outer somewhat smaller), obovate or oblong, 0.8 — 1.3 mm. long, (0.4–) 0.6 — 0.8 mm. broad, rounded at the tip, subentire to minutely fimbriate, the midrib unbranched. Disk absent. Ovary ovoid, c. 0.8 — 1.2 mm. in diameter at anthesis, rugulose, not stipitate, of 3 or rarely 2 carpels; styles connate at the base into a column c. 0.3 — 0.5 mm. high, bifid to the column, the flattened acute tapering tips spreading or ascending, 1.8 — 2.3 mm. long. Staminodia absent.

Fruit mostly oblate spheroidal, 3-celled (rarely 2-celled), (5–) 6 — 8.5 mm. high, (5.5–) 6 — 8.5 (–10.5) mm. broad, obtusely lobed, indehiscent, dry and woody, the outer layer soft and pithy, the inner hard and bony. Fertile carpels usually 1 or 2 per fruit, each with a single seed. Seeds flattened, smooth, the brittle testa pale brown or stramineous, c. 3 — 3.5 (–4) mm. long, (2–) 2.2 — 2.4 (–2.7) mm. broad; hilum conspicuous, c. 0.7 — 1 mm. across, dark reddish-brown, triangular or roundish.

Collected in flower January through March; in fruit April through December.

Type: Tobago, Auchenskeoch Beach, March 25, 1914, *W. E. Broadway 4789* (US 759650; lectotype). The specimen in the U. S. National Herbarium is here designated as the lectotype, as it is the only sheet seen of the type collection; the original specimen in Urban's herbarium at Berlin-Dahlem presumably was destroyed during World War II.

Distribution: low forests along lagoons and rivers, usually near sea-level, northern South America to southern Mexico (Map III).

TOBAGO: Auchenskeoch Beach, *Broadway 4789* (US, lectotype), *5910* (MO); Studley Park, near the sea, *Broadway 4557* (F, GH, MO, US). TRINIDAD: Erin, sea shore, *Broadway 7845* (MO, S), *9112* (A, MO); Rousillac Swamp, *Swabey* (TRIN 12558).

Because of the variability and interesting distribution of this species, the following representative specimens are cited from throughout its range.

MEXICO: Nayarit: Mexcatitlan, nearly at sea level, shallow lagoons, growing in water, *Mexia 1005* (A, US); same locality, *Ortega 5545* (US). Guerrero: near sea beach, Acapulco, *Palmer 595* (A, US). Chiapas: Paredon, Tonala, *Matuda 16274* (US).

BRITISH HONDURAS: Belize River, *Record B.H.52* (US).

EL SALVADOR: Santa Ana: El Desagüe, Laguna de Quija, alt. 440 m., *Pittier 1902* (US). San Miguel: Laguna de Olomega, alt. c. 75 m., *Standley 20983* (GH). Sonsonate: Izalco, in park, *Standley 22234* (GH).

PANAMA: Canal Zone: banks of Chagres River, below Gatun, near sea-level, *Maxon 4797* (US); forest along the Rio Indio de Gatun, near sea-level, *Pittier 2776* (US).

COLOMBIA: Bolivar: San Martin de Loba, *Curran 409* (GH); river-marsh, Magangue, *Pennell 3954* (US). Santander: Puerto Wilches, *Daniel 1178* (US).

VENEZUELA: Delta: Rio Manimo, Buelta Triste, *Bond, Gillin, & Brown 158* (GH, US), *163* (GH).

BRITISH GUIANA: Botanic Gardens, Georgetown, *Archer 2576* (US).

SURINAM: swamp, Nickerie, Nanni-creek, near Kaaimancreek, common, *Geyskes 154* (A).

The broad distribution of *P. elsiae*, which is probably locally common in numbers of mainland littoral areas along the Caribbean, has not been recognized heretofore because of the confusion between it and *P. acidus*. Since the original publication of the species by Urban, all of the collections cited above with the exception of that of Swabey have either been mistaken for *P. acidus* or left unnamed. Lanjouw and Lindeman, however, have independently come to the conclusion that the tree of the Surinam swamps discussed by Lindeman (Veg. Coastal Reg. Suriname, Table II. 1953) under the name *P. acidus* actually represents a different species (personal communication).

The habitat of *P. elsiae*, as reported by Lindeman, is the swamp woods or moist forest which often occurs near the coastline directly behind the mangrove belt, and only a few feet above sea-level. Only the collection made in El Salvador by Pittier records the species at an elevation of greater than 100 meters. It is probable that further collecting will show the range of *P. elsiae* to be almost continuous along the coast from Surinam to British Honduras and, on the Pacific side, from Panama to Mexico. As far as can be determined, however, the species does not occur along the Pacific Coast of South America.

The resemblance between *P. acidus* and *P. elsiae* is so close that the past confusion is quite understandable. Both plants are cauliflorous trees with tetramerous flowers and similar indehiscent fruits. However, the differences between the two species are so important that they seem best assigned to separate sections. In contrast to the West Indian representatives of *P. acidus*, which are monoecious, with a well-developed floral disk and drupaceous fruit, *P. elsiae* is dioecious, with no floral disk and with a woody rather than fleshy fruit. Even sterile specimens of the two species are readily separable, *P. acidus* having branchlets with 25—40 leaves and ovate leaves gradually narrowed to the tip, while *P. elsiae* has branchlets with 10—20 leaves and more rotund leaves which are usually abruptly narrowed at the tip. Furthermore, *P. elsiae* is always perfectly cauliflorous (the leafy branchlets invariably being sterile), while *P. acidus* usually has flowers produced on the leafy branchlets as well as the aphyllous thyrses.

Much more closely related than *P. acidus* is the type species of *Aporosella*, *P. chacoensis*. This plant, native to the Chaco region of Argentina and Paraguay, resembles *P. elsiae* so closely that one might almost consider the two taxa as subspecies of a single species. However, the fruits of *P. chacoensis* are always 2-celled, and although this character is not invariable in distinguishing it from *P. elsiae* (which rarely has a few 2-celled fruits in addition to the usual 3-celled ones), the styles furnish an adequate diagnostic feature. They are much broader and shorter (less than 1 mm. long) in *P. chacoensis* than in *P. elsiae*. It appears best, therefore, to consider the plants in question as two closely related but distinct species.

Sect. 7. **Emblica** (Gaertn.) Baill. Etud. Gen. Euphorb. 626. 1858.

Emblica Gaertn. Fruct. **2**: 122–123, *pl. 108, fig. 2.* 1790.
Dichelactina Hance in Walp. Ann. **3**: 375. 1852–53.

Trees with phyllanthoid branching; branchlets often fascicled at the nodes; leaves oblong to linear, closely distichous. Monoecious; flowers in axillary cymules at the proximal nodes of branchlets. Male flower: calyx-lobes usually 6; disk of 6 small segments, or absent; stamens normally 3, filaments united into a column; anthers sessile atop the column, dehiscing vertically; pollen grains subglobose to subprolate, 4- or 5-colporate. Female flower: pedicel very short; calyx-lobes 6; disk a lacerate cup enveloping the ovary; ovary smooth, of 3 carpels; styles shortly connate, twice bifid, distally dilated. Capsule with a fleshy exocarp, the cocci rather thick and massive, eventually separating from a well-developed columella. Seeds 2 in each locule, trigonous, somewhat unequal.

TYPE SPECIES: *Emblica officinalis* Gaertn. loc. cit. (= *Phyllanthus emblica* L.).

This section of a few Old World species is here given the same circumscription as that of Hooker (Fl. Br. Ind. **5**: 286, 289–290. 1887), who excluded from the section all the species listed by Mueller (DC. Prodr. **15**(2): 352–355. 1866) except those with fleshy fruits. Pax and Hoffmann (Naturl. Pflanzenf. **19c**: 64. 1931) have also accepted the section in this sense. Beille, on the other hand (Fl. Gen. L'Indo-Chine **5**: 572. 1927), has continued the usage of Mueller, without however showing any convincing distinction between sect. *Emblica* sensu Mueller and sect. *Paraphyllanthus.*

It appears to me that only by adopting the narrow circumscription can sect. *Emblica* be maintained. Hooker described three new species, and two others have more recently been proposed; but all of these appear quite similar to one another and to *P. emblica.* Possibly the populations belonging to this section should be interpreted as a single widespread, variable species native from India to Malaya and China.

The present classification of sect. *Emblica* is provisional, for it does not approach very near to any of the three other sections included in subg. *Cicca.* The arboreal habit and fleshy fruit are only superficial resemblances and do not indicate any close affinity, particularly since the fruit of *Emblica* is still fundamentally capsular, in contrast to the truly drupaceous fruits of sects. *Cicca* and *Aporosella.* Furthermore, the pollen grains of sect. *Emblica* appear to differ considerably from those of the other three sections.

In the present treatment sect. *Emblica* is retained within subg. *Cicca* primarily on grounds of convenience, for it does appear to fit here better than in any other West Indian subgenus. The natural relationships of sect. *Emblica* are doubtless with Indian species of the sect. *Paraphyllanthus* sensu Mueller, such as *P. polyphyllus, P. lawii,* and *P. columnaris.*

9. **Phyllanthus emblica** L. Sp. Pl. 982. 1753; Muell. Arg. in DC. Prodr. **15**(2): 352. 1866; Hook. f. Fl. Br. Ind. **5**: 289. 1887. (PLATE XV, *figs. J–L*).

Myrobalanus emblica Bauh. Pinax 445. 1623.
Nili-camarum Rheed. Hort. Malabar. 1: 69, *pl. 38.* 1672.
Phyllanthus foliis pinnatis floriferis, caule arboreo, fructu baccato L. Fl. Zeyl. 158. 1747.
Emblica officinalis Gaertn. Fruct. 122–123, *pl. 108, fig. 2.* 1790.
Emblica grandis Gaertn. op. cit. 123.
Emblica arborea Raf. Sylva Tellur. 91. 1838.
Diasperus emblica (L.) O. Ktze. Rev. Gen. 2: 599. 1891.

A deciduous tree up to c. 15 m. high, with flaking bark; annotinous branches smooth or hirsutulous, terete or somewhat angled, greyish or brownish, 2 — 5 mm. thick, with internodes mostly 1 — 3 cm. long. Cataphylls inconspicuous, subpersistent, dark reddish brown, scarious and brittle; stipules triangular-ovate, c. 1.3 — 2 mm. long, 0.8 — 1.3 mm. broad, acuminate, margins entire or denticulate, ciliolate when young, subauriculate at the thickened base; blades basally convex and much thickened, attenuate-acuminate, c. 1.5 — 1.9 mm. long. Deciduous branchlets (5–) 10 — 25 (–30) cm. long, pale brown, furrowed, copiously hirsutulous, terete, sterile or floriferous (and then shorter), with (15–) 30 — 100 (–150) leaves, the internodes very much shorter than the imbricate leaves (i.e., mostly 1 — 3 mm. long); fertile branchlets with leaves greatly reduced in proximal floriferous portion. Leaves: stipules triangular, 0.8 — 1.5 mm. long, 0.3 — 0.5 mm. broad, apex attenuate, ciliolate, minutely denticulate, becoming dark reddish-brown and scarious. Petioles stout, 0.3 — 0.7 mm. long. Leaf blades smooth, chartaceous, linear-oblong, obtuse, slightly oblique and subcordate at the base, mostly 12 — 20 mm. long and 2 — 5 mm. broad (reduced leaves associated with flowers considerably smaller); above olivaceous, the midrib and laterals often raised and conspicuous, beneath greyish or brownish, the midrib raised, the laterals (4 — 7 on a side) straight, steeply ascending; margin firmly thickened and sometimes scarious, more or less inflexed or involute, the scarious tip of the blade more or less inflexed.

Monoecious; first few proximal nodes of floriferous branchlets barren, with leaves reduced to dark brown scarious cataphylls; succeeding nodes with green but reduced leaves subtending cymules of male flowers, followed by nodes each with a cymule of one central female flower and several lateral males, the reduced leaves of this vicinity grading into normal leaves; distal half of floriferous branchlets normally sterile, with typical leaves, less commonly the distal portion not developed.

Male flower: Pedicel glabrous, slightly thickened above, c. 1 — 2.5 mm. long (up to 4 mm. long ex Mueller). Calyx-lobes 6, oblong-obovate or spathulate, 1.2 — 2.3 mm. long, 0.5 — 1 mm. long, obtuse or rounded, convex above, entire or obscurely denticulate, membranous, yellowish white, the midrib unbranched or with a few inconspicuous branches. Disk-segments 6, clavate, crenulate, foveolate, c. 0.2 — 0.3 mm. across; or disk sometimes obsolete. Stamens 3; filaments completely united into a terete column (0.2–) 0.3 — 0.7 mm. high; anthers sessile atop the column but discrete, erect, oblong, minutely apiculate, 0.5 — 0.9 mm. long, 0.5 — 0.6

mm. broad; anther-sacs parallel, dehiscing vertically, discrete, the slits not confluent; pollen grains (ex *Broadway 5258*) subglobose, 17.5 — 19 μ in diameter, 4- or 5-colporate, the colpi short, not bordered.

Female flower subsessile, the ill-defined pedicel 0.5 mm. long or less. Calyx-lobes 6, oblong or spathulate, 1.6 — 2.5 mm. long, 0.7 — 1.3 mm. broad, obtuse or rounded at the tip, more or less obscurely denticulate, thicker than the male, the scarious margin ill-defined or obsolete. Disk urceolate, investing the ovary, up to c. 1 mm. high, 6-ribbed, the ribs alternate with the calyx-lobes and projecting as marginal fimbrillae, the rim often with smaller teeth between the projecting ribs. Ovary smooth, ovoid; styles rather fleshy, shortly connate at the base, c. 2.5 — 4 mm. long, ⅓-parted to bifid, the branches bifid, remaining terete or flattened and conspicuously dilated and petaloid, usually spreading and distally reflexed.

Capsule with a firm fleshy greenish white or yellowish white epicarp, c. 2.5 — 3 cm. in diameter when fresh, the endocarp (cocci proper) rather massive and thick-walled, c. 1 cm. in diameter, the cocci at length separating from the columella; columella trigonous, slender below the dilated apex, c. 7 — 8 mm. high. Seeds of the pair in each coccus more or less unequal; the smaller plano-convex, 3.9 — 4.3 mm. long, c. 2.5 mm. radially, c. 2 mm. tangentially; the larger asymmetrically trigonous (carinate on one side), c. 4.5 mm. long, 3.1 — 3.2 mm. radially, c. 3 mm. tangentially; seed-coat dark chestnut brown, smooth, at high magnification with close-set rounded slightly convex flecks.

TYPE: left undesignated. There appears to be no specimen of *P. emblica* in the Hermann Herbarium (BM), and indeed Linnaeus cited none in the "Flora Zeylanica." There is a sterile specimen, number 1105–11, in the Linnaean Herbarium (LINN), which is probably this species; it is marked "H U," presumably indicating that it was grown in the botanic garden at Upsala. However, in view of the taxonomic uncertainty with regards to the limits and subspecific variation of *P. emblica,* it seems unwarranted to designate either this specimen or such illustrations as those of Rheede as representing the holotype. Typification of this Linnaean species must await a thorough study of the entire sect. *Emblica.*

DISTRIBUTION: *P. emblica,* in the present inclusive (though not necessarily correct) sense ranges from India and Ceylon to Hainan, Borneo, and Java. Mueller's reports of the species from Japan and the Mascarene Islands appear to be based on cultivated specimens. In the West Indies *P. emblica* is found only in cultivation and shows no signs of becoming part of the spontaneous flora.

BERMUDA: Public Garden, St. George's, *Brown, Britton, & Wortley 1732* (GH, NY).

CUBA: PINAR DEL RIO: Pinar del Rio City, Finca del Obispo, *Ekman 18643* (S). HABANA: Habana, *Marie-Victorin 45025* (MT). LAS VILLAS: Soledad, *Jack 4246* (NY, S).

PUERTO RICO: MAYAGUEZ: Agricultural experiment station, Mayaguez, *N. L. & E. G. Britton 7441* (NY).

LESSER ANTILLES: GRENADA: Botanic station, *Broadway* (NY).
TRINIDAD: Botanic gardens, St. Ann's, *Broadway 5238* (MO, S).

This species, widely cultivated in tropical regions, is perhaps the most economically important in the genus. Because of the use of the fruits as a purgative, it was the first species of ***Phyllanthus*** to become familiar to Europeans; pharmacists knew it as "emblic myrobalan" in Medieval times. However, it is also of some value as a timber tree (Pearson & Brown, For. Ind. **2**: 878–881. 1932), and as a source of tannin (Burkill, Dict. Econ. Prod. Mal. **1**: 920. 1935).

The great variability of the species is apparent even from the small sample of West Indian specimens, on which the description is mainly based. Both Mueller and Hooker reported the disk as absent in the male flowers, but in two of the flowering collections from the West Indies it is well developed as in the floral illustration of Wight (Icon. Pl. Ind. Or. **5**: *pl. 1896.* 1852). The fruit of the tree in the garden at Soledad, as observed from both herbarium (*Jack 4246*) and fresh material, is at least 2.5 cm. in diameter, which is much larger than that allowed by Hooker and better matches his *Phyllanthus pomiferus* [*Cicca macrocarpa* of Kurz]. The pollen grains of *Jack 4246*, not included in the description because they seem abnormally wrinkled, are subprolate, measuring c. 21 — 23 by 19 — 21 μ, and appear all to be 5-colporate.

The West Indian specimens appear to deviate from the norm of *P. emblica* somewhat in the longer branchlets with often an unusually large number of leaves. In *Broadway 5238* many of these long sterile branchlets are associated at a node with an abbreviated floriferous branchlet in which the distal leafy portion has been suppressed; such a marked dimorphism between fertile and sterile branchlets appears, however, to be rare. The fascicled branchlets which account for part of the characteristic appearance of the branches of *P. emblica* are, on close inspection, invariably found to be grown out from several collateral buds at a node from which the branchlet of the previous year has fallen.

Despite all these deviations, however, the West Indian collections show a close agreement in the apiculate anthers, unusual hypogynous disk, branchlet structure, and leaves; it therefore appears likely that they represent only variations of a single species.

(*To be continued*)

PLATE XV

LEAVES, MALE FLOWERS, AND FEMALE FLOWERS IN SUBG. *Cicca.*[13]

FIGS. A–C. *Phyllanthus pseudocicca* Griseb. (*Clemente & Alain 4079* [MICH]). FIGS. D–F. *Phyllanthus acidus* (L.) Skeels (cult., Kingston, Jam.). FIGS. G–I. *Phyllanthus elsiae* Urb. (G, H, *Matuda 16274* [US]; I, *Palmer 595* [GH]). FIGS. J–L. *Phyllanthus emblica* L. (J, K, *Broadway 5238* [S]; L, *Tsui 118* [A]).

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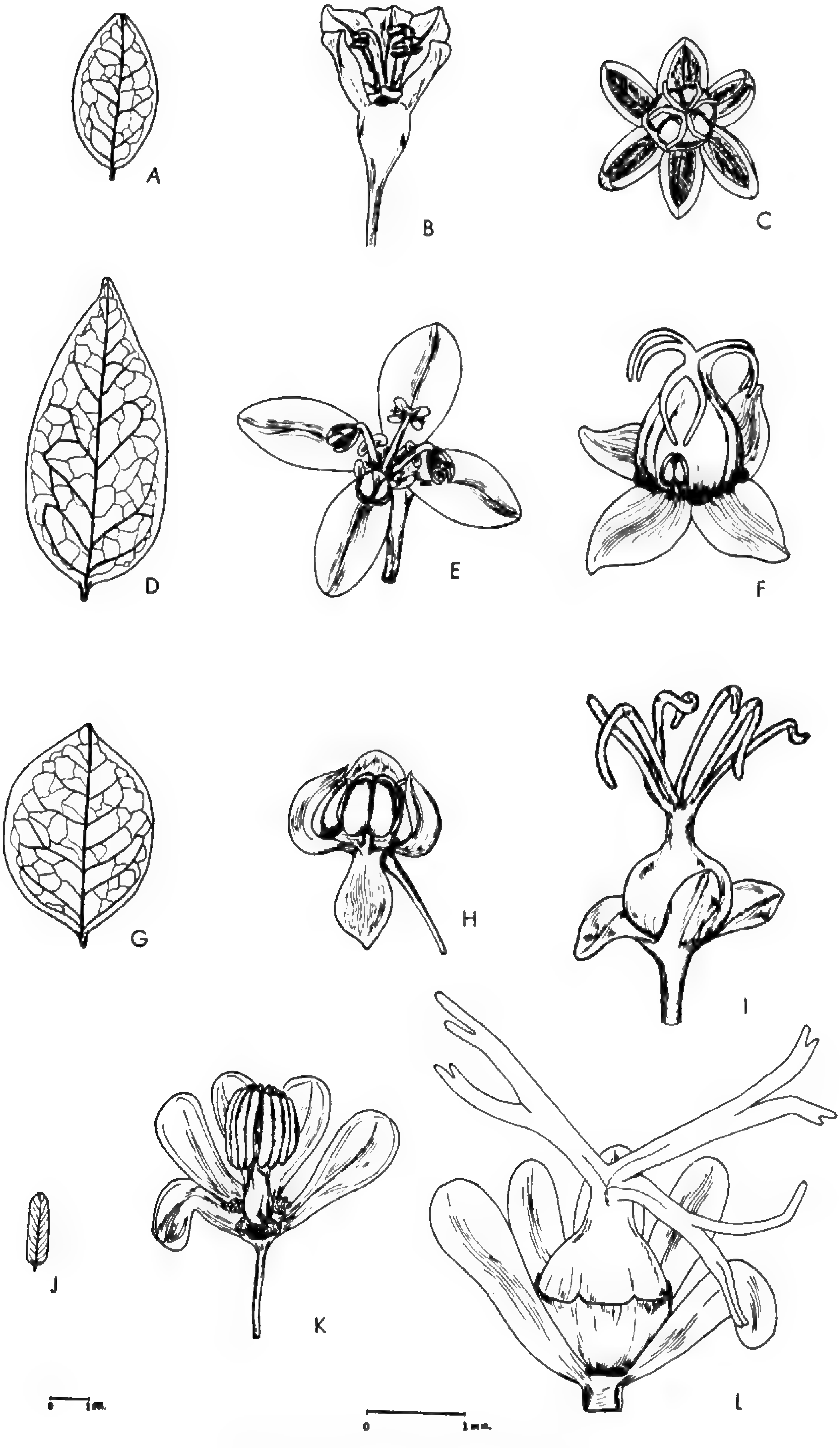
[13] Male and female flowers are drawn to the same scale.



WEBSTER, WEST INDIAN PHYLLANTHUS

STUDIES IN THE GENUS COCCOLOBA, III. THE JAMAICAN SPECIES

Richard A. Howard

In a revision of any West Indian genus of plants having wide-ranging species, the taxonomist invariably must center part of his study on the vegetation of the island of Jamaica. The specimens and the writings of the early botanists and naturalists in Jamaica, men like Hans Sloane and Patrick Browne and Olaf Swartz were accepted by Linnaeus and became the types and starting points for study of important taxa in the Caribbean vegetation. In the difficult genus *Coccoloba*, it has been necessary to spend a disproportionate amount of time on the few wide-ranging species and the great variety of names and applications given them. The lack of consistency in the successive publications of Lindau as the most recent monographer of the genus, Grisebach, Eggers, Britton and others has increased the task of assigning the proper name to each taxon. The failure of these writers to understand the normal and abnormal variations of these plants as seen in herbarium sheets has added to the difficulties of modern identification and definition.

Fawcett & Rendle, in preparing a treatment of the genus for the Flora of Jamaica, examined the Linnaean species of *Coccoloba* and published a note on these in the Journal of Botany in 1913. This was followed in 1914 with a treatment of the genus as it occurs in Jamaica and in this work eighteen species were recognized and defined in addition to one species which was recorded as "insufficiently known." Since that time only one species has been described as new to the flora of Jamaica and no species have been added to the flora by published extensions of ranges, although many erroneous herbarium identifications might have been so considered.

Fawcett & Rendle's treatment of the genus in the Flora of Jamaica is unfortunately based on an inadequate knowledge of the genus as indicated at the beginning in the generic description. The functionally unisexual flowers; the occurrence of pistillate flowers singly and the staminate flowers in multiples at the nodes of the inflorescence; the variation between adventitious and normal growth in pubescence, leaf size and leaf shape; the ability of the plants to flower in juvenile or adventitious leaf condition; the phenomenal morphological variation following injury and the frequent occurrence of hybrids, particularly those involving *Coccoloba uvifera*, are characteristics which only careful field experience could evaluate and which have not been taken into account in the generic treatment in the Flora of Jamaica.

In preparation for this paper, I have had the unusual opportunity of field work expressly for the study of *Coccoloba* populations, as well as trips which permitted attention to species of this genus. I am indebted to the American Philosophical Society for a grant from the Penrose Fund which made possible an extended field trip in 1950 and a study of this genus from Trinidad to Cuba in the West Indies. More recently, with the aid of grants from the Institute of Jamaica and the support of both the Reynolds Jamaica Mines Company and the Kaiser Bauxite Company, I have made several field trips to Jamaica in order to study plants growing on bauxite soils, among them species of *Coccoloba*. I am grateful to the directors of these organizations for the support and cooperation offered during my visits. In the summer of 1955 while in Europe to attend the International Horticultural Congress, it was possible to visit many herbaria and gardens where the species of *Coccoloba* in the herbaria and under cultivation were studied. In addition, I have borrowed herbarium material from many botanical organizations and am appreciative of the use of material from the following herbaria cited in this paper: Arnold Arboretum (A), Berlin Botanical Garden (B), British Museum (BM), Copenhagen (C), Chicago Natural History Museum (F), University of Göttingen (Gott.), Gray Herbarium (GH), University College of the West Indies (J), Institute of Jamaica (IJ), Kew (K), Linnaean Society of London (L), Missouri Botanical Garden (MO), New York Botanical Garden (NY), Naturhistoriska Riksmuseum, Stockholm (S), U.S. National Herbarium (US). Only the basic synonymy and most important references are given for each species. The older references for these species are published in Lindau's monograph.

Coccoloba P. Br. ex L. Syst. Nat. ed. 10, 1007, 1367. 1759. Taxon 3: 114, 156, 233. 1954, nom. conserv.

Guaiabara Miller, Gart. Dict. ed. 4, 2: 1754.
Coccolobis P. Br. Civ. Hist. Jam. 209, *pl. 14, f. 3.* 1756.

Shrubs or trees, often with scandent branches or vines; branches terete, often geniculate, or arranged in one plane, short shoots commonly developed laterally or the terminal shoots of limited growth becoming long shoots; nodes commonly tumid; ochreae characteristically developed, membranaceous or coriaceous, deciduous or persistent, or so in part, glabrous, puberulent or pilose; leaves alternate, minute to large, membranaceous, chartaceous or coriaceous, the margin entire to undulate, flat or revolute, the primary veins straight to the margin, much branched at the apex becoming reticulate or arcuate and anastomosing or arcuate and bifurcate-anastomosing, the secondary venation obscure or coarsely to minutely reticulate, the upper leaf surface commonly pitted, rarely pubescent, the lower leaf surface glabrous to pilose, short multicellular glands present or the glands depressed in the lamina producing resinous secretions; petioles terete to stout, broadly and shallowly canaliculate above, pilose to glabrous, the base often tumid, attached at the base of the ochreae or above the base to two-thirds the length of the ochreae; plants dioecious or monoecious; inflorescence racemose or sub-spicate, spicate or paniculate, terminal on the primary or lateral branches, few-flowered and short to many-flowered and several times the length of the leaves, the rachis glabrous, puberulent, pilose or with glandular excretions; flowers unisexual or functionally so, the staminate flowers in clusters of two to four at each node of the inflorescence, occasionally solitary, the pistillate flowers solitary; bracts subtending each node, the flowers developing in a membranaceous sheath which ruptures irregularly or regularly to become an ochreola, the ochreolae membranaceous, generally one per flower, occasionally more by abortion of flowers, rarely stalked, the flowering pedicels shorter than the ochreolae to many times as long, the flowers articulated at the apex of the pedicel; perianth campanulate at the base forming a hypanthium, the lobes 5, imbricate, the outer three slightly larger than the inner, the stamens 7 or 8 borne on the hypanthium, the filaments united at the base, the anthers introrse, the stamens in the pistillate flowers rudimentary, the pistil rudimentary in the staminate flowers, trigonous in the pistillate flowers, the styles 3, dilated at the apices, the ovary 1-celled, the ovule solitary, attached basally; perianth expanding in fruit, the lobes surrounding the achene or the hypanthium expanding surrounding the achene with the perianth lobes appressed against the apex of the achene or coronate on the achene, the achene with a hard shiny outer layer, the inner layer papery; seed with ruminated endosperm, the major lobes 3, the minor lobes and involutions numerous, the embryo centrally located, the cotyledons orbicular, flat, rarely folded, the radicle small, terete.

TYPE SPECIES: *Coccoloba uvifera* L.

KEY TO THE SPECIES FOUND IN JAMAICA

A. Inflorescence paniculate.
  B. Pedicels 0.5 mm. long, shorter than the ochreolae in flower, to 1.5 mm. long, slightly exceeding the ochreolae in fruit; leaves rounded to cordate at the base, deciduous, the tree often barren of leaves for short periods. .... 1. *C. plumieri.*
  BB. Pedicels 3–6 mm. long, exceeding the ochreolae in flower and in fruit; leaves broadly cuneate at the base, the tree apparently never devoid of leaves. .... 2. *C. proctori.*
AA. Inflorescence racemose, the racemes solitary or rarely with 1 or 2 smaller ones at the base.
  B. Leaves thick, generally broader than long; plants of sea coast. .... 3. *C. uvifera.*
  BB. Leaves membranaceous to thinly coriaceous, longer than broad.
    C. Pedicels shorter or only slightly exceeding the ochreolae.
      D. Ochreolae several, persistent, conspicuous; rachis stout; pedicels very short; leaves usually turning black on drying. .... 4. *C. swartzii.*
      DD. Ochreolae solitary, deciduous; leaves buff or tan on drying.
        E. Inflorescence shorter than the leaves; the blades ovate, acuminate at the apex, cordate at the base, usually exceeding 7 cm. in length; inflorescence rachis conspicuously angled; with pedicels ascending; fruit ovoid, averaging 9 mm. long and 8 mm. in diameter. .... 5. *C. troyana.*

EE. Inflorescence exceeding the leaves; blades ovate-oblong, acute at the apex, obtuse or rounded at the base, usually less than 5 cm. long; inflorescence rachis not angular, the pedicels diverging at right angles; fruit strongly 3-lobed at the base, 5 mm. long and 3 mm. diameter on the average. .... 6. *C. krugii.*

CC. Pedicels conspicuously exceeding the ochreolae in flower and fruit.

- D. Leaves borne above the base of the ochreae, the base of the ochreae at leaf attachment generally conspicuously swollen.
  - E. Leaves appearing to be clustered on short lateral shoots, membranaceous, ovate-elliptical; inflorescence generally curved or drooping, pedicels thin. .... 7. *C. tenuifolia.*
  - EE. Leaves coriaceous, oblong elliptic, generally spaced on the branches which are often wand-like or scrambling; inflorescence stout, generally straight and erect; pedicels stout. .... 8. *C. longifolia.*
- DD. Leaves borne at the base of the ochreae without conspicuous swelling evident.
  - E. Leaf blades usually oblong-elliptic, rounded at the apex, generally darkening on drying but uniform in color on both sides. .... 9. *C. diversifolia.*
  - EE. Leaf blades broadly elliptic to rounded-elliptic, the apex acute or acuminate; blades turning black above on drying, usually lighter below. .... 10. *C. zebra.*

1. **Coccoloba plumieri** Griseb. Fl. Brit. W.I. 162. 1859; Lindau, Engl. Bot. Jahrb. 13: 134. 1890, Symb. Antill. 1: 220, 1899; Fawcett & Rendle, Flora Jam. 3: 113. 1914.

Coccoloba polystachya Wedd. var. *jamaicensis* Fawcett & Rendle, Jour. Bot. **51:** 125. 1913, Flora Jam. **3:** 112. 1914.
Uvifera plumieri O. Ktze. Rev. Gen. **2:** 562. 1891.

Trees to 60 ft. tall, trunk diameter breast height 18 in.; bark scaly; crown dense, branches spreading; the branchlets stout, terete, lightly striate; nodes only slightly enlarged; ochreae large, 10–15 mm. long, obliquely truncate, membranaceous at the apex and deciduous, coriaceous and persistent at the base, puberulent when young, soon glabrate; petioles 3–5 cm. long, attached at the base or below the middle of the ochreae, puberulent or glabrate; leaf blades oblong-elliptic, broadly ovate or oval, membranaceous to subcoriaceous 32 × 20; 27 × 16; 20 × 13, 13 × 7 cm. glabrous; apex obtuse to bluntly acuminate; base cordate, rarely truncate; margin entire, flat or slightly undulate; midrib and primary veins evident above, prominent below, primary veins 7–9 pairs, arcuate ascending, anastomosing near the margin, ultimate venation reticulate, evident but not prominent on both surfaces; inflorescence terminal paniculate, often uniformly branched from the base, the branches 15–25 cm. long and broad, rachises angular, puberulent or glabrate; flower nodes distinct; bracts semiorbicular, minute, less than 0.5 mm. long; ochreolae membranaceous, minute, less than 0.5 mm. long; flowering pedicels minute, less than 0.5 mm. long; fruiting pedicels to 1.5 mm. long; pistillate flowers always solitary; staminate flowers 1 to few at each node, perianth tube 1.5–2 mm. long, perianth lobes broadly ovate to suborbicular 2–3.5 mm. long and wide, functional stamens with filaments 3 mm. long at anthesis, the anthers 1 mm. long; pistillate flowers with rudimentary stamens 0.5–1 mm. long; functional pistil 2–3 mm. long, the pistil of staminate flower rudimentary 1 mm. long; fruit ovoid, rounded or subtruncate at the base, slightly narrowed at the apex to the subcoronate perianth lobes, 15–17 mm. long, 10–13 mm. thick, the lobes 2–3 mm. long; fruit perianth heavily and coarsely fibrous; achene pale brown, obtusely 3-angled, strongly apiculate at the apex.

Clarendon: Spaldings *Dignum 68* (IJ). **Manchester:** Mandeville, *Britton 3233* (NY); Moorlands Estate, 2 miles NE of Spur Tree, *Howard & Proctor 14439* (A), *Proctor 10593* (IJ). **St. Ann:** Soho, *Harris 12023* (F, MO, NY, US); Lydford Post Office, *Howard & Proctor 13398* (A, IJ), *14247* (A), *Proctor 8637* (IJ), *8687* (A). **St. Elizabeth:** Pepper, *G. S. Miller 1366* (US). **Westmoreland:** *Purdie s.n.* (K, TYPE of *C. polystachya* var. *jamaicensis;* NY, drawing). Without locality: *Alexander*, collected in 1850 (Gott. TYPE*;* NY, B, G), *March 1941* (B, Gott.).

COMMON NAME: Wild Grape. Collected in flower: January, July. Collected in fruit: December, January and April.

Coccoloba plumieri is the only species of the genus in Jamaica which is completely deciduous. Harris in his field notes reports plants from St. Ann to be in leafless condition in April and May. Proctor and I found plants with very young leaves just developing on plants in St. Ann in late December. As in many tropical trees, the young leaves of *C. plumieri* are limp and hanging when young and increasing in size. They become firm and coriaceous only when fully developed in size. The young leaves seen were often attractively colored red or bronze.

In the original description of *C. plumieri* Grisebach described the inflorescence of these plants as "racemes compounded at the base." His description was based on collections by Prior and March in the herbarium at Göttingen which I have seen. In both of these specimens the central axis of the inflorescence is not well developed. Lindau considered the inflorescence a panicle and placed the species in his section *Eucoccoloba* on this basis. I have now seen the specimens cited above and numerous plants in the field and agree with Lindau and Fawcett & Rendle that the inflorescence should be considered a panicle in that the central axis is dominant in most specimens but can be weak and less conspicuous than the basal branches in others. The dominance of the basal branches seems exaggerated in the fruiting condition with the weight of the mature fruit on the inflorescence diminishing the evidence of the panicle form.

Lindau's elaborate description of *C. plumieri* is confused through his failure to recognize the functionally unisexual condition of the flowers. Both staminate and pistillate flowers have been seen in the field and are represented in the collections cited. Few of the staminate flowers are clustered and the pistillate flowers are always solitary at the nodes. Flowers of both sexes are articulated to the pedicels. The staminate flowers dehisce from the pedicels after shedding the pollen and the pedicels remain small. The pedicels of the pistillate flowers, however, increase slightly in length and thickness as the fruit develops until at maturity they are several times the length of the ochreolae. Grisebach emphasized with italics in the original description the "pedicels jointed at the base." Examination of the specimens in the Herbarium at Göttingen indicates that Grisebach had confused the scar left by the deciduous ochreolae for an articulation at the base of the fruit-bearing pedicel. While the pedicel bearing the fruit is smaller at the basal end, there is no true articulation present at that point.

Harris has suggested the common name of wild grape for this plant in the vicinity of Soho, St. Ann. I have not found a common name in legitimate use in the areas where I have collected specimens. The few fruits seen in the field were dark purple in color and astringent to taste.

A collection by Gerrit S. Miller was identified as *Coccoloba rugosa*, but should be referred to the present species. The specimen is sterile and was collected apparently from a fast-growing shoot. The single leaf available is suborbicular in shape and 32 × 32 cm. long and broad. Adventitious shoots were seen on several large trees on the Moorlands Estate and younger plants with fast-growing branches and leaders were also abundant. In all of these specimens studied in the field, the shape of the leaves on these fast-growing shoots tended to be broadly ovate to oblong-elliptical. Typical leaves from these shoots reached 40 × 20 cm. in size.

Fawcett & Rendle described a specimen collected by Purdie in 1844 in the interior of Westmoreland as *Coccoloba polystachya* var. *jamaicensis*. The specimen is from a staminate plant and can be referred without hesitation to *C. plumieri* Griseb.

2. **Coccoloba proctori,** sp. nov.

Frutex, ramulis crassis teretibus; nodis non tumescentibus; ochreis membranaceis, glabris, 10–17 mm. longis, ad basim persistentibus coriaceis, ad apicem obliquis, membranaceis; petiolis crassis, 2–3 cm. longis, glabris; lamina ovata vel elliptici-ovata, 17 × 12 vel 19 × 15 cm. longa et lata, apice obtusa, basi late cuneata vel rotundata, glabra, coriacea, nerviis primariis 4 vel 5, arcuatis inconspicue anastomosantibus; inflorescentibus terminalibus, paniculatis, ♂ ad 15 cm. longis, fructibus ad 25 cm. longis; floribus ♂ 2–4 per nodulum, floribus ♀ 1 per nodulum, rhachi glabra, bracteis 0.5 mm. longis, ochreolis membranaceis 1 mm. longis, pedicellis floriferis 3–4 mm. longis, pedicellis fructiferis 5–6 mm. longis; fructu globoso, 1 cm. diametro, lobis perianthii basi subcoronata, hypanthii 13–15 vascularibus cristis, basim versis rotundata, substipitata. Achenia pallida fulva.

Tree, branches stout terete, nodes not swollen; ochreae 10–17 mm. long, glabrous, membranaceous above and deciduous, coriaceous and persistent below, oblique and slightly bilobed; petiole inserted at the base, petiole stout, 2–3 cm. long, glabrous, blade ovate to elliptical-ovate 17 × 12, 19 × 15 cm. long and broad, apex obtuse, base broadly cuneate to rounded, glabrous, coriaceous, primary veins 4–5 pairs, arcuate, inconspicuously anastomosing; inflorescence terminal, paniculate, staminate to 15 cm. long, fruiting to 25 cm. long, glabrate, staminate flowers in clusters of 2–4, pistillate flowers solitary, bracts less than 0.5 mm. long, ochreolae less than 1 mm. long; flowering pedicels 3–4 mm. long, glabrate, fruiting pedicels 5–6 mm. long; fruit globose, 1 cm. diameter, fruiting perianth with 13–15 vascular ridges, slightly coronate at the apex, base rounded, very slightly stalked, achene tan.

St. Elizabeth: Wooded area on limestone outcrop near Pit 101 of Kaiser Mines, south of Gutters, *Howard and Proctor 14555* (A, IJ), *15718* fruit (TYPE A), *14719* ♂ (A).

Several plants are known of this new species, but it has been found on only two limestone outcrops in the valley south of Gutters. The two largest trees were 50 and 65 feet tall and three feet in diameter at breast height. One of these has been collected in fruit twice (December and January) and the other has not been found in fertile condition. The collection *14719* was a slender tree 30 feet tall and 6 inches in diameter at breast height. Its perilous position on eroded limestone necessitated felling this tree to collect material and it was the only staminate tree seen. Numerous small trees have been located in this area and vigorous shoots of these, as well as of the larger trees, show the typical larger leaves now expected in this genus on thick shoots. The largest leaves of the adventitious shoots were on petioles of 5 cm. with blades 40 × 25 cm.

This species is named in honor of Mr. George Proctor of the Institute of Jamaica, who has been my companion on many recent field trips in Jamaica. His efforts in collecting have already resulted in making the flora of Jamaica better known.

Coccoloba proctori is similar to *C. plumieri*, differing, however, in the more strict branches of the inflorescence, the globose fruit and the leaves with cuneate bases and fewer veins.

3. **Coccoloba uvifera** L. Syst. Nat. ed. 10, 1007. 1759; Lindau, Engl. Bot. Jahrb. 13: 204. 1890, Symb. Antill. 1: 231. 1899; Fawcett & Rendle, Fl. Jam. 3: 119. 1914.

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

Tree of strand areas, 2–15 m. tall; branches terete, stout, papillose to pilose, the nodes not tumid; ochreae rigid, coriaceous at the base, membranaceous at the apex, 3–8 mm. long, puberulent to pilose; petioles stout, 7–10 mm. long, papillose to pilose; leaf 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 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, secondary venation minutely reticulate or obscure; apex rounded, truncate or emarginate, the base rounded to broadly cordate, one lobe often extended around the petiole; leaves of adventitious or fast-growing shoots usually variable in size and shape, but commonly obovate; inflorescence stout, 15–13 cm. long, rachis puberulent; staminate flowers in clusters of 1–7, the pistillate flowers solitary, the bracts ovate, 1–1.5 mm. long, 2 mm. broad, puberulent, the ochreolae 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, the 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, perianth rose-purple when mature, the achene black.

DISTRIBUTION: General along beaches of Florida, Bermuda, the Bahamas through the Caribbean area to South America.

Manchester: Alligator Pond, *Miller 1403* (S). **Portland:** Port Antonio, *Fredholm 3039* (US), *Proctor 11884* (IJ), *Shreve 25674* (Wisc.); Bennett Point, *Proctor 11844* (GH); Buff Bay, *Maxon 10337* (S, US). **St. Ann:** *Hunnewell & Griscom 14306* (GH); Runaway Bay, *Pierce 26* (IJ); Dunn's River, *Barkley 22J360* (IJ). **St. James:** Montego Bay, *Maxon & Killip 1639* (A, F, GH, US), *Barry s.n.* (IJ), *Davis s.n.* (Mich.). **St. Mary:** Rio Nuevo, *A. von der Porten s.n.* (IJ). **Westmoreland:** Negril Point, *M. L. Farr s.n.* (IJ). Parish uncertain: Glenwood, *Harris 5978* (F).

LOCAL NAME: Sea Grape, Seaside Grape, Beach Grape. Collected in flower in March. Collected in fruit in September.

As frequently happens with well-known and widely distributed species, *Coccoloba uvifera* has been neglected by collectors in Jamaica and is poorly represented in herbaria. The sea grape, however, is a common and often picturesque component of the strand and beach floras of Jamaica and is probably found in every coastal parish. On the north coast the sea grape has been observed only along the immediate coastline, but on the southern side of the island in the vicinity of Kingston and again on the Lititz savannah in St. Elizabeth, *C. uvifera* has been found growing several miles inland.

4. **Coccoloba swartzii** Meisner, DC. Prodr. **14**: 159. 1856; Lindau, Engler Bot. Jahrb. **13**: 157. 1890, Symb. Antill. **1**: 227. 1899; Howard, Jour. Arnold Arb. **30**: 420. 1949, **37**: 324. 1956.

Coccoloba barbadensis, authors not Jacq.
Coccoloba diversifolia Fawcett & Rendle, Flora Jam. **3**: 115. 1914 and all recent authors not Jacq.

Coccoloba neglecta Fawcett & Rendle, Jour. Bot. 51: 124. 1913, Flora Jam. 3: 116. 1914.
Uvifera swartzii Ktze. Rev. Gen. 2: 562. 1891.

Tree 8 to 20 m. tall; branches terete, the youngest puberulent, becoming glabrate, the nodes slightly tumid; ochreae 10–12 mm. long, the persistent coriaceous basal portion 3–5 mm. long, the upper deciduous portions membranaceous, puberulent or glabrate; petiole attached at the base of the ochreae, glabrous or puberulent becoming glabrate, 10–18 mm. long; leaf blades ovate to elliptic, 7 × 5, 11 × 9, 15 × 7.5 cm. long and broad, coriaceous, usually turning black on drying, glabrous, the apex acute or rounded, the base narrowed, rounded or slightly obliquely cordate; midrib and veins inconspicuous above, prominent to inconspicuous below, the primary veins 6–7 pairs, arcuate, anastomosing, ultimate venation conspicuous reticulate; margin entire, slightly recurved; leaves of adventitious shoots with petioles 1.5–2.5 cm. long, the blades ovate to lanceolate, the apex acute to acuminate, 23 × 8.5 to 45 × 18 cm. long and broad; inflorescence terminal 10–15 cm. long, the rachis glabrous or with glandular exudates, rarely papillose, staminate flowers in clusters of 3–5 with tightly concentric membranaceous ochreolae forming a truncate or flattened cylinder after flowering; pistillate flowers solitary, ochreolae erect in flower, flattened against the rachis in fruit; bracts ovate, 1–1.5 mm. long, ochreolae membranaceous 1–1.5 mm. long, flowering pedicels shorter than the ochreolae, hypanthium 0.5 mm. long, perianth lobes ovate, 1–1.5 mm. long and broad, fertile stamens 1 mm. long; fruit ovoid 8–10 mm. long, 6 mm. in diameter; perianth lobes 1–1.5 mm. long in fruit, coronate; achene dark brown.

DISTRIBUTION: Rare in the Bahamas and Cuba, most abundant in Jamaica and less so in Hispaniola, Puerto Rico, the Virgin Islands, Leeward Islands and Windward Islands south to St. Lucia.

Clarendon: Savoy, *Harris 11639* (C, F, GH, NY, MO, US); Peckham Woods, *Harris 11194* (US, NY); Croft's Mts., *Harris 11219* (F, NY, US). **Hanover:** Quashiba Mt., *Webster & Wilson 5086* (A). **Manchester:** New Green, *Britton 3757* (NY); Mandeville, *Britton 3732* (NY), *3236* (NY). **Portland:** Green Ridge *Eggers 3732* (C); Claverty Cottage, *Harris 5088* (C, US); Mt. Pleasant, Stony Hill, *Harris 11133* (F, NY, US). **St. Andrew:** Long Mt., *Webster 4983* (GH); Hardware Gap near New Castle, *Britton & Hollick 1806* (NY); Clydesdale to Chesterdale, vicinity of Cinchona, *Britton 334* (F, NY); Constant Spring to Bardowie, *Harris 12110* (F, GH, MO, NY, S, US); Port Royal Mts., Content Road, *Harris 5092* (US), *5263* (S, US); Lower Davids Hill, *Harris 5091* (C, US); Liguanea Hills, *Prior s.n.* (NY); Moody's Gap, *Britton 3337* (NY), *3364* (NY); Brandon Hill, *Fawcett 8062* (F, NY). **St. Ann:** Union Hill near Moneaque, *Howard 12031* (GH), *12022* (GH), *12013* (GH), *Prior s.n.* (NY); Mt. Diablo, *Hunnewell 19335* (GH); Lydford P.O., *Howard and Proctor 13536* (A, IJ), *13544* (A, IJ), *14586* (A). **St. Catherine:** Juan de Bolas, *Proctor 7146* (IJ); Holly Mount, *Harris 8901* (NY); Charlton, *Harris 6699* (F, NY); Bogwalk, *Proctor 8185* (IJ). **St. Elizabeth:** Malvern, *Howard & Proctor 13722* (A, IJ), *Britton 1195* (NY); Malvern, Bideford District, *Webster & Proctor 5328* (GH).

St. Thomas: Big Level, John Crow Mts., *Webster & Proctor 5529* (GH); Bath, *Britton 3492* (NY), *Harris 6055* (F, NY); Green Valley, *Harris 5233* (C, NY), *12126* (F, GH, MO, NY, S, US); Mansfield, *Britton 3556* (NY); Blue Mts., *Harris 5274* (US),*5094* (B, BM — TYPE of *C. neglecta*, C, J, US); Without location, *Britton 3656* (NY). **Trelawny:** Oxford, *Britton 430* (NY); Troy, *Britton 919* (NY), *Harris 90994* (F, NY, US), *Howard & Proctor 14119* (A). Parish uncertain: Cedar Hurst, *Harris 5500* (C); "Portland," *Bancroft 11* (US). Without definite location: *Swartz s.n.* (De Candolle Herb., TYPE, S, NY).

COMMON NAME: Wild grape. Collected in flower in July, August and September. Collected in fruit in January, February, March, September and November.

A full discussion of the polymorphic species *Coccoloba swartzii* has been published as the second paper in this series (Jour. Arnold Arb. 37: 317–339. 1956). The Jamaican populations of this taxon are remarkably uniform, although they do grade into the variations found on other islands. The type of the species, a Swartz collection described by Meisner and located in the De Candolle Herbarium, is from Jamaica.

I cannot understand how Fawcett & Rendle, in their comprehensive treatment of the genus for the Flora of Jamaica, overlooked this species and failed to consider it. The specimens recognized here as *Coccoloba swartzii* were called *C. diversifolia* Jacq. in the Flora of Jamaica.

5. **Coccoloba troyana** Urb. Symb. Antill. 6: 8. 1909; Fawcett & Rendle, Flora Jam. 3: 116. 1914.

Tree of inland areas, generally on limestone, 7–15 m. tall, commonly branched from the base with several trunks; ultimate branches terete, glabrous with nodes only slightly enlarged; ochreae cylindrical, 10–13 mm. long, glabrous, membranaceous, almost completely deciduous; petioles attached at the base of the ochreae, 1.5–2 cm. long, glabrous; blades cordate-ovate to ovate-elliptic, 7 × 4.5, 8 × 6, 9 × 6, 10.5 × 8 cm. long and broad; apex short acuminate, the base cordate; margin entire, flat, chartaceous, drying buff or tan; midrib and primary veins inconspicuous to prominent on both surfaces, arcuate, anastomosing; primary veins 6–9 pairs, the secondary venation reticulate on both surfaces, glands few, inconspicuous; inflorescence terminal, 5–9 cm. long, generally shorter than the leaves, the rachis glabrous or with glands, the pedicels decurrent so that the axis is angular, ridged and grooved; bracts broadly ovate, less than 1 mm. long, glabrous, the ochreolae membranaceous, to 1 mm. long, pedicels glabrous, at most 1.5 mm. long in fruit; staminate flowers 1–3, the pistillate flowers usually solitary, the hypanthium 1 mm. long, perianth lobes oblong-ovate, 1.5 mm. long and broad, the functional stamens 1.5 mm. long; fruit ovoid, 8 mm. long and 5 mm. in diameter, stalked at the base, becoming fusiform to fusiform-ovoid; perianth lobes appressed, 4–5 mm. long, not coronate; achene chestnut brown, shiny.

DISTRIBUTION: Endemic to Jamaica.

Portland: 2½ mi. SW of Ecclesdown, *Proctor 11375* (IJ). **St. Thomas:** John Crow Mts., *Harris & Britton 10764* (F, NY, US). **Trelawny:** Troy, *Harris 9439* (TYPE B, F, NY, US), *9474* (B, F, NY, US), *10653* (C, F, NY, US), *Britton 600* (F, NY, US), *639* (NY); Ramgoat Cave, *Howard and Proctor 14142* (A), *14383* (A, IJ), *Howard, Proctor & Stearn 14659* (A), *Proctor 10616* (IJ).

Collected in flower in March. Collected in fruit in September and November.

This species is easily recognized even in sterile condition by the cordate leaf shape, the long, pale buff petioles and the buff or tan blades. The angular inflorescence axes with the decurrent pedicels mark the species in flowering and fruiting condition. Despite these apparent characters, the species appears to be very similar to some specimens of *Coccoloba krugii* and it is possible that further collections will show complete transition between the two. Attempts to germinate the seeds of *C. troyana* and *C. krugii* have not been successful and the cytological relationship of these species is not known. There is a possibility that *C. troyana* may be a polyploid race of *C. krugii.*

Urban's original description has not been significantly altered by Fawcett & Rendle. More recent collections show that Urban examined only a fragment of the ochreae and that his report of ochreae 3 mm. long is erroneous.

I have seen a dozen specimens of *C. troyana* in the field between Troy and Kimloss in the Cockpit country. Each specimen was in an isolated and sparsely populated area and was not cut or injured. There were neither trauma-induced adventitious shoots nor spontaneous ones and the nature of the larger leaves generally characteristic of juvenile and fast-growing shoots is not known for this species.

The collection by Harris and Britton from the John Crow Mountains, presumably the southern shoulder of this range, extends the known range of the species in Jamaica from the center at Troy to the opposite and eastern end of the island. The specimens collected by Harris and Britton are in full bud or young flowers and appear to agree in all characters with the more numerous material from Trelawny. More recent collections by Proctor from the John Crow Mountains above Ecclesdown are sterile. I have seen the plants in this area and believe they are correctly assigned here.

6. **Coccoloba krugii** Lindau, Engl. Bot. Jahrb. **13**: 145. 1891, Symb. Antill. **1**: 222. 1899; Fawcett & Rendle, Flora Jam. **3**: 115. 1914.

Coccoloba børgesenii Schmidt, Fedde Repert Sp. Nov. **24**: 75. 1927.
Coccoloba børgesenii forma *ovato-lanceolata* Schmidt, Fedde Repert Sp. Nov. **24**: 76. 1927.

Shrub or small tree to 6 m. tall; branches terete, glabrous, slightly nodose; ochreae membranaceous, persistent, 3–5 mm. long, petiole attached at the base of the ochreae, 5–6 mm. long; leaf blade ovate, suborbicular, 2 × 1.8, 2.5 × 2.5, 4 × 3.5 cm. long and broad, the apex obtuse or rounded, the base cordate or rounded, thin coriaceous, entire, flat or recurved margin, glabrous or rarely with a few hairs near the attachment of the petiole, the midrib flat above, slightly prominent below, the secondary venation minutely reticulate below, smooth above; adventitious shoots with ochreae to 1 cm. long, petioles on shoots to 1 cm. long, the leaf blades generally elliptic, 6 × 4, 7 × 6 cm. long and broad; inflorescence terminal, 5, 6, 8 cm. long, the rachis glabrous, the bracts broadly ovate, membranaceous, less than 1 mm. long, the ochreolae membranaceous, less than 1 mm. long, the pedicels shorter than the ochreolae; pistillate flowers solitary, the staminate flowers 1 or 2 at a node on the axis, hypanthium 1 mm. long, the perianth lobes ovate, 2 mm. long, the fertile stamens 1–1.5 mm. long; fruit ovoid or fusiform, generally 3-angled, 4–5 mm. long, 3–3.5 mm. in diameter, the perianth lobes appressed, about half the length of the fruit; achene dark brown.

DISTRIBUTION: Bahamas, Hispaniola, Jamaica, Puerto Rico, the Virgin Islands and some of the Leeward Islands.

Clarendon: Portland Ridge, *Lewis 52* (IJ), *80* (IJ), *Webster 5122* (GH). **St. Andrew:** Lower Valley Cave River, *Proctor 10208* (IJ); Long Mt. on road to Wareka, *Harris 10008* (F, NY, US), *10014* (F, NY, US), *Maxon 10521* (GH, NY, S, US), *Webster 5002* (GH); Long Mt., *Howard 12033* (G), *Webster & Wilson 4861* (GH). **St. Catherine:** Great Goat Island, *Harris 9335* (A, F, NY, US). **St. Elizabeth:** Lovers Leap, Santa Cruz Mts., *Britton 1149* (NY); Yardley Chase, *Harris 9667* (B, F, NY, US); Southfield, *Proctor 11337* (IJ). **St. Thomas:** Albion Mt., *Harris 11690* (F, GH, MO, NY, US), *11681* (F, GH, MO, NY, US). **Trelawny:** Ramgoat Cave, *Howard and Proctor 14395* (A, IJ), *Howard, Proctor & Stearn 14683* (A).

COMMON NAME: Big Family, Crabwood. Collected in flower in July. Collected in fruit in February and March, June, July, August, September and November.

A conspicuous taxon easily recognized in the field and in the herbarium by the ashen gray petioles and ochreae, the yellowish brown or tan leaves and the strongly triangular fruit.

The two Harris collections from Albion Mountain, *11680* and *11681,* were presumably made at the same time and place and probably from adjacent trees which looked different. The second collection consists of specimens distinctly short pilose on all parts and with the leaves rounded and emarginate at the apex. This is the most exaggerated pubescent condition seen in the species, although the same leaf shape has been found with all transitions. The Harris collection from Great Goat Island, *9335,* probably showed the greatest variation in the sheets available for study. Other workers had previously and erroneously labelled several of these sheets *C. pyrifolia.*

7. **Coccoloba tenuifolia** L. Syst. Nat. ed. 10, 1007. 1759, Amoen.

5: 397. 1760, Sp. Pl. ed. 2, 524. 1762; Fawcett & Rendle, Flora Jam. **3**: 119. 1914, Jour. Bot. **51**: 124. 1913.

Coccoloba leptostachyoides Lindau, Engl. Bot. Jahrb. **13**: 207. 1890.
Coccolobis ? frutescens, foliis subrotundis, fructu minore trigone Brown, Hist. Jam. 210, *t. 14, f. 3.* 1756.
Coccoloba excoriata L. Syst. Nat. ed. 10, 1007. 1759; Fawcett & Rendle, Flora Jam. **3**: 121. 1914.
Coccoloba bahamensis Britton, Bull. N.Y. Bot. Gard. **4**: 116. 1905, as *Coccolobis.*

Shrub, rarely a small tree 6 to 15 feet tall; branches terete, light brown in color, glabrous or puberulent; ochreae membranaceous above and deciduous, coriaceous and persistent below, puberulent; the leaves characteristically borne on lateral shoots and crowded, the petioles short persistently puberulent, 6–9 mm. long, arising from a conspicuous base above the base of the ochreae, the blades generally elliptic, occasionally obovate, oval, oblong or sublanceolate, 3.5 × 2, 7 × 4.5, 8 × 6, 9.5 × 6 to 12 × 10 cm. long and broad, membranaceous to subcoriaceous, the apex acute, short acuminate or rarely obtuse, the base narrowed and unequally rounded to subcordate, the margin entire to undulate, the blade often conspicuously umbonate in the field; midrib and veins flat or impressed above, prominent beneath, primary veins 4–6 pairs, arcuate, the ultimate venations finely reticulate, glabrous above, finely puberulent below, generally tomentose in the axils of the veins and extending on to the lamina persisting or evident as clear hair bases; adventitious shoots with leaves evenly distributed, petioles 2–5 cm. long, the blades 7 × 9 to 18 × 16 cm. long and broad; inflorescence terminal from the lateral leafy shoots, to 8 cm. long, weak and hanging generally strongly curved, the rachis puberulent becoming glabrate; staminate flowers 1–4 at the node, the pistillate flowers usually solitary, bracts broadly ovate, to 0.5 mm. long, the ochreolae membranaceous, 0.5 mm. long, the pedicels 1 mm. long, the hypanthium 1–1.5 mm. long with apparent basal stalk more conspicuous in the pistillate flower, the perianth lobes 1–1.5 mm. long and broad, the functional stamens 1–1.5 mm. long, the functional pistil 1.5 mm. long; fruiting pedicels 1–1.5 mm. long, the fruit ovoid 5–6 mm. long and 4 mm. in diameter with a short stalk 0.5 mm. long, the perianth lobes appressed, the achene tan in color.

DISTRIBUTION: Bahamas, Cuba and Jamaica.

Manchester: Spur Tree Hill, *Britton 1064* (NY), *1665* (NY), Marshall's Pen, *Britton 3706* (NY). **St. Andrew:** Green Valley, *Harris 5391* (US), *12129* (F, GH, MO, NY, S, US); Long Mountain, *Harris 8862* (F, NY, US), *Britton 810* (NY), *Howard 12034* (GH), *12035* (GH), *Webster & Wilson 4880* (A), *4890* (A); Mona, *West & Arnold 559* (GH), Berwick Hill, *Harris 5343* (F, US), *6517* (B, F, NY), *Perkins 1194* (A, GH). **St. Ann:** Falls River, *Harris 5228* (Leiden, US). **St. Elizabeth:** Malvern, *Harris 9808* (F, NY, US); Potsdam, *Britton 1264* (NY); Shooters Hill, *Howard & Proctor 14106* (A); Hampton School, *Webster & Proctor 5307* (GH). **St. Thomas:** Blue Mts., *Harris 5272*

(US); Morant Bay, *Barry s.n.* (IJ). **Clarendon:** Portland Ridge, *Howard 12010* (GH). **Trelawny:** Ramgoat Cave, *Howard & Proctor 14143* (A), *14420* (A). Location uncertain: *March 1989* (TYPE of *C. leptostachyoides*, B, Gott.); *Swartz s.n.* (S), *Hart s.n.* (F, NY). Linnaean Herbarium types of *C. tenuifolia* and *C. excoriata* (Patrick Browne).

COMMON NAME: Wild grape. Collected in flower in July, August, September. Collected in fruit in January, February, August, September, October and November.

Fawcett & Rendle have made the greatest contribution in straightening out the nomenclature of this species which has been confused for many years.

Lindau, the earliest monographer of the genus *Coccoloba*, apparently never saw the specimen of *Coccoloba tenuifolia* L. in the Linnaean Herbarium. Lindau refers only to the description in Linnaeus's Amoenitates Academicae 5 in citing this species in a category of uncertain species (Engl. Bot. Jahrb. 13: 220. 1890). The Linnaean specimen is in excellent flowering condition and is easily recognized. Lindau, however, described two species from Jamaica, *C. jamaicensis* and *C. leptostachyoides* which Fawcett & Rendle consider identical and synonymous with *C. tenuifolia*. I agree only in part with this conclusion, as I consider *C. jamaicensis*, as based on a March specimen, a hybrid and the same as *C. litoralis* Urban.

There remains one species, *Coccoloba excoriata* L., to be disposed of properly before the terminology of this taxon can be considered stable. Linnaeus based *C. excoriata* on a Patrick Browne specimen which is today in the Linnaean Herbarium. As Fawcett & Rendle report in reviewing this species (Jour. Bot. **51**: 123. 1913 and Flora Jam. 3: 121. 1914), the specimen labelled *C. excoriata* in Linnaeus's handwriting is a "stout shoot, apparently a young sucker 14 cm. long and 0.5 cm. thick with white bark and brown lenticels; leaves 7.5–10 cm. long, 6–7 cm. broad, broadly elliptical, very shortly acuminate, base sometimes unequal, rounded, nerves on both sides prominulous, veins inconspicuous, dark brown on upper surface, light brown beneath; petioles and ochreae puberulous; ochreae dark brown, broadly tubular, 1 cm. long, permanent base 5–7 cm. long, leaf inserted about the middle of the permanent base."

Fawcett & Rendle sought to identify this species through the common name of "The Mountain Grape Tree" supplied by Patrick Browne and, being unsuccessful, left this taxon as "species insufficiently known" in the Flora of Jamaica. Lindau completely misinterpreted the description and considered *C. excoriata* the same as *C. nivea* Jacquin. He placed the species as a synonym in the section *Campderia*. *Coccoloba nivea* Jacquin is now known as *C. venosa* L. and is a very distinct species.

To identify *C. excoriata* L. it is necessary to consider the adventitious shoots of the common species of *Coccoloba* in Jamaica. I have a collection of such shoots made over a period of five years representing most of the species of the genus known from the island. The specimens which agree most closely with Linnaeus's description and the specimen in the Linnaean Herbarium were collected on Long Mountain just outside of Kingston and are *Howard 12034, 12035, Britton 810* and *West and Arnold 559.* A Harris specimen, *6517,* from Berwick Hill also matches the sterile Patrick Browne specimen. The vegetation on the dry hillsides of Long Mountain is cut with regularity for fuel and the stumps which produced the adventitious shoots here considered are referable in fertile condition to *C. tenuifolia.* There is no doubt that the Patrick Browne specimen of "The Mountain Grape Tree" and the type of *C. excoriata* is an adventitious shoot of *C. tenuifolia.* Both of these names are published on page 1007 of Linnaeus's Systema Natural. edition 10, in 1759. As the Linnaean specimen of *C. tenuifolia* is an excellent flowering specimen, it is desirable to select this as the type and to consider *C. excoriata* based on a sterile adventitious shoot as a synonym.

Coccoloba tenuifolia is distinctive in having tenuous and characteristically curved inflorescence axes. The clustering of the leaves on short lateral branches gives this taxon a distinctive appearance in the field. The swollen ochreae bases, heavily veined near the attachment of the petiole, are also of diagnostic value.

Anomalies have been seen in this species, also, with fasciated and branched inflorescences relatively common. In one specimen the inflorescence axis is thin at the base, becoming flattened and broad about the middle of its length and dividing into ten branches near the apex. The flowers in the Perkins specimen (*1194*) are monstrous in size and the stamens, numbering from four to seven in various flowers examined, are variously united.

8. **Coccoloba longifolia** Fischer ex Lindau, Engl. Bot. Jahrb. **13:** 161. 1890; Ettingschausen, Denkschriften K. Acad. der Wissenschaften, Vienna **15:** *229, tab. 27, fig. 2.* 1858; Fawcett & Rendle, Flora Jam. **3:** 117. 1914.

Coccoloba venosa Griseb. ex Lindau, Engl. Bot. Jahrb. **13:** 152. 1890, not Linnaeus.
Coccoloba venosa major Lindau, Engl. Bot. Jahrb. **13:** 152. 1890.
Coccoloba rumicifolia Britton, Bull. Torrey Bot. Club **42:** 514. 1915.

Erect shrub, scrambling shrub or tree to 15 m.; branches often scrambling, terete, striate, the nodes not conspicuously swollen; ochreae 4–6 mm. long, obliquely truncate, sparsely to densely short yellow pubescent or glabrate, membranaceous above and evanescent, coriaceous below and persistent, the petiole arising slightly above the base, 14 mm. long, glabrous, puberulent or pilose on the adaxial surface; leaf blades oblong-ovate to sublanceolate-ovate, 7 × 2.5, 8 × 5, 13 × 5, 17 × 7 cm. long and broad, subcoriaceous, glabrous, the margin slightly recurved, the primary veins 6 pairs, arcuate, anastomosing near the margin, the ultimate venation reticulate and evident on both surfaces, the base rounded, cordate or rarely cuneate, the apex obtusely acuminate to long acuminate; adventitious shoots with internodes to 10 cm. in length, ochreae 2.5–3.5 cm. with petiole attached from near the base to about the middle, the petioles to 2.6

cm. in length, the blades ovate, ovate-lanceolate or ovate-elliptic 13 × 9, 21 × 8, 26 × 11, 32 × 12, 40 × 19 cm. long and broad; inflorescence racemose, generally exceeding the leaves, 6, 10, 18, 26 cm. in length, basal ochreae to 6 mm. long, the axis puberulent or glabrate, the bracts triangular, obtuse to 0.5 mm. long, the ochreolae membranaceous generally flaring slightly truncate or obliquely truncate, about 1 mm. long, the pedicels in flower 2 mm. long; staminate flowers 1–4 at each node, the pistillate flowers normally single, rarely 2 at each node, the pedicels and perianth puberulent, the hypanthium campanulate 1–2 mm. long, perianth lobes ovate, generally 2 mm. long and broad; fertile stamens to 2 mm. long; functional pistil 2–3 mm. long; fruiting pedicels 2.5–4 mm. long, fruit bright red, ovoid 10–12 mm. long, 6–7 mm. in diameter, apex slightly turbinate, the base contracted to a short stipe, fruiting perianth conspicuously vascular; achene dark brown or black.

DISTRIBUTION: Endemic to Jamaica.

Clarendon: Leicesterfield, *Harris 10840* (F, GH, NY, US); Peckham Woods, *Harris 10873* (F, GH, NY, US), *11174* (F, MO, NY, US), *12785* (F, MO, NY, US); *Proctor 8227* (IJ). **Hanover:** Kempshot, *Britton 2437* (NY). **Manchester:** Martins Hill near Mandeville, *Harris & Britton 10617* (F, NY, US); New Green near Mandeville, *Harris & Britton 10597* (NY, US), *Harris 6317* (B); Mandeville, *S. Brown 241* (NY). **Portland:** 1.5 mi. SW of Ecclesdown, *Howard, Proctor & Stearn 14778* (A); Swift River District, West Hope Bay, *Harris 6009* (F, NY). **St. Ann:** Union Hill near Moneague, *Britton & Hollick 2736* (NY), *2773* (F, NY), *2777* (NY), *Howard 12029* (GH); Grierfield near Moneague, *Britton 2665* (NY), *2667* (NY); Soho, *Harris 11984* (F, NY, US), *11986* (F, GH, MO, NY, US); Liberty Hill, St. Anns Bay, *Britton 2502* (NY), Mt. Diablo, *Maxon 2219* (NY, US), *Webster & Wilson 5013* (A); Lydford P.O., *Howard & Proctor 13420* (A), *13534* (A), *14579* (A), *Howard, Proctor & Stearn 14600* (A), *Proctor 6397* (IJ), *8642* (A, IJ); Linton Estate near Claremont, *Howard & Proctor 14191* (A); Prickly Pole, *Howard & Proctor 14318* (A). **St. Andrew:** Bogwalk, *Hitchcock s.n.* (MO); Constant Spring, *Campbell 5714* (F, NY). **St. Catherine:** Luidas Vale, *Hunnewell 19334* (GH), *Hunnewell & Griscom 14305* (GH); Hollymount, *Britton 730* (NY), *Harris 6489* (B). **St. Elizabeth:** Pepper, *G.S. Miller 1331* (US); Stanmore Hill, Santa Cruz Mts., *Britton 1308* (NY). **St. Mary:** Gayle, *Proctor 5093* (IJ). **St. Thomas:** John Crow Mts., *Britton 3991* (NY), *Harris & Britton 10689* (F, NY, US), *10758* (F, NY, US), *10756* (F, GH, NY, US); Big Level, *Webster & Proctor 5532* (GH), *5545* (GH); Bath, *Britton 3649* (NY), *Howard, Proctor & Stearn 14808* (A); Bachelors Hill, *Britton 3616* (F, NY); Amity Hall Hill, *Harris & Britton 10716* (F, NY). **Trelawny:** Troy, *Harris 8719* (NY), *8772* (NY); between Troy and Oxford, *Britton 680* (F, NY); Oxford, *Harris 9489* (F, NY); Tyre, *Harris 9462* (F, NY), *Britton 545* (NY); Windsor, *G.S. Miller 1475* (US); Hectors River, *Harris 6005* (B), Troy, *Howard & Proctor 14117* (A); Ramgoat Cave, *Howard & Proctor 14146* (A), *14147* (A), *14153* (A), *14393* (A); Burnt Hill, *Barkley, 22J241* (IJ). **Westmoreland:** Negril, *Britton & Hollick 2034* (NY); Beeston Spring to Bog House, *Webster & Wilson 5032* (A); Teague Gulley, Newmarket, *Britton 1592* (TYPE of *C. rumicifolia*, N.Y.), *Harris 9837* (B, F, NY, US). Locality not certain: *Willdenow 7698* (B); *March 1568* (GH), *674* (Gott.)

Swartz s.n. (S), *Hansen s.n.* (NY), *Prior s.n.* (B, GH, NY). **Cultivated:** Hort. Berlin 1828 (US), 1843(B).

COMMON NAMES: Wild Grape, Bastard Cherry. Collected in flower in March, April, May and July. Collected in fruit in December, February, March, April and May.

Lindau in his monograph of the genus supplies the first complete description of *Coccoloba longifolia* and attributes the name to Fischer. He cites as the first publication of his name the reference "Cat. Pl. Razoum. à Gor. p. 25" and notes that it was without description. I was unable to locate any reference to that publication in the United States and am indebted to the staff of the library at the Royal Botanic Gardens at Kew for their assistance in finding this little book. It is, correctly, "Catalogue du Jardin des Plantes du son excellence Monsieur le comte Alexis de Razoumeffsky a Gorenki." This catalogue was compiled by F. Fischer and was published in Moscow in 1812. The name in question was published in a list on page 16, not 25, as "Coccoloba ? longifolio." It is a nomen nudum. Lindau cites further references for this name, the next being H. F. Link in his Enumeratio Plantarum Horti Regii Botanici Berolinensis 1: 386. 1821, where for the first time the plant is credited to English Gardens. No description is given. Steudel in Nomenclator Botanicus, page 210 in 1821 and again in the 1840 edition on page 290 lists this plant under cultivation as "C. longifolia Fisch." To the latter listing is added the information "Hort. Ang." and "Ind. Occ." and a symbol indicating the species is not well known.

In 1858 C. von Ettingshausen in a preliminary work on the interpretation of fossil plant remains (Denkschriften K. Acad. d. Wiss. Wien. **15**: 229, *tab. 27, fig. 2.* 1858) gives a brief description of the vascular pattern of the leaves of "C. longifolia Link" and an illustration. It is obvious that the material he studied originated in the Botanical Garden in Berlin bearing the name from Link's catalogue. It would be permissible, but of doubtful value, to consider the description and illustration of Ettingshausen as the first valid publication of the name *C. longifolia*.

Lindau's complete description has been taken as the starting point for this species by Fawcett & Rendle (Flora Jam. 3: 117. 1914), who refer to *C. longifolia* Fisch. ex Lindau. It would be noted, however, that Fawcett & Rendle literally compile a new description and concept for this species, combining as they do two species and one variety recognized by Lindau in one description. The correct citation for this species should probably be *Coccoloba longifolia* Fisch. ex Lindau emend. Fawcett & Rendle. Lindau recognized *C. venosa* which he attributes to Grisebach. It is based on a manuscript name in the herbarium at Göttingen. Two specimens are cited, *March 674* without locality and an Alexander Prior specimen without number from Moneague. However, *C. venosa* Griseb. ex Lind. is a later homonym for *C. venosa* L. Lindau also described a variety *major* for this species based on another Alexander Prior specimen without location or number. I have seen all three specimens cited in the Grisebach Herbarium at Göttingen. Lindau distinguished this species and its variety from his newly described "C. longifolia Fisch." as having an inflorescence rachis tomentellose, while *C. longifolia* had the rachis glabrous.

The typification of this species is as difficult as the definition. Lindau cites three specimens from Jamaica, *Cuming 49*, *Purdie* and *Wullschlagel 1389* and a specimen from a locality not indicated on the sheet and collected by "Sivart." This latter specimen according to Lindau is in the herbarium at Leningrad. Although Lindau twice refers to the "Sivart" specimen in his treatments of this species, it seems obvious that this is an error of transcription for "Swartz." One specimen in the herbarium at Stockholm referable to this species bears the annotation "Ind. Occ." and the name "Swartz" written in longhand in such a way that "Sivart" could be implied. Lindau saw this sheet, for it bears his annotation label with the printed date of 1889 and the reference to *Coccoloba longifolia* Fisch. I have seen three of the four specimens cited by Lindau in the first complete description of *C. longifolia*. However, not one of these specimens bears flowers as were described in the original publication of the name. The selection of a lectotype must be deferred until the specimen not seen (*Wullschlagel 1389*) can be located and even then it may be desirable to select a lectotype from a more modern collection.

Fawcett & Rendle broaden the concept of *Coccoloba longifolia* as described by Lindau to include the pubescent forms which Lindau treated as *C. venosa* Griseb. *Coccoloba venosa* var. *major*, the specimens cited by Fawcett & Rendle in the Flora of Jamaica are extremely diverse in the size and shape of the leaves and the amount of pubescence on the stem, ochreae and rachises. Likewise Fawcett & Rendle broaden the concept to allow for more than a single pedicel per node on the inflorescence axis, a character now recognized as sexual. However, since they did not include a discussion, I felt a field study of this species-complex was essential to clarify the differences in these treatments. Between 1950 and 1956 I have had the opportunity of studying *C. longifolia* plants in many parts of Jamaica on five separate trips to the island at different times of the year. Numerous collections were made and cited, but many field observations were not supported with voucher specimens of this relatively common species. I have studied an abundance of living specimens in St. Ann, St. Elizabeth and St. Catherine parishes from near the seacoast at Ocho Rios to altitudes of about 3,000 feet at Griermount. *Coccoloba longifolia* appears to be a weak tree reaching at most a height of 30 feet and occurring often with several erect trunks. The most common occurrence is in cut-over thickets or secondary woodlands. The branches show a tendency toward a scrambling habit. As is true in most species of *Coccoloba*, adventitious branches develop readily following injury and in the case of *C. longifolia*, any distortion of a branch from its normal attitude tends to incite the development of adventitious shoots with longer internodes and larger leaves, petioles and ochreae. As it occurs commonly in disturbed woodlands which are frequently cut for building poles and fire wood, the number of plants with larger leaves considered atypical is greater than the number of plants encountered with smaller and more pubescent leaves and considered as typical of the species. Collections from the more remote or undisturbed areas of the island of Jamaica tend to exhibit the smaller leaf size and the more abundant phases of pubescence. Thus, collections by Harris (*9462*) and Britton (*545*) from Tyre near Troy in the Cockpit Country, Harris (*12785*) from Peckham Woods and Prior (*s.n.*) from Moneague exhibit what Lindau considered as *C. venosa* Griseb. var. ***typica***. It is interesting that an older collection by A. S. Hitchcock (Dec. 17, 1890) from Bogwalk, an historic location, shows the same characteristics, but has never been re-collected in this area. Of the many living plants of this species seen along the gorge of the Rio Cobre below Bogwalk, all illustrate the more rampant growth form. I likewise revisited the Moneague area, particularly Union Hill, where Britton and Hollick (*2773*) in 1908 collected the same growth form of *C. longifolia* as did Prior. In the protected forested area I was able to find specimens which duplicated the earlier collections, but at the edge of clearings and in areas of regrowth the full range of variation was found, from small and pubescent leaves with short inflorescences to large and essentially glabrous leaves with long inflorescences. These variations were found on many occasions and often on one plant (*Howard 12029*, GH). The most striking contrast on one tree was found in the Claremont area of St. Ann, where specimens were made (*Howard 14191,* A) of a single tree which had one shoot showing normal growth form and many adventitious shoots from the base and from stumps of other branches, showing the full range of variation.

One can conclude from a careful field study that *C. longifolia* is a common species showing considerable variation in leaf size, shape, texture and venation pattern and in the length, thickness and pubescence of the inflorescence, as well as the length of the pedicels. Anomalous inflorescence axes are to be expected in this species, for field study showed elephantine development producing rachises which were longer than the leaf and which, on drying, were 5–7 mm. thick while on the same branch another inflorescence axis might be ¼ to ¾ the length of the leaves, but extremely thin and delicate. Several of the thicker inflorescence axes were branched at the apex, as in *Harris 9489*, indicating a teratological development.

Coccoloba rumicifolia described by Britton and based on a collection (*1592*) he made while collecting with Harris (*9837*) at Teague Gulley near New Market (published incorrectly as "Tea Gulley") represents the more fragile aspect of *C. longifolia*. The plants, described by Britton as three meters tall and growing on a wooded hillside, have membranaceous leaves as well as weak, short inflorescence axes with short pedicels. There is no doubt that this species should be referred to the synonymy of *C. longifolia*.

There remains some question as to why this species was in cultivation in the gardens and greenhouses of Europe in the early nineteenth century. Certainly the plant does not have the horticultural possibilities of *Coccoloba uvifera*, *C. rugosa* or *C. pubescens* which were in cultivation at the same time. The oldest horticultural herbarium specimen known to me is currently in the U.S. National Herbarium (*617174*). This specimen is labelled

"*Coccoloba longifolia* Hort. Angl." and "ex. hort. bot. berol. 1828", thus agreeing with the citation of Link's catalogue of 1821. The erroneous annotation "28 Cocc. caracasana Meisn." in an unidentified handwriting is also on the label. The specimen was sent from the Botanic Garden at Berlin to the Herbarium of the Bureau of Science in Manila and eventually was transferred to the U.S. National Herbarium. It is interesting to note that this specimen bears Lindau's annotation label of 1889. In the herbarium of the Berlin Botanical Garden there is another specimen apparently cultivated under the name of *Coccoloba barbadensis* which was growing in the garden at Berlin in May 1843. This specimen was annotated by Lindau as *C. longifolia*. There is also a specimen of *C. longifolia* in the Kew Herbarium bearing the information, "Hort. Kew 1857." Although Lindau annotated all of these sheets, he did not cite them in his monographic treatments of the genus. All three specimens represent the fast-growing aspect of the species with larger, thin leaves and long, slightly puberulent rachises. All are pistillate specimens, raising the question of how these early cultigens were propagated if they did not all come from the same seed lot. If the latter is true and these were all one seed collection, then further unanswered questions are raised regarding the inheritance of sex in these dioecious plants.

9. **Coccoloba diversifolia** Jacq. Enum. Pl. 19. 1760, Hist. Stirp. Amer. 114, *pl. 76*. 1763; Howard, Jour. Arnold Arb. **30**: 421. 1949.

Coccoloba laurifolia Lindau, Engl. Bot. Jahrb. **13**: 158. 1891, Urban, Symb. Antill. **1**: 227. 1901; Fawcett & Rendle, Flora Jam. **3**: 116. 1914 and all recent authors, not Jacquin.

Coccoloba longifolia Schmidt, Fedde Rep. Sp. Nov. **24**: 73. 1927, not Fischer.

Guaiabara laurifolia House, Am. Midl. Nat. **8**: 64. 1922 (as Guaibara).

Shrub or small tree to 7 m. tall; branches terete, often geniculate by limited growth, glabrous, the nodes rarely slightly tumid; ochreae coriaceous in the persistent lower portion, membranaceous and deciduous above, 3–5 mm. long; petioles 7–10 mm. long, glabrous; leaf blades ovate, oblong, elliptic, lanceolate or obovate, variable on a single shoot, the apex rounded, obtuse, acute or acuminate, the base cuneate to rounded or subcordate, 4 × 3.5, 7 × 5.5, 8× 4.5, 12 × 8 cm. long and wide, coriaceous, often shining above, dull beneath, glabrous, the 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, the margin entire, commonly slightly recurved; leaves of adventitious shoots similar in shape to those of normal growth but larger in size, 17 × 8, 24 × 13, 32 × 12.5 cm. long and wide on petioles 1–2.5 cm. long; leaves of windswept specimens often much smaller than those of normal shoots, 2 × 1.3, 3 × 2 cm. long and wide; inflorescence terminal 4.9, 9, 11 to 18 cm. long; rachis glabrous; staminate flowers in clusters of 2–5, the pistillate flowers solitary; bracts ovate, less than 0.5 mm. long, 1 mm. broad, glabrous; ochreolae membranaceous, less than 0.5 mm. long, glabrous, the flowering pedicels 2–4 mm. long, glabrous; hypanthium 1 mm. long, the perianth lobes 2 × 2, to 3 × 1 mm. long and broad, filaments of functional stamens 1 mm. long, fruiting pedicels 3–4.5 mm. long; fruit globose to obpyriform 10 × 7, 12 × 8, 13 × 8 cm. long and thick, perianth lobes appressed at the apex of the achene.

DISTRIBUTION: Florida and the Bahamas, through the West Indies to South America.

Clarendon: Portland Ridge, *Howard 12004* (GH). **St. Andrew:** Gordon Town, *Harris 6032* (F, NY, US). **St. Elizabeth:** Pepper, *G.S. Miller 1354* (US), *1365* (US); Malvern, *Howard & Proctor 13689* (A, IJ), *13724* (A, IJ); Gutters, *Howard & Proctor 13821* (A, IJ). **St. Thomas:** Sheldon, *Harris 5093* (US).

Collected in flower in July and in fruit in February and November. This species, particularly abundant in the Bahamas, Cuba and Hispaniola, is of infrequent occurrence in Jamaica. It is apparently limited to the south coast and specimens were not abundant in the one region, Portland Ridge, where I have collected it. The plant was not known to others of our party and no common name was offered by the residents of the area.

10. **Coccoloba zebra** Griseb., Fl. Brit. W.I. 162. 1859; Lindau, Engl. Bot. Jahrb. **13**: 135. 1890, Symb. Antill. **1**: 220. 1899; Fawcett & Rendle, Flora Jam. **3**: 113. 1914.

Coccoloba harrisii Lindau, Urb. Symb. Antill. **1**: 228. 1899; Fawcett & Rendle, Flora Jam. **3**: 117. 1914.
Coccoloba priorii Fawcett & Rendle, Jour. Bot. **51**: 124. 1913, Flora Jam. **3**: 120. 1914.

Tree to 30 feet tall; branches terete, slender, glabrous; ochreae subcoriaceous, persistent, slender and cylindrical but flaring and oblique at the apex, 8–14 mm. long, glabrous; petiole attached at the base of the ochreae, slender, 11–14 mm. long on normal shoots, glabrous; leaf blades elliptic to elliptic-ovate, 7 × 4, 8 × 6, 10 × 7 cm. long and broad, coriaceous, glabrous, flat, dull turning black on drying, the midrib and primary veins flat above, prominent below, the veins 5–7 pairs, arcuate, anastomosing, the secondary venation densely reticulate, the apex short acuminate, the base rounded to truncate; leaves of adventitious shoots similar in shape, 15 × 9 cm. long and broad on petioles to 2.4 cm. long; inflorescence terminal 5–14 cm. long, the ochreae of rachis flaring, 8 mm. long, puberulent, the rachis puberulent; bracts and ochreolae less than 0.5 mm. long, glabrous or puberulent, the pedicels 1.5–2.5 mm. long, puberulent, the pistillate flowers borne singly, the perianth puberulent, the hypanthium 1.5 mm. long, the perianth lobes 1.5 mm. long and broad, the stamens rudimentary, the pistil 1.5 mm. long; staminate flowers not known; fruiting pedicels 3–4 mm. long; fruit fusiform, 17 mm. long, 8 mm. in diameter; perianth fibrous; achene dark brown.

DISTRIBUTION: Endemic to Jamaica.

St. Ann: Union Hill near Moneague, *Prior 338* (K, TYPE of *C. priorii*, B). **Manchester:** below St. Georges, *Watt s.n.* (NY). **Portland:** 2.5 mi. SW of Ecclesdown, *Howard, Proctor & Stearn 14754* (A); *Webster & Wilson 5133* (A); *Proctor 11371* (IJ); Vinegar Hill, *Harris 5481* (C, BM, TYPE of *C. harrisii*), *7667* (B, BM, F, NY, US). Parish not certain: Blue Mts., *Harris 5089* (B, BM). Locality not certain: *Wilson 168* (Gott. TYPE of *C. zebra*, B, K); *March 679* (Gott.)

COMMON NAME: Zebra wood (ex Grisebach). Collected in flower in July and September. Fruiting date not known. The type specimen of *Coccoloba zebra* is a fruiting branch of a vigorous shoot. The internodes are long and the leaves larger than in the other collections cited. The type specimens of *C. harrisii* and *C. priorii* are shoots of normal growth. It is clear to me that these collections represent one taxon and that *C. zebra*, being the older name, must be used. Lindau distinguished *C. harrisii* from *C. zebra* primarily on the assumption that *C. harrisii* had a glabrous rachis. I have seen all the material Lindau cited and annotated and conclude he was in error on this point.

Fawcett & Rendle do not discuss their new species *C. priorii* in the original description, but in the Flora of Jamaica they distinguish it from *C. harrisii* as having "veins on the upper surface only seen with a lens when dry" while *C. harrisii* has "veins on the upper surface evident." These two species form a section of the key headed "leaves small, not exceeding 8 cm." while *C. zebra* is distinguishable from this section by having "leaves large, exceeding 8 cm." These are not reliable characters.

The specimens cited from the crest of the John Crow Mountains near Ecclesdown represent an extension of the range of the species and unfortunately are sterile. However, the vigorous and normal growth aspects of these bridge the variation expressed in the earlier collections. *Coccoloba zebra* is not adequately known and additional material is needed. Only one fruiting specimen is known and this consists of very old fruit. The fruits are all detached and are in a pocket on the sheet. If the fruits belong with the vegetative parts, the shape of the fruit is an additional diagnostic character for the species. Staminate plants or flowers with functional anthers have not been seen. The specimens recently collected are the only modern collections and as this location is known to botanists in Jamaica, it is hoped that the additional characters can soon be added to this description.

HYBRIDS AND SPECIES EXCLUDED FROM THE FLORA OF JAMAICA

Coccoloba × jamaicensis Lindau (stat. nov.) Engler Bot. Jahrb. **13**: 206. 1890, Symb. Antill. **1**: 232. 1899.

Coccoloba litoralis Urban, Symb. Antill. **6**: 9. 1909; Fawcett & Rendle, Flora Jam. **3**: 117. 1914.

Coccoloba leoganensis Griseb. ex Lindau Engl. Bot. Jahrb. **13:** 206. 1890, not Jacquin.

Tree to 13 m. tall; branches terete glabrous, the nodes not conspicuously enlarged; ochreae subcoriaceous, glabrous or with minute puberulence, persistent, the apex oblique, 6–9 mm. long; petiole inserted above the base, stout, 1.5 cm. long, glabrous or minutely puberulent; leaf blades broadly orbicular-ovate, 7 × 6, 11 × 9, 15 × 11, 16 × 12 cm. long and broad, the apex acute or rounded and slightly mucronate; the base rounded to cordate, thin coriaceous, glabrous, sunken glands sparsely distributed above, dense below, these black when dry, the midrib and primary veins prominent on both surfaces, primary veins 5–6 pairs, arcuate, anastomosing, ultimate venation minutely and densely reticulate; margin undulate to entire and flat; inflorescence terminal, solitary or with reduced inflorescence at the base, 12, 18, 35 cm. long, the axis puberulent, the bracts ovate above, 1 mm. long, the ochreolae 1 mm. long, both puberulent, the pedicels 1–1.1 mm. long in flowering condition; staminate flowers 2–4 per node, the pistillate flowers solitary, the hypanthium 1–1.5 mm. long, the perianth lobes 1.5–2 mm. long and broad, the fertile stamens 1.5 mm. long; fruits immature and abortive, stalked and similar in size and shape to those of *C. uvifera.*

DISTRIBUTION: Endemic to Jamaica.

St. Catherine: Great Salt Pond, *C. B. Lewis s.n.* (IJ 3231). **St. Elizabeth:** Slipe district, 2–4 mi. SW of Lacovia, *Howard & Proctor 14509* (A), *14512* (A); 1.5 mi. N of Fullerwood in Black River Swamp, *Howard & Proctor 14508* (A). **Westmoreland:** Negril, *Harris 10228* (B, TYPE of *C. litoralis*, BM, F, N.Y. US), *Britton & Hollick 2057* (NY). Locality uncertain: *March s.n.* (Gott., TYPE, B, GH).

Unfortunately considerable shifting and re-sorting of names is required to establish the correct epithet for this taxon which is now recognized as a hybrid. *Coccoloba jamaicensis* was described by Lindau and one collection, March without number, was cited. Lindau saw two specimens, one in the Grisebach Herbarium at Göttingen and the other in the Krug & Urban herbarium in Berlin. Both of these collections are fragmentary, with the specimen in the Krug & Urban herbarium consisting of one leaf and two pencil tracings. A third specimen of this collection has been found in the Gray Herbarium and is more complete and in better condition than either of the others. After careful comparison of these three collections, I have no doubt of their origin from the same plant. They represent a flowering branch with relatively young leaves.

In his original monograph of the genus *Coccoloba* Lindau was unable to identify *C. tenuifolia* L. and listed this species in a category of uncertainty at the end of his publication. He did describe *C. jamaicensis* and *C. leptostachyoides*, the latter based on a numbered March collection from Jamaica. In a treatment of *Coccoloba* in the West Indies published in 1899 in Symbolae Antillanae, Lindau concluded that his species *C. leptostachyoides* was the same as his *C. jamaicensis* and listed the former in synonymy. Fawcett & Rendle, in studying the Linnaean species of *Coccoloba* from Jamaica, recognized that *C. tenuifolia* L. "is the species which has been recently described by Lindau as *C. jamaicensis* in Engl. Bot. Jahrb. xiii. 206. 1890." This is the treatment which Fawcett & Rendle published in the Flora of Jamaica and which I followed in a treatment of the genus *Coccoloba* in Cuba (Jour. Arnold Arb. **30**: 407. 1949). After having studied the March collection which is the type of *Coccoloba jamaicensis* and having compared it with the March collection *1989*, the type of *C. leptostachyoides*, and the Browne collection in the Linnaean Herbarium, the type of *C. tenuifolia* L., I find it necessary to agree with Lindau that two taxa are represented in the two March collections. *Coccoloba tenuifolia* L. is the same as *C. leptostachyoides* Lindau. *Coccoloba jamaicensis* Lindau, however, based on the March collections cited, is different from *C. tenuifolia* L., but is the same as the material currently recognized as *C. litoralis* Urban.

Coccoloba litoralis as described by Urban was based on specimens collected by Harris at Negril. Harris reported the plant as a tree of 40 feet growing near the rocky seacoast among coconut plantings. Urban's observations compared this new species with *C. polystachya* of South America, *C. laurifolia* Jacq. and *C. verruculosa* of Hispaniola. It is clear after examining the specimens which Urban had for study in Berlin and additional specimens in the field that *C. litoralis* is a hybrid between *C. uvifera*, the common sea grape, and *C. tenuifolia* of the dry coastal areas of Jamaica.

The specimen by Britton & Hollick was collected on the same area, Negril, from the same size tree and in the same condition, during the same period. It is suspected that Britton & Hollick were with Harris on this day and that their collection is from the same tree as the Harris specimen, the type of *C. litoralis*.

In July of 1955 Mr. George Proctor and I had opportunity of collecting in the Black River Swamp area of southern St. Elizabeth parish. Where the one road crosses the Broad River there was a well developed stand of *C. uvifera* of characteristic appearance and scattered among them were trees noticeably different to one familiar with the sea grape. Five or six of these trees were seen, the largest being 25 feet tall. All had the general sprawling habit of the sea grape, but differed in having generally smaller and thinner leaves much more green in color. The inflorescences of these plants were long and tenuous and generally weak and drooping. Both staminate and pistillate plants were seen in flower, but all fruits were either abortive or immature. In fact, the largest fruits seen were on staminate inflorescences and all of these fruits were hollow and obviously sterile. One collection in the herbarium of the Arnold Arboretum (*Howard & Proctor 14509*) was deliberately prepared to show the variation possible on one tree. The branches were selected and mounted to show specimens that looked as much like *C. tenuifolia* and as much like *C. uvifera* as possible. In fact, the specimen cited would key out to *C. tenuifolia* or *C. uvifera* in the key given, but would look unlike the species. Most of the plants possessed conspicuous adventitious shoots and these and their leaves were thinner in aspect than is typical for *C. uvifera.* Closer study of the herbarium specimens prepared indicates that these specimens are identical with those named *C. litoralis* by Urban. It is clear from field observation of the living plants and from study of the specimens prepared that *C. litoralis* is a hybrid between *C. uvifera* and *C. tenuifolia* and that the correct name for this taxon is *C.* × *jamaicensis* Lind. No specimens of *C. tenuifolia* have been collected from the immediate vicinity of the plants seen in the Black River swamp, although this species was observed about 4 miles away on dry hummocks in the same swamp.

Several populations of hybrids involving *C. uvifera* as one parent are known from the Antilles. In all cases the characteristics of *C. uvifera* dominate those of the other parent in appearance, both of the plant, the habit and the leaves. The inflorescence character, as is the case in *C. litoralis,* is that of the other parent. The fruit in all of the hybrids observed have been sterile, but the specimens seen in the field are relatively numerous. It appears that *C. uvifera* is receptive to cross pollination from other species of *Coccoloba,* but there is some genetic disturbance preventing the formation of fertile fruits and viable embryos.

COCCOLOBA PYRIFOLIA Desf., Fawcett & Rendle, Flora Jam. **3**: 114. 1914 (as *C. pirifolia*).

Lindau (Symb. Antill. 1: 222. 1899) refers a Wilson specimen from Jamaica to this species. No locality is known for this specimen. Fawcett & Rendle cite two specimens from the Great Valley in the parish of Manchester collected by Purdie and by Wilson. I cannot determine whether Lindau and Fawcett & Rendle refer to the same Wilson collection. Both George Proctor of the Institute of Jamaica and I have searched and collected extensively in this area and have found only *Coccoloba krugii* in the region. After the publication of the treatment of the genus *Coccoloba* in the Flora of Jamaica, Harris collected additional material which has been referred to *C. pyrifolia.* All such specimens that I have seen from Jamaica I believe to be identified incorrectly and should be referred to *C. krugii.* It seems probable that the Purdie and Wilson collections may also prove to be from adventitious shoots of *C. krugii.* At the present time *Coccoloba pyrifolia* is not known from Jamaica.

COCCOLOBA PUBESCENS L., Fawcett & Rendle, Jour. Bot. **51**: 123. 1913, Flora Jam. **3**: 118. 1914.

This is a common species of eastern Hispaniola, Puerto Rico and islands of the Lesser Antilles. There are no modern records of this plant from Jamaica. Fawcett & Rendle reported seeing a Wright specimen which I was not able to locate at the British Museum. They also emphasize the fact that Patrick Browne reported this species as common between Kingston and Bull Bay. Browne commented that the plants were of low size, seldom rising above 5 or 6 feet. The area between Kingston and Bull Bay, while populated and subject to heavy traffic, has not been drastically altered by man for cultivation because of the extreme dry conditions prevalent. *Coccoloba pubescens* in adventitious growth is not one of the better woods and it is difficult to believe that the species, if it occurred there, could have been exterminated either by cultivation or by use. I feel that there is an error in ascribing *C. pubescens* to the flora of Jamaica.

COCCOLOBA VENOSA L., Fawcett & Rendle, Jour. Bot. **51**: 123. 1913, Flora Jam. 3: 120. 1914.

It is acknowledged in the Flora of Jamaica that no specimens of this plant have been reported from Jamaica since the time of Browne and Swartz. The Browne diagnosis, based on a Plukenet description and drawing, is the basis of this report, as well as a great deal of confusion in the genus *Coccoloba*. The Plukenet material, preserved in the Sloane Herbarium at the British Museum, is the same as *C. nivea* Jacq. and *C. venosa* L. A fruit cluster illustrated by Plukenet is the basis for the epithet "punctata" later applied to the species by Linnaeus. (This was used by Lindau in Symbolae Antill. 1: 228. 1899.) The fruit does not belong with the foliage, is not that of *Coccoloba* and has not been preserved with the leaves. I have not found material in the Swartz herbarium which could be attributed to Jamaica and I believe the ancient report of this species from Jamaica, unsupported by more recent collections, is in error and that *Coccoloba venosa* L. should be deleted from the list of species found in Jamaica.

COCCOLOBA NIGRA, Fawcett & Rendle, Jour. Bot. **51**: 124. 1913; Flora Jam. 3: 121. 1914.

The type of this species is in the herbarium at the Royal Botanic Garden, Edinburgh and, as reported by Fawcett & Rendle, bears only the annotation "Jamaica" without the collector's name or other data. I have examined this specimen and conclude that it did not come from Jamaica. In fact, it appears certain to be part of a collection by Schomburgk (*531*) collected in the Guianas in 1838, which is the type collection of *Coccoloba ovata* Benth. The Schomburgk collection is also represented in the Edinburgh herbarium and the type of *Coccoloba nigra* appears to match the Schomburgk material even to the foliose lichens on the stem. This species should not be recognized from Jamaica.

COCCOLOBA EXCORIATA L., Fawcett & Rendle, Jour. Bot. **51**: 123. 1913, Flora Jam. 3: 121. 1914.

This species is referable to *Coccoloba tenuifolia* L. and is discussed under the latter species.

COCCOLOBA RUMICIFOLIA Britton, Bull. Torrey Bot. Club **42**: 514. 1915.

This is the only species attributed to Jamaica described since the publication of the Flora of Jamaica and this I refer to synonymy and discussion under *C. longifolia* Fisch. ex Lindau.

THE NODAL ANATOMY AND THE PRIMARY VASCULAR CYLINDER OF THE CALYCANTHACEAE

ABRAHAM FAHN AND I. W. BAILEY

With two plates

THE VASCULAR ANATOMY of the Calycanthaceae has long been known to be of a peculiar character, owing to the presence in the internodes of most stems of four [1] inverted "cortical" vascular bundles. These bundles [2] which first appear in the epicotyl of the seedling extend throughout the stems of mature plants and have branches which enter the opposite leaves at the nodes.

In the past, investigators in studying the anatomy of the stem have focused their attention largely upon the structure and behavior of the aberrant cortical bundles.[3] Less attention has been given to tracing the course of the strands in the normal part of the eustele. There is evidence in some dicotyledons which may be interpreted as indicating the derivation of cortical bundles by modification of the lateral traces of plants having trilacunar or multilacunar nodes. It is important in studying the relationships of the Calycanthaceae to determine whether the cortical bundles of the family have evolved in this way or have developed by the addition of a superimposed system of vasculature in plants having fundamentally unilacunar nodal structure. In this connection we have made a detailed investigation of the primary vascular cylinder of the Calycanthaceae which we report in the following pages.

MATERIAL AND METHODS

Material of both *Calycanthus* and *Chimonanthus* was examined. Branches of *Calycanthus fertilis* Walt. (*C. glaucus* Willd.), Arnold Arboretum 12946, *C. fertilis* Walt. var. *laevigata* (Willd.) Bean (*C. fertilis* var. *ferax* (Michx.) Rehd.) A. A. 13400, *C. floridus* L., A. A. 5255 and *C. floridus* L. var. *ovatus* (Ait.) D.C., A. A. 1542 were obtained from shrubs growing at the Arnold Arboretum. Branches of *Chimonanthus praecox* (L.) Link. (*C. fragrans* Lindl.) were secured from the garden of Dr. H. L. Blomquist, Durham, N. C.

The youngest parts of the growing shoots — the vascular system of which consisted of primary tissue only — were cleared by heating in lactic acid, and were examined, after removal of the hairy epidermis, while

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[1] Baillon (3) refers to the occurrence of five such bundles in a specimen of *Chimonanthus fragrans* (= **C. praecox**). This rapidly elongating specimen had a 2/5, instead of the usual decussate, phyllotaxis.

[2] Van Tieghem (13) claimed that they develop in the pericyclic tissue of *Chimonanthus*.

[3] In this connection see Baillon (3), Boureau (4), Lignier (6), Quinlan (10), Tieghem (13), Woronin (14) and Worsdell (15).

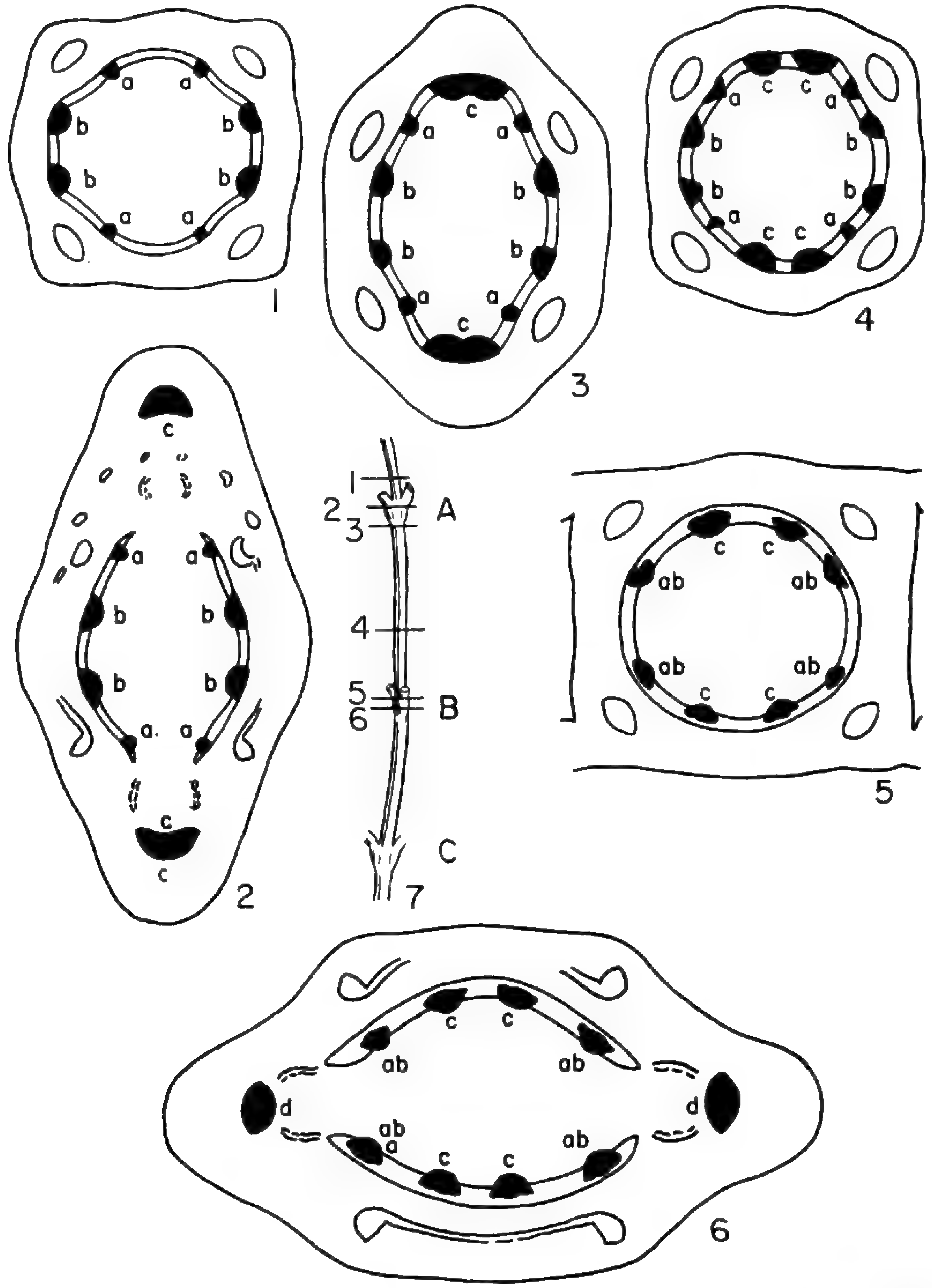
preserved in the acid. In some cases, it was necessary to treat the cleared material for about 20 minutes with a 10% solution of sodium hydroxide in order to remove crystals which appeared after clearing with lactic acid. In addition, the terminal parts of growing stems were embedded in paraffin and serially sectioned through 3–4 nodes from the apex downward. These serial transverse sections were stained with safranin and fast green. Parts of branches having secondary vascular tissues were serially cross-sectioned through three nodes. The sections were made from living stems with a sliding microtome without embedding. They were arranged serially on slides in glycerine mounts.

OBSERVATIONS

The primary vascular pattern in the stems of the species examined was found to be basically the same in both genera of the Calycanthaceae. The chief differences observed were in the levels of "branching" and "fusing" of the vascular bundles of the eustele. In both genera, it was possible to follow successive stages in the "fusing" of pairs of leaf traces during the development of the unilacunar nodes and during the elongation of the internodes.

In the terminal parts of cleared growing shoots, *Plate I, A & B*, the developing leaf traces reveal no appearance of approximation or fusing below the levels of attachment of the leaves. In serial cross sections of such immature parts of the stems, there are two discrete strands of xylem and phloem. No procambial tissue could be detected between them, indicating that two independent strands of procambium develop at an early stage. At lower, more laterally expanded levels of the shoot, *Plate I, B*, approximation of the vascular strands of each foliar pair is attained by the downward extension of additional longitudinal files of tracheary cells. This appearance of ontogenetic fusing is obvious in comparing successively formed pairs of leaf traces in the same orthostichy of the decussate phyllotaxis. Each trace of a foliar pair also fuses with a trace of another leaf, approximately two nodes below the level of the leaf which it vascularizes, *Plate I, B*.

In serial cross sections of older parts of the stem, the existence of a similar pattern of primary vasculature may be traced. For example in cross sections of *Calycanthus fertilis* var. *laevigatus*, *Fig. 7*, there are eight primary bundles in the eustele just above the level of node A, *Fig. 1*; two pairs of traces labeled (a) and two pairs marked (b). At the nodal level of A, there are two additional large vascular strands (c) located opposite two conspicuous gaps in the eustele, *Fig. 2*. Just below the nodal level of A, these strands (c) form integral parts of the eustele, *Fig. 3*, which now consists of 10 traces. Lower in the internode the inherent doubleness of strands (c) becomes increasingly apparent, *Fig. 4*, and there are 12 well separated traces. At the base of the internode, *Fig. 5*, the number of discrete strands is reduced to eight by the approximation or "fusion" of four pairs of the (a) and (b) strands. At node B, *Fig.* 6, the arrangement



FIGURES 1–6. Cross sections of the mature part of a shoot of *Calycanthus fertilis* var. *laevigatus*, cut at the successive levels shown in FIGURE 7. The primary xylem of the eustele and the median vascular strand of the leaf-base are shown in solid black. The cortical bundles, the vascular strands of the buds and the secondary xylem are merely outlined.

described at node A recurs except that the axis of the leaf gaps is now at right angles to that at node A.

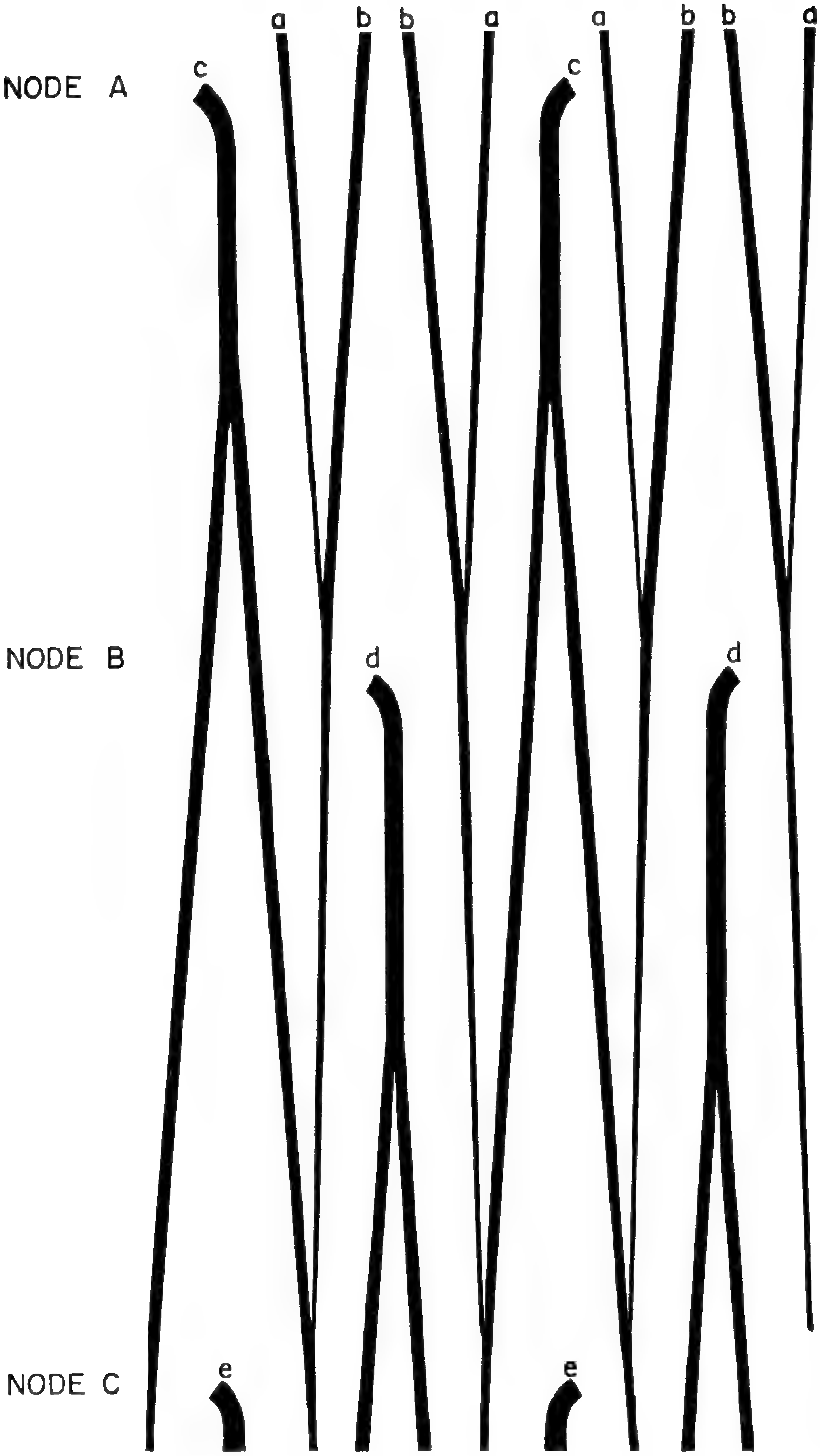


FIGURE 8. Diagrammatic reconstruction of the longitudinal course of the vascular strands of the eustele in *Calycanthus fertilis* var. *laevigatus*.

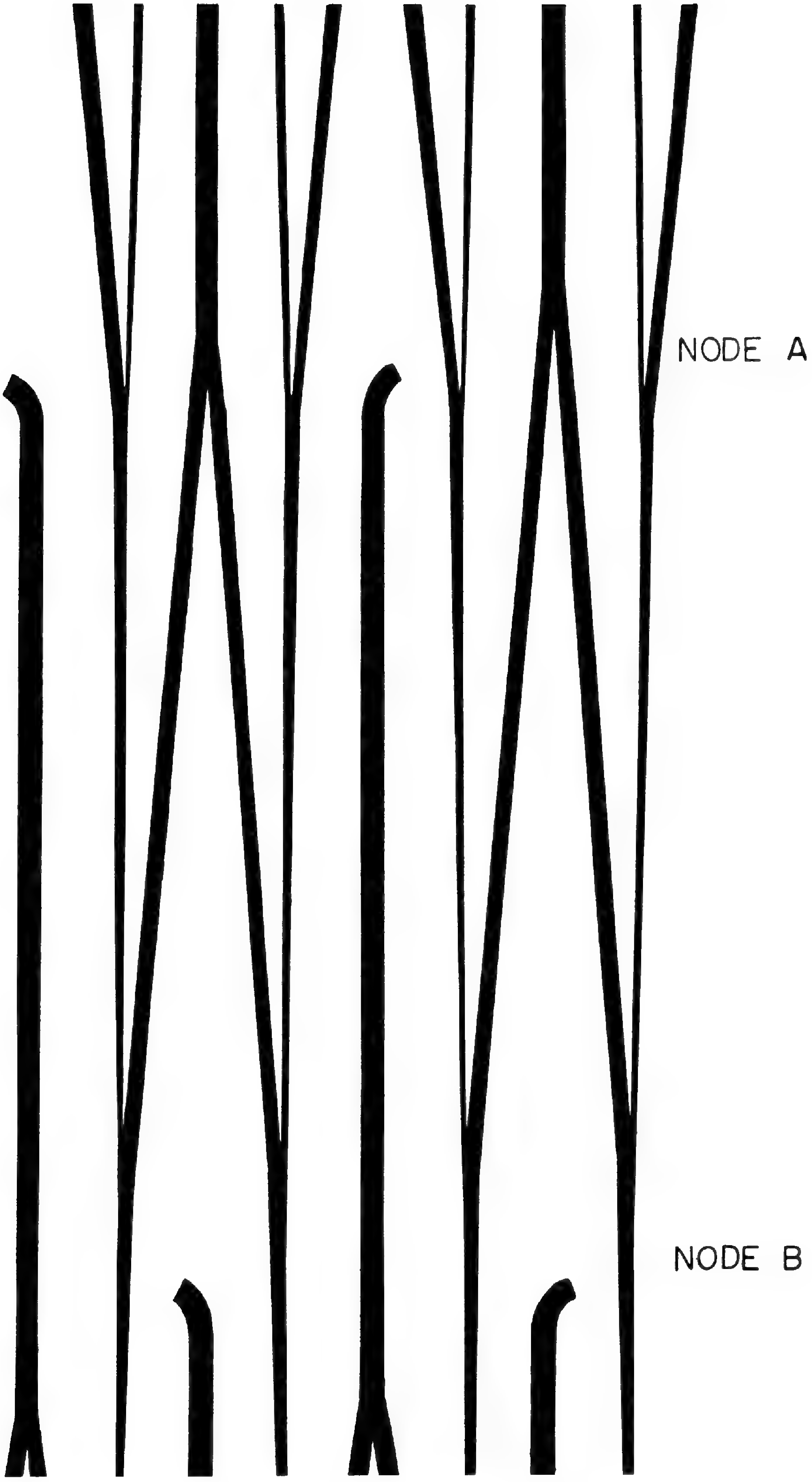


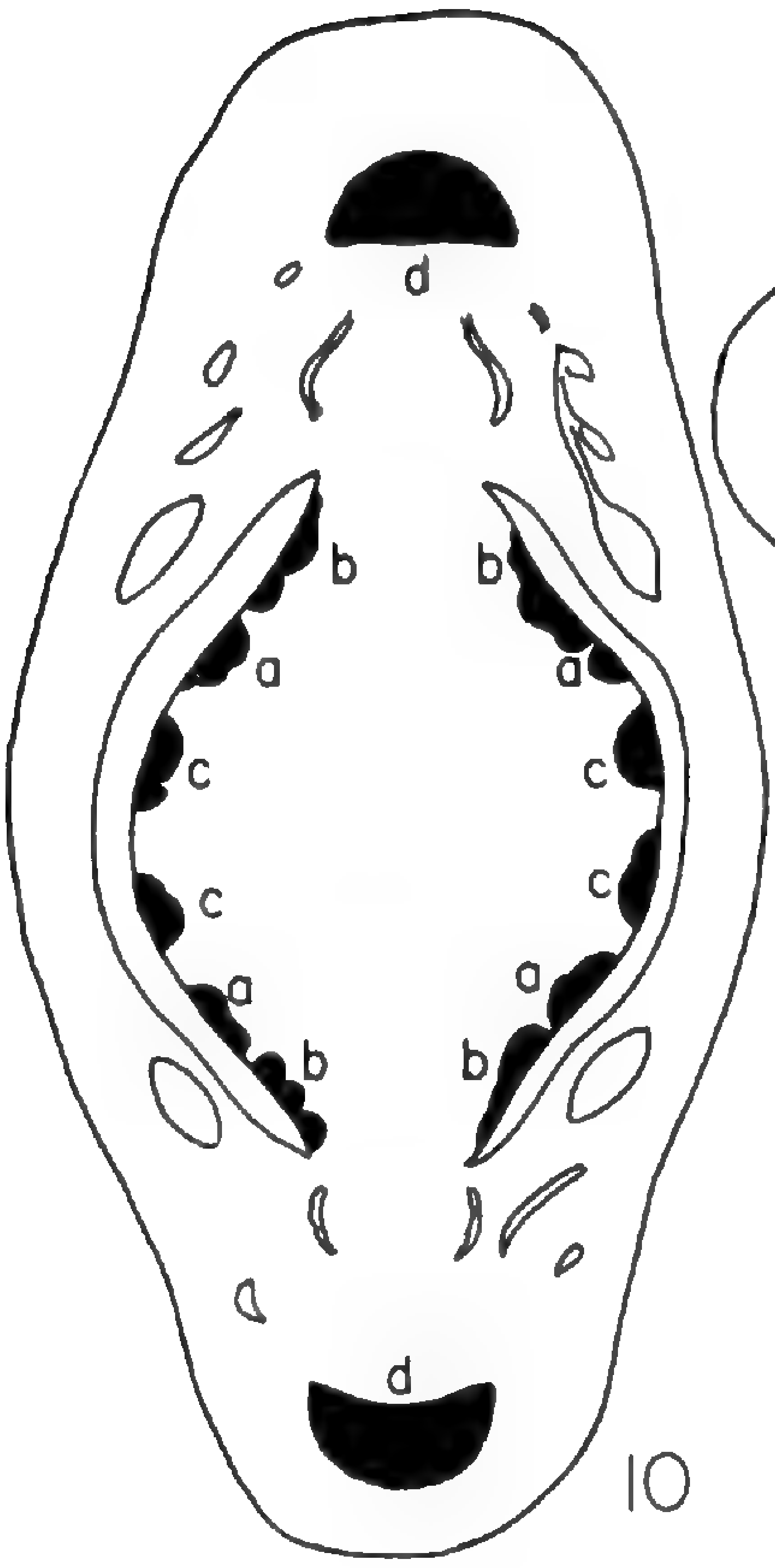
FIGURE 9. Diagrammatic reconstruction of the longitudinal course of the vascular strands of the eustele in *Calycanthus floridus* var. *ovatus*.

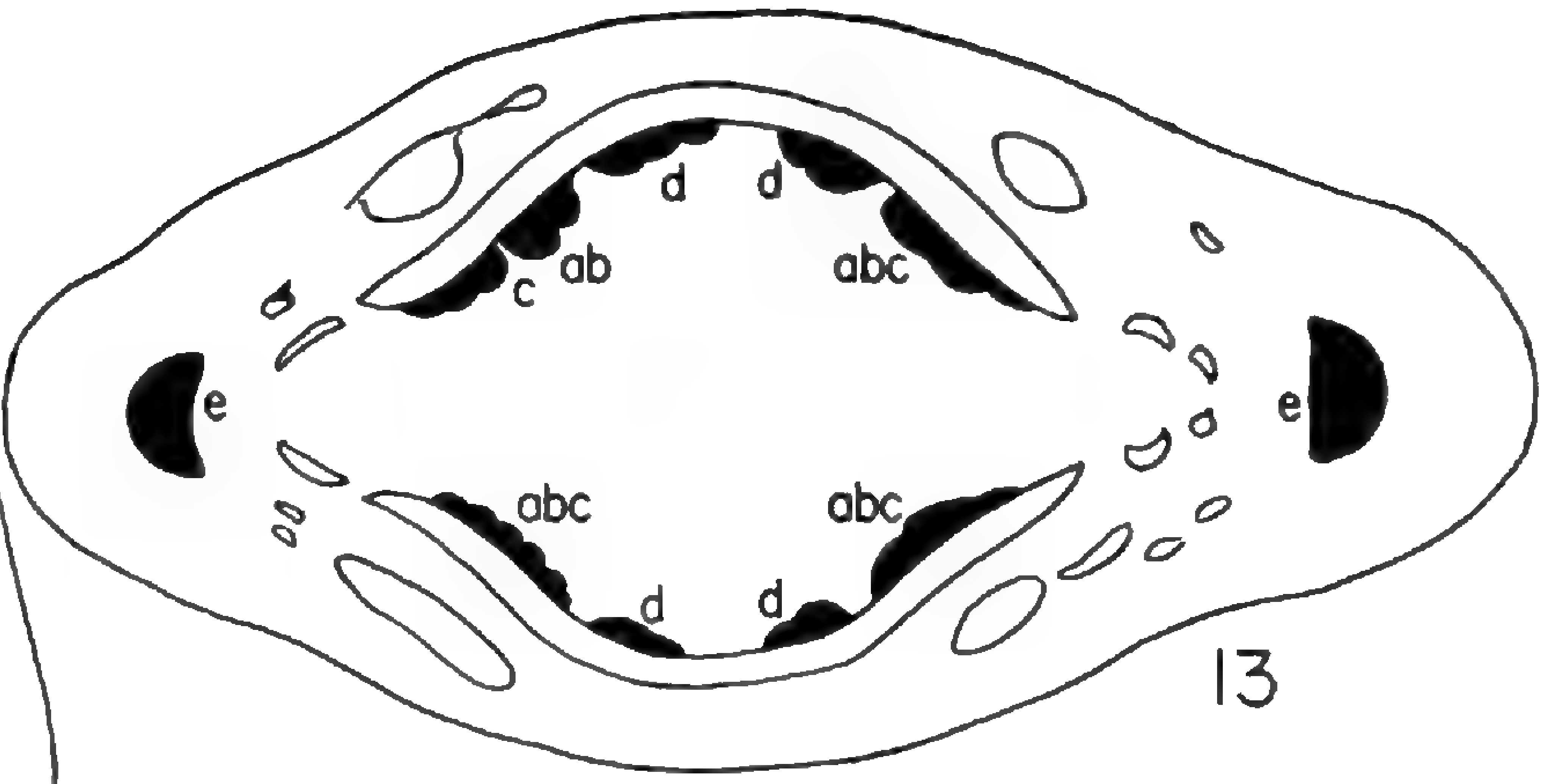
The longitudinal course of the leaf traces in the mature stem may be reconstructed from serial cross sections, and is diagrammatically shown in *Fig. 8.* The pattern is in agreement with ontogenetic evidence obtained from the elongating, immature, terminal parts of the axis, *Plate I, B.*

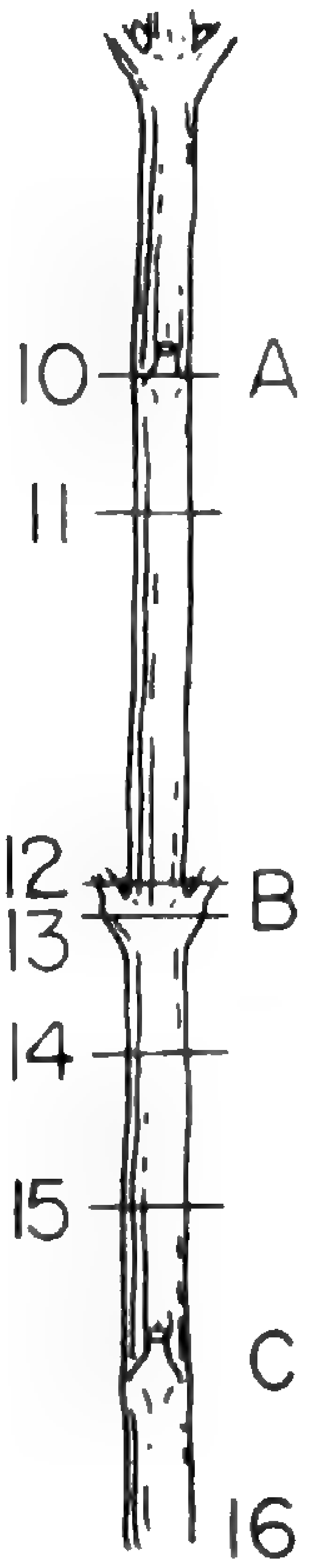
In fully matured stems, the paired leaf traces commonly approximate or apparently "fuse" in the middle part of the first subtending internode below the level of attachment of a leaf. In early ontogenetic stages, the fusing of the two principal foliar strands, as previously mentioned, occurs only within the leaf itself, *Plate I, B.*

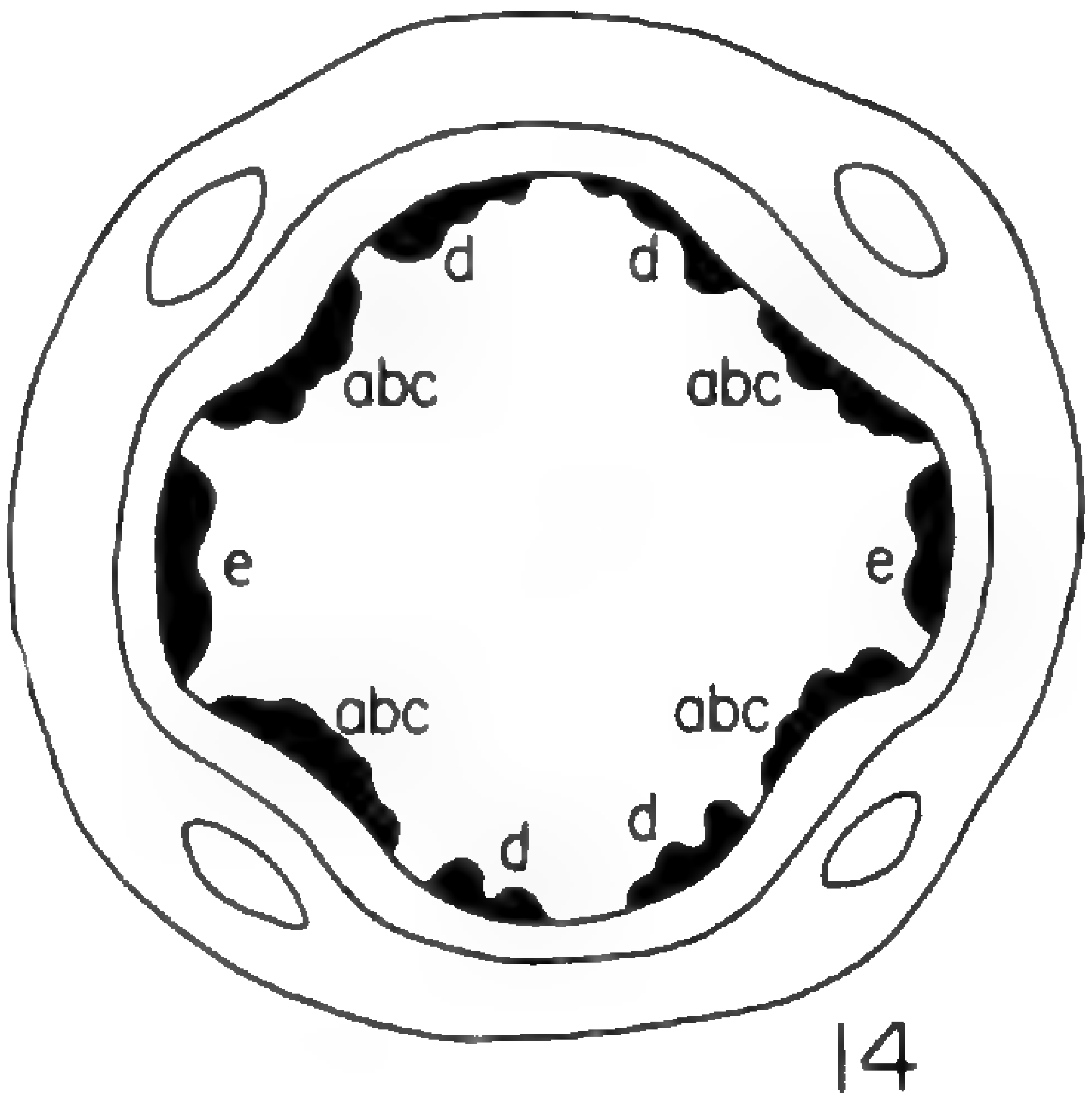
As in the case of *Austrobaileya*, *Trimenia*, *Ascarina* and other plants having fundamentally double-trace unilacunar nodes, there is considerable individual and interspecific variation in the levels at which fusing of the two leaf traces occurs and in the levels at which these traces join the traces of other leaves, compare *Figs. 8 and 9.* Thus, the number of discrete strands visible in cross sections of mature stems varies at times even at corresponding levels. For example, as shown in *Fig. 8*, there commonly are in stems of *Calycanthus fertilis* eight bundles in cross sections cut immediately above the node, twelve bundles at a slightly higher level and ten strands in the upper part of the internode. In branches of *Calycanthus floridus* and in some stems of *C. fertilis*, the number of vascular strands differ from this at corresponding levels. For instance, in *Fig. 9*, there are only six bundles immediately above node B and eight strands immediately below it. In some stems there may be as many as fourteen discrete strands at certain levels. In this connection, it is desirable to consider the effects of variations in internodal elongation.

In branches of *Chimonanthus praecox*, obtained through the courtesy of Dr. Blomquist, the primary vascular bundles, as seen in transverse sections, are relatively broad and the interfascicular spaces of the eustele are comparatively very narrow. This feature develops very early in the ontogeny of the axis, *Plate II, B.* It makes it difficult at times to follow the course of individual traces during later stages of the maturation of the stem. However, careful analysis of serial cross sections makes it possible to reconstruct the following pattern. At node A, *Fig. 10*, there are twelve bundles and two large detached strands opposite the two conspicuous gaps in the eustele. Somewhat below the node there are eleven or ten strands, *Fig. 11*, due to the inclusion of the two (d) traces and the fusion of three or four pairs of (a) and (b). In some cases the (a) and (b) strands fuse at a lower level and there are fourteen bundles at this level. At a lower level the number of bundles is commonly twelve due to separation of the (d) strands into their constituent halves and the fusion of all four pairs of (a) and (b) strands, *Fig. 12.* At nodes B and C, the fusing of the bundles (ab) and (c) occurs above the nodal level. The total number of bundles at these levels was therefore eight only, *Figs. 13 & 17.*









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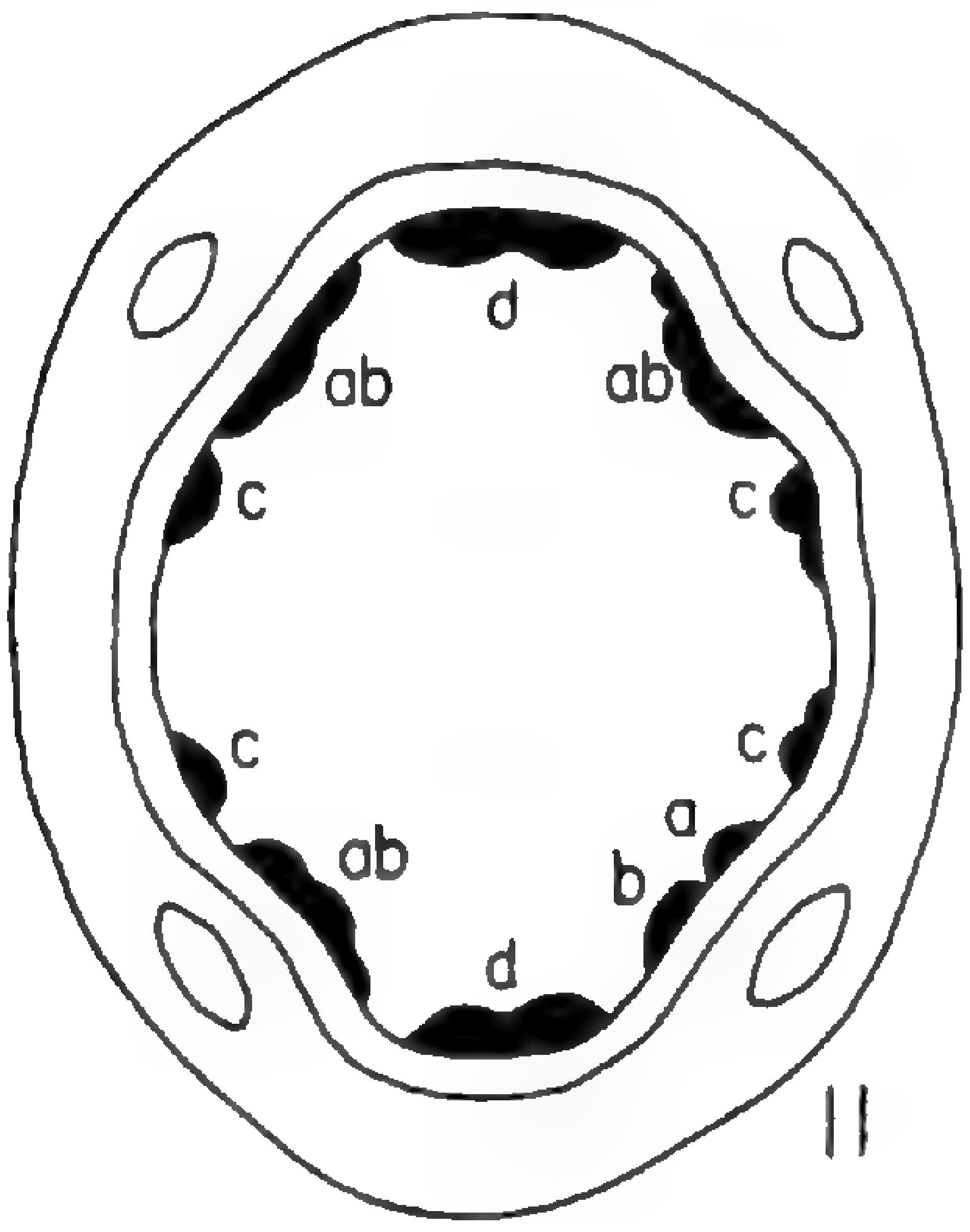

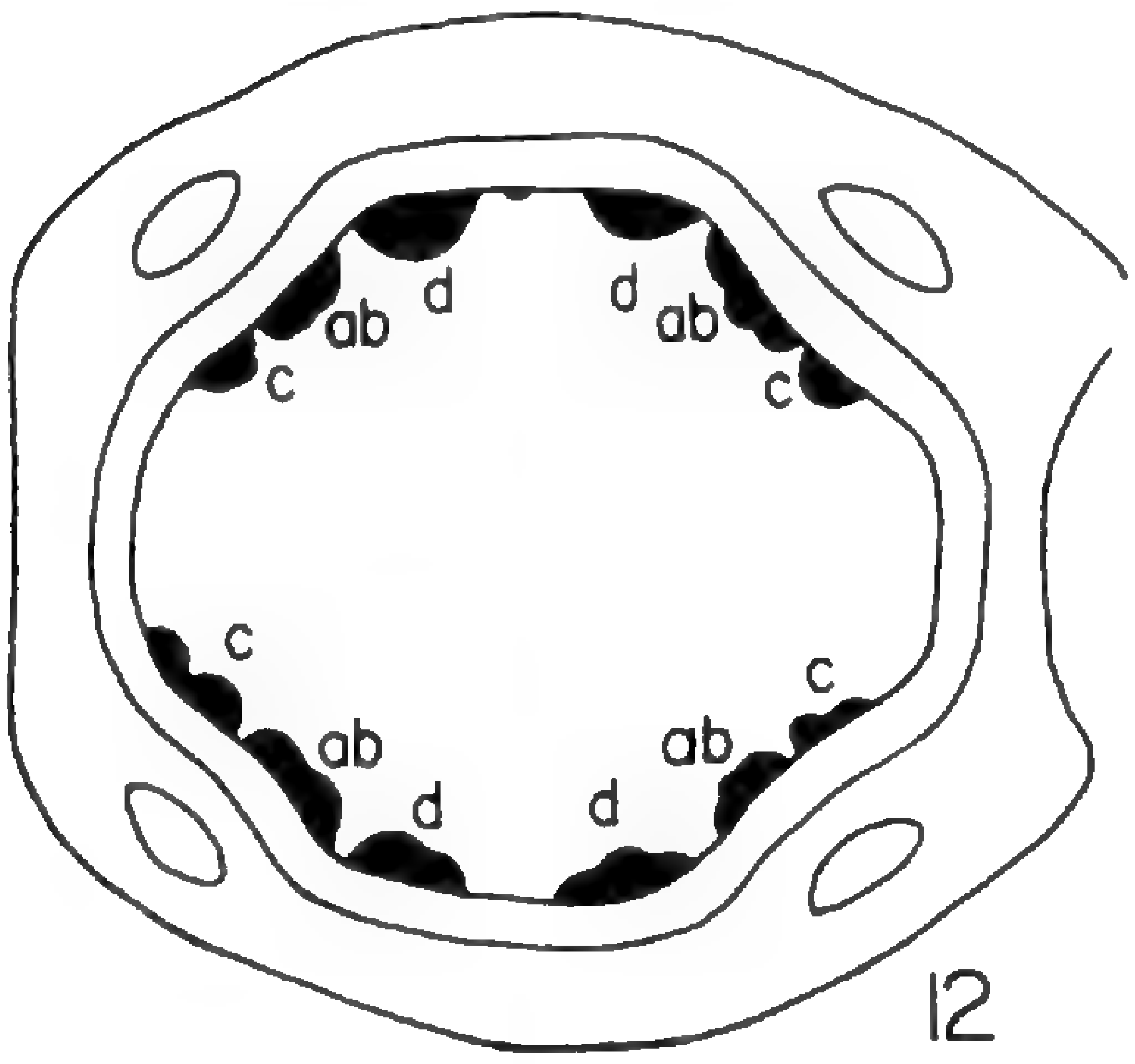

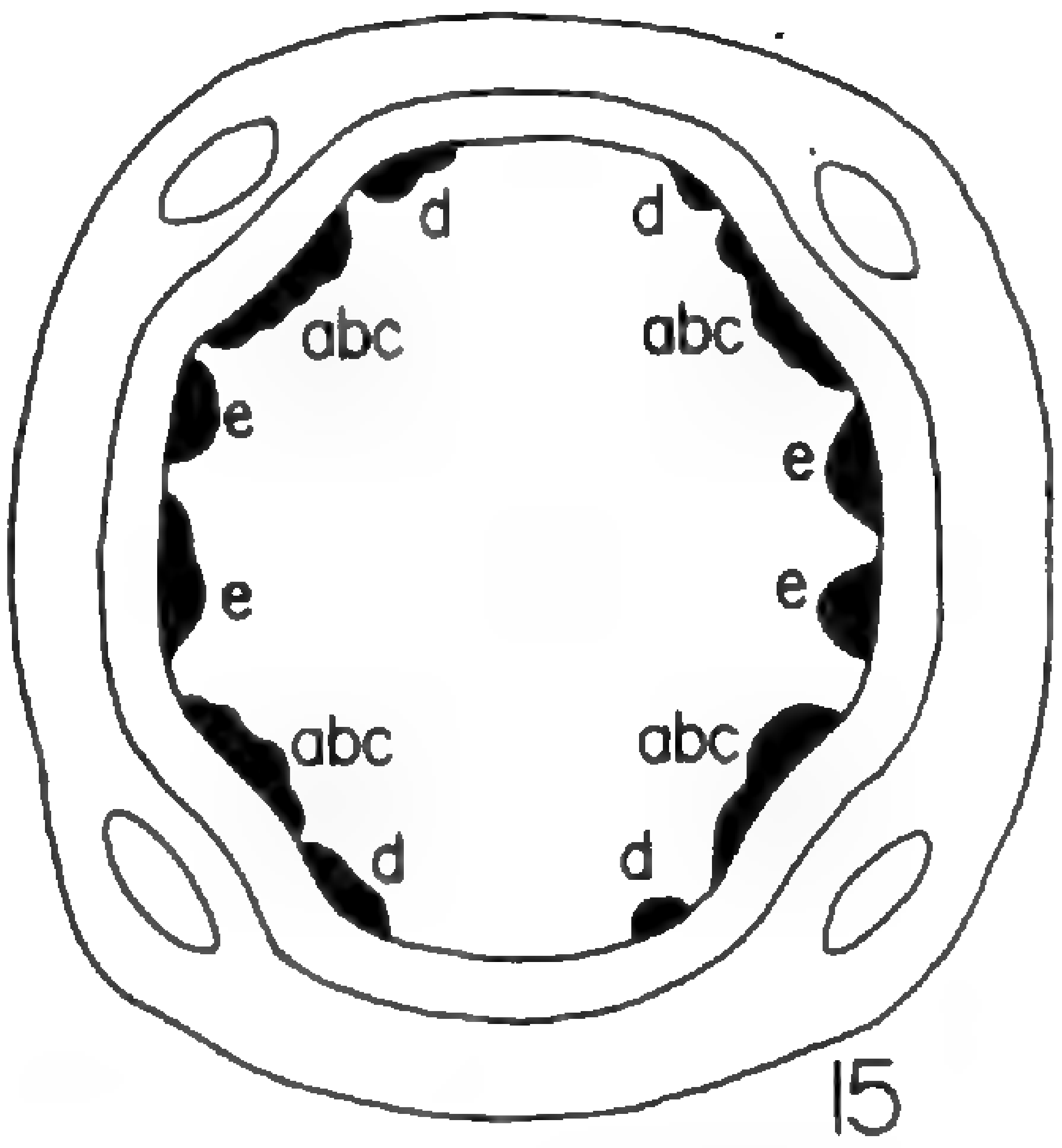

FIGURES 10–15. Cross sections of the mature part of a shoot of *Chimonanthus praecox*, cut at the successive levels shown in FIGURE 16. The primary xylem of the eustele and the median vascular strand of the leaf-base are shown in solid black. The cortical bundles, the vascular strands of the buds and the secondary xylem are merely outlined.

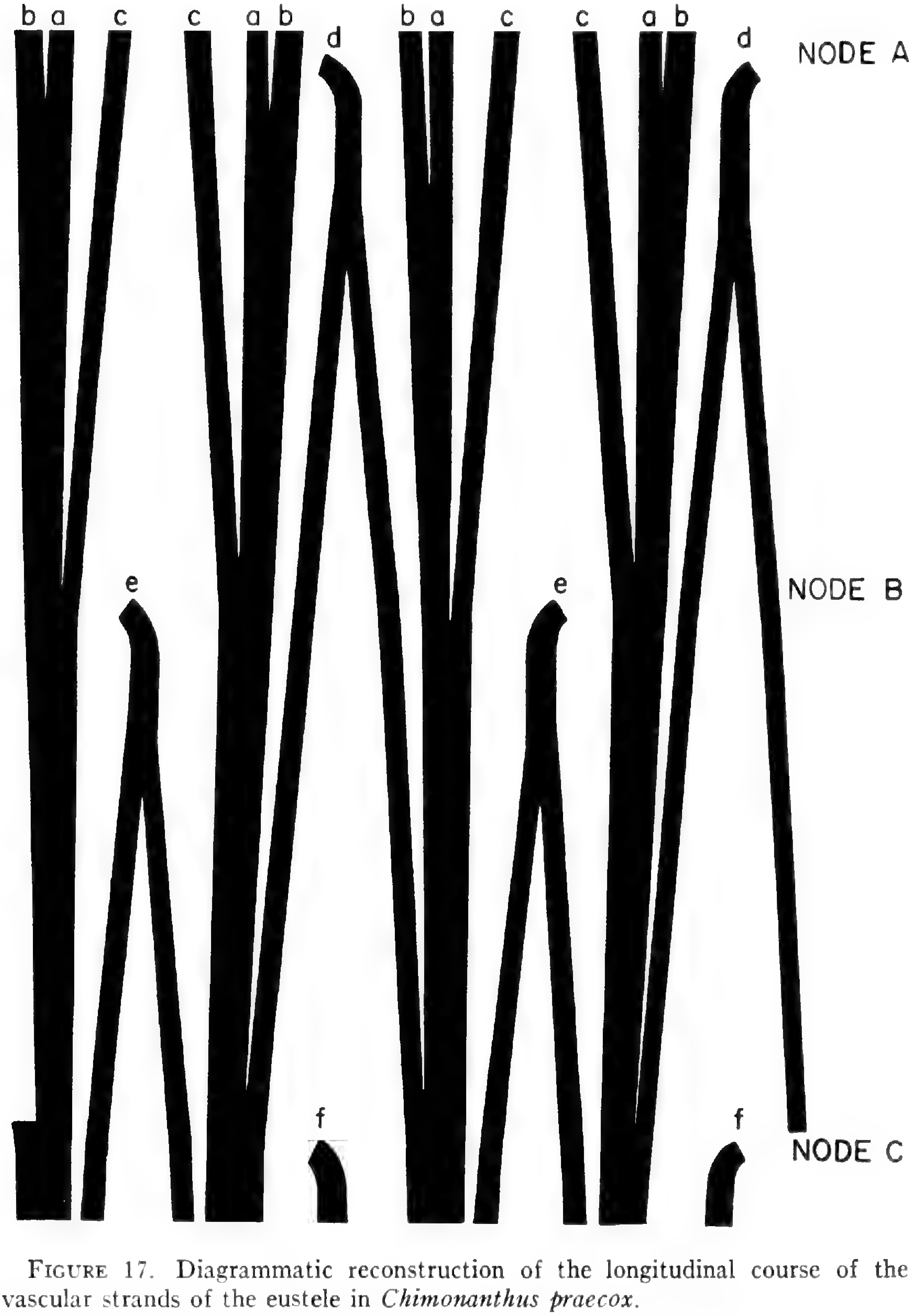

FIGURE 17. Diagrammatic reconstruction of the longitudinal course of the vascular strands of the eustele in *Chimonanthus praecox*.

INDEPENDENCE OF THE CORTICAL SYSTEM OF VASCULATURE

The course and behavior of the cortical vascular strands in our material — we have not studied the floral axis as yet — is in general agreement with that reported by previous investigators. Each of the four cortical strands has three lateral branches at the nodal level, *Plate II*. One of these runs independently through the petiole and into the marginal basal part of the lamina. The other two unite with the large median strand in the base of the petiole. There are in addition two transverse connections between the cortical strands at the nodal level in stems of *Calycanthus, Plate II, A*. These connections occur in the two opposite sides of the stem which do not form foliar gaps at the node, *Fig. 6*. However, in our specimens of *Chimonanthus praecox* they are very tenuous in some of the immature nodes. They are absent in others and in all mature stages examined, *Plate II, B*. In some cases, there are indications that early tenuous inter-strand connections may possibly have been disrupted during subsequent lateral enlargement of the stems. There are no connections in our material of immature and mature stems between the cortical vascular strands and the central eustele, except in the epicotyl between the cotyledonary node and the first foliar node.

Seedlings grown from seed labeled *Calycanthus floridus* and *C. laevigatus* have the fundamental, double-trace, unilacunar, cotyledonary structure that occurs in so many dicotyledonous families, Bailey (1). The branches of the two discrete traces may extend independently throughout the lamina of a cotyledon or certain of their branches may approximate giving the appearance of a midvein.

DISCUSSION AND CONCLUSIONS

Our investigations of both genera of the Calycanthaceae indicate that these plants belong in the category of unilacunar dicotyledons which have been shown in recent years [4] to have leaves and cotyledons that are vascularized by ramifications of two traces that are related to independent parts of the eustele. In certain representatives of this category, e. g. *Ascarina*, *Austrobaileya*, *Trimenia*, the two traces and their branches extend at times independently throughout the stem, petiole and lamina of the leaf. In many others, approximation or apparent fusion of the two vascular strands, or of certain of their branches, occurs at various levels of the stem, petiole or lamina,

The Calycanthaceae are significant in the latter connection exhibiting various stages of approximation and fusion in mature cotyledons and during the ontogenetic development and maturation of the stem and its foliar appendages. In addition, the two genera of the family are of interest in illustrating a special trend of modification of the basic double-trace, uni-

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[4] In this connection see Bailey and Swamy (2), Money, Bailey & Swamy (9), Swamy & Bailey (12), Swamy (11), Marsden & Bailey (7), Bailey (1).

lacunar form of vasculature, viz. the development of a superimposed independent system of cortical strands. In none of our material of seedlings and adult plants is there any evidence indicative of the derivation of the cortical system by modification of trilacunar or multilacunar structure.

The double-trace, unilacunar structure of the primary vascular cylinder of the Calycanthaceae, which so clearly resembles that of representatives of the Austrobaileyaceae, Trimeniaceae, Chloranthaceae and Lactoridaceae, is suggestive of relationship between these families, but taken *by itself* is not conclusive proof of *close* affinity since the structural similarities might be due to parallel or convergent evolution or to the persistence of a primitive form of vasculature — such as occurs in *Ginkgo biloba*, Gunckel & Wetmore (5), certain species of *Ephedra*, Marsden & Steeves (8), and other gymnosperms — in dicotyledons of relatively remote relationship. It should be noted in this connection that a fundamentally similar form of vasculature occurs within the Verbenaceae, Labiatae and Solanaceae. Only when considered in connection with the *totality* of evidence from all organs and parts of the plant do vascularization patterns become reliably significant in studying problems of phylogeny and natural relationships.

As emphasized by Money, Bailey & Swamy (9), there are two distinct categories of woody ranalian families which have ethereal oil cells and monocolpate pollen or pollen which has evolved by phylogenetic modification of such grains. One of these groups of families — the Winteraceae, Degeneriaceae, Magnoliaceae (sensu stricto), Himantandraceae, Annonaceae, Eupomatiaceae, Myristicaceae — are characterized by having trilacunar or multilacunar nodes. The other category — the Austrobaileyaceae, Amborellaceae, Trimeniaceae, Monimiaceae, Gomortegaceae, Lauraceae, Hernandiaceae, Chloranthaceae, Lactoridaceae — have double-trace unilacunar nodes or unilacunar modifications of this basic form of vasculature. Our investigations of the eustele of the Calycanthaceae when considered in the light of a summation of collateral evidence indicates that the family belongs in the second category of ranalian families and is more closely related to them than to any of the families in the first category.

ACKNOWLEDGMENTS

We are much indebted to Dr. C. E. Wood, Dr. H. L. Blomquist and Dr. R. B. Channell for kind assistance in helping us obtain material of the Calycanthaceae.

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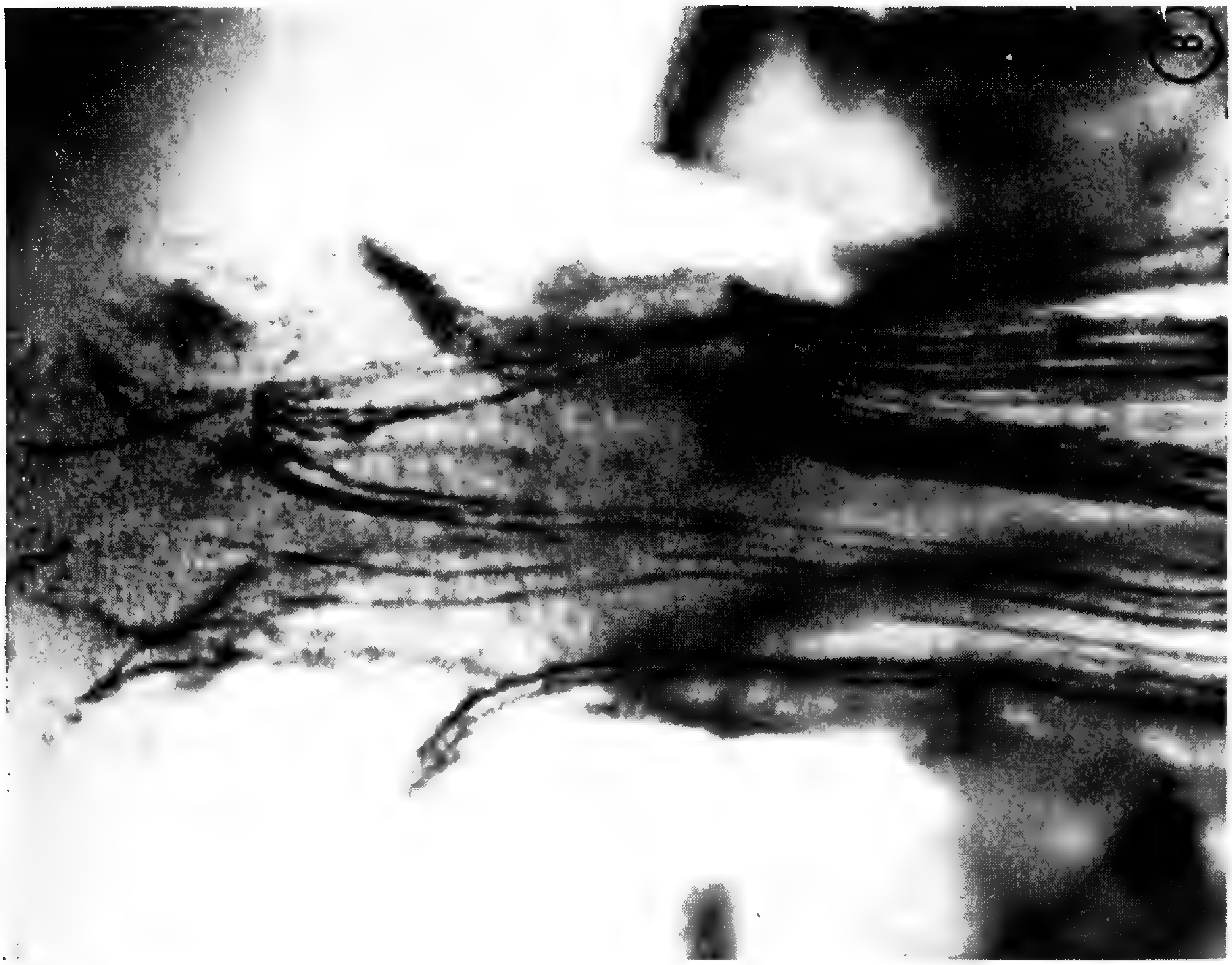
DESCRIPTIONS OF PLATES

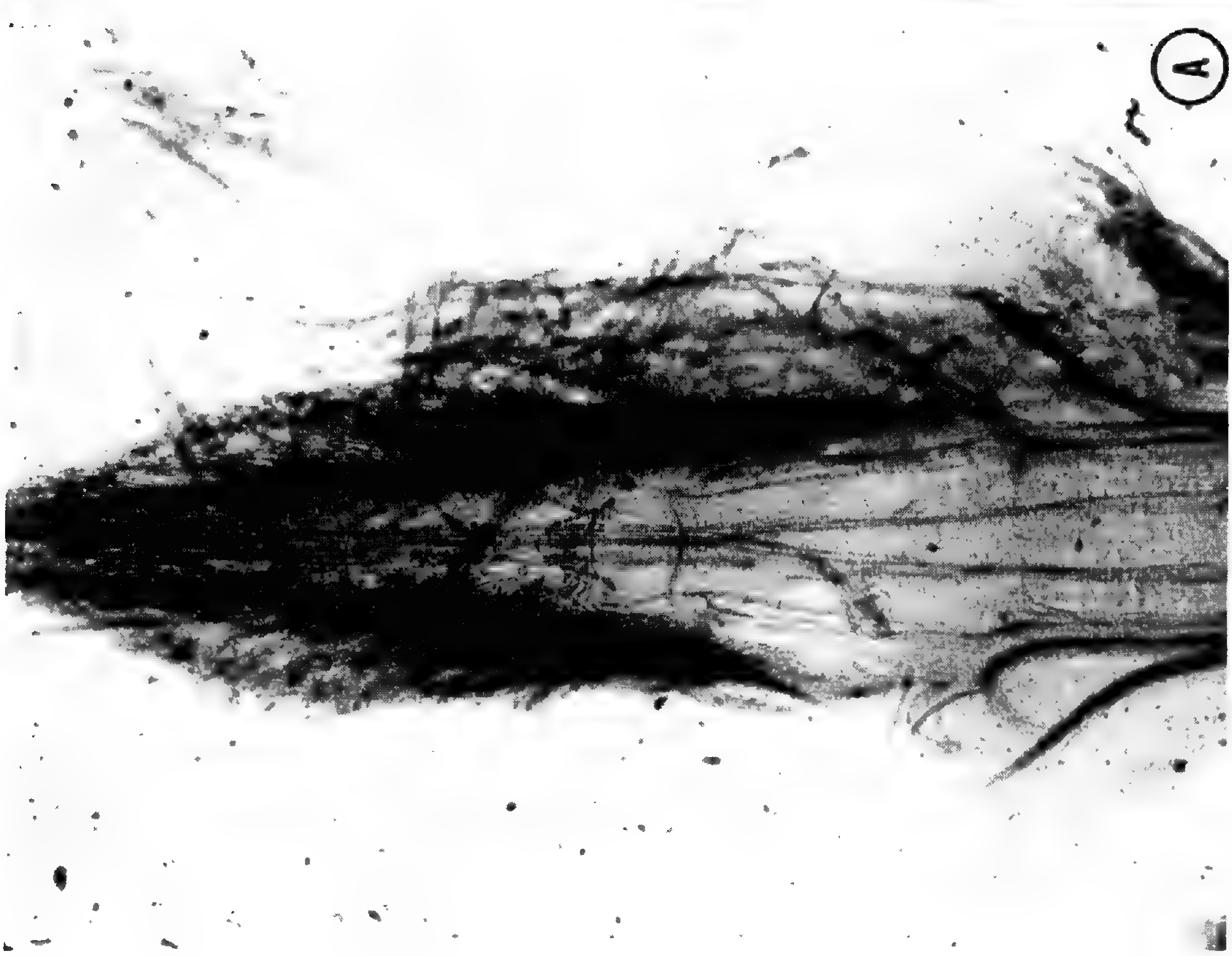
PLATE I

Cleared terminal parts of young shoots. The epidermis and some of the cortical tissue have been removed. A. *Calycanthus fertilis* var. *laevigatus*, showing two separate traces entering a young leaf. B. *Chimonanthus praecox*, showing the vascular strands of the eustele.

PLATE II

Mature nodes after clearing and removing the epidermis. A. *Calycanthus floridus* var. *ovatus*, showing lateral connection between two cortical strands and the branches which enter the leaves. B. *Chimonanthus praecox*, showing the absence of transverse connection between the two cortical strands.





Fahn and Bailey, Calycanthaceae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THE GENUS JUGLANS IN MEXICO AND CENTRAL AMERICA

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WALNUTS AND BUTTERNUTS, *nogal* or *nogales* in Latin America, well known important timber and nut trees belonging to the genus *Juglans*, of the Juglandaceae, occur in the New World from eastern Canada to Argentina and from the West Indies and Florida to California. The genus is missing in the modern flora from the northwestern states. In Central America walnuts have not been reported as native from Salvador, Nicaragua, Costa Rica, and Panama. The trees grow primarily in a humid, temperate climate, so that those which grow in the tropical latitudes are restricted to rather high altitudes with good rainfall, and those of arid regions are restricted to the canyons of streams. Consequently, the localities where *Juglans* occurs in Mexico and Central America are comparatively few and the trees are difficult to locate.

The species of Latin America are closely related to those of the United States and two of them occur in both Mexico and the United States. In the United States Sargent (1933) recognized six species, and gave an excellent treatment of these, with illustrations. Some authors recognize five species, others four. The writer recognizes five species: *J. cinerea* L. and *J. nigra* L. in the east, and *J. microcarpa* Berlandier (formerly called *J. rupestris* Engelmann ex Torrey), *J. major* (Torr.) Heller (included by many under *J. rupestris* as a variety), and *J. californica* S. Watson (including *J. hindsii* Rehd.) in the south and southwest. Of these species of the United States, *J. cinerea* clearly does not enter Mexico; *J. nigra* and *J. californica* approach the border of Mexico but have not been reported within that country; the other two species occur in north-central and northwestern Mexico.

The first species published for Mexico and Central America was *J. pyriformis*, described in 1850 by the Danish botanist F. Liebmann from the region of Mount Orizaba, near Coscomatepec, in the state of Vera Cruz, Mexico. The first treatment of *Juglans* of Latin America as a whole was that of Dode (1906–1909), who, in his comprehensive fully illustrated survey of the genus *Juglans* of the world, lists only two species for Mexico and Central America: *J. pyriformis* Liebm. and *J. mollis* Engelm. Standley, in his thorough treatment of the trees and shrubs of Mexico in 1920, gave four species, the two above for eastern Mexico, and *J. rupestris* Engelm. ex Torrey and *J. major* (Torr.) Heller extending from Texas, New Mexico and Arizona into north-central and northwestern Mexico. Definite descriptions were not made of any species of the genus from Central America until Standley and Williams described *J. olanchana* from Honduras in 1950. Manning, in Standley & Steyermark's Flora of Guatemala (1952), described *J. guatemalensis* and *J. steyermarkii* from that country.

Since the time of Dode many collectors, primarily from the United States, have made trips to Mexico and Central America. In 1953 the writer and his wife made a trip of over 5000 miles in Mexico under the auspices of the American Philosophical Society, primarily to collect and study *Juglans* and *Carya*. As a result of these activities, we have acquired a much better idea of the species of *Juglans* in the area under consideration, and of the distribution of these species.

All species of *Juglans* of the new world, with one exception,[1] belong to the section Rhysocaryon of Dode, typified by *J. nigra*. Dode (1909, p. 166) gives a description of the section. It is characterized by having, (1) a secondary as well as a primary partition in the nut so that the lower part of the nut is 4-celled; (2) each staminate flower with a stalk, and with the floral receptacle round; (3) the husk persistent on the nut; (4) the nut surface ridged or striate in various ways, but never smooth or rugose; (5) the nut dehiscent only at germination; (6) the scales of the embryo of the seed and younger part of the seedling spiral, gradually increasing in size until the normal leaves are reached; (7) the embryos of the seeds with shoulders or lobes near the apex ("shoulder region of the embryo lobes concave" according to Scott, 1954), so the embryo is 5-lobed and the nut 5-celled near the apex; (8) the leaflets serrate; (9) the leaf-scar without a hairy fringe or "mustache," but with a definite notch, along its upper edge. Some of these features were not given by Dode, but have been added by Nagel (1914), Manning (1948), and Scott (1954).

The species of *Juglans* of the world, as well as those of the other genera of the family, arranged by sections, are listed by the writer in his paper on the staminate flowers of the family (Manning, 1948). Two species mentioned there were not published until 1952 and another of those listed will be described in this paper. *Juglans glabrata*, mentioned there, is here reduced to a variety.

All of the species of Mexico and Central America, as well as in the New World as a whole, are so closely related that it is difficult to distinguish them. The writer recognizes five species in Mexico, and two others in Central America, one of the latter represented by a variety in southern Mexico. Two taxa from western Mexico, here described as varieties, may, upon further study, prove to be distinct species.

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[1] *Juglans cinerea*, the butternut, is a member of the section Trachyocaryon of Dode; the writer does not consider this section distinct from Dode's section Cardiocaryon of Asia, an opinion shared by Nagel, 1914, who, however, uses different sectional names.

Although Dode (1906–1909) did little work on the Mexican and Central American walnuts themselves, his contribution is the only comparatively recent world-wide study of the genus, and the only one on the *J. nigra* section. Furthermore, he studied intensively the species which occur in Texas, New Mexico, Arizona, and northern Mexico. Consequently we must examine carefully his criteria for distinguishing species. It should be pointed out, however, that most students of *Juglans* have ignored most of Dode's species, apparently because he based his new taxa on extremely variable features, so that almost every fruiting specimen constituted for him a new species. His treatment does bring out the amount of possible variation along certain lines.

The key of Dode (1909, pp. 166–168) to species of the section Rhysocaryon is based on nuts. He states that this key has only relative value, it presumably being necessary to use the key along with vegetative and floral features found in the descriptions. In this key he divides the species into three groups: A, nuts with ridges more or less sharp (*J. nigra*); B, nuts with ridges more or less obtuse (*J. pyriformis, J. elaeopyren,* etc.); C, nuts with striations (*J. mollis, J. torreyi, J. rupestris,* etc.). These features are important. They are, however, rather difficult to define, and there are wide variations within the species.

Additional but more unreliable features used by Dode in his key are the shapes of nuts, the compression of nuts, the wings of nuts, the size, shape, and number of lacunae (cavities in the outer wall of the nut as observed in a cross-section through almost the exact center of the nut, at least as used by Dode), and the height of dorsal or secondary partition (high, medium, low). On these additional features Dode has divided what most authors consider one species, *J. nigra,* into six species, and what most authors consider one or at most two species (*J. microcarpa* or *J. rupestris,* and *J. major*) into six species.

We can study *Juglans nigra,* the basic taxon for the section, as a criterion for many of these characters.

Certainly there is a decided variation in shape of nuts from tree to tree of *J. nigra,* from subglobose to depressed to elongate, these variations recognized by all American botanists as belonging to one species. Most nuts of *J. nigra* are compressed parallel to the primary partition, but the amount of compression varies.

The wings or dorsal lips of the nut along the suture, resembling those of the nuts of *J. regia,* seem to be variations on individual trees and of no value for specific distinctions in this section.

The writer has made an intensive study of the lacunae of the nuts of *J. nigra* and finds that the number and shapes of lacunae vary, not only in the nuts of trees side by side, but also from level to level of the same nut (typically 8 near the base of the nut, 4 elongate ones in the middle because of the fusion of these in pairs, then 8 toward the apex, with suppression of lacunae and intermediate conditions in different nuts). Scott (1954) has illustrations of consecutive cross sections of one nut of *J. major,* which is similar to, but somewhat less complicated than, *J. nigra.*

There is a possibility that the presence or absence of primary wall lacunae (at each end of the primary partition) may be distinctive, but more study of this feature is required.

The height of the dorsal partition, as seen in a carefully made longitudinal section of the nut along the secondary partition or, better yet, the section seen along the half of the nut following the natural dehiscence at germination, has been used by Dode in separating various species. It is true that the dorsal partition is high in all nuts of *J. nigra* observed by the writer, but the difference in height in the nuts of different species is so slight in the Latin American species, or else the variation is so great, that this feature is difficult to use.

There are other fruit features (husk and nut) not given by Dode in his key, though some of these are given in his descriptions. The writer has found the pyriform condition of the fruit (fruit with a basal or apical projecting neck or both) extremely unreliable, with fruits varying in trees side by side. The thickness of the husk is an uncertain feature, as very few fruits have been collected in the fully mature stage, with dependable notes, and the husk shrinks in drying. All Latin American fruits seem to have a husk thinner than that found in *J. nigra*. In some species, such as *J. pyriformis* and *J. olanchana*, the husk is conspicuously verrucose due to the presence of large, open, flat-topped warts. In other species, as in *J. nigra*, the warts are more numerous, smaller, raised, but not open and only give the fruit a rough appearance. In still other species the warts are very inconspicuous, partly because of the presence of numerous hairs. Strangely enough, Dode did not use the size of the fruit and nuts as criteria in his key. Although this feature must be used with caution because of the overlapping extremes due to variations on individual trees and to climatic conditions, it is important.

The length of the pistillate spike and the type of hairiness of the individual pistillate flowers are of some value.

In the staminate inflorescences the length of the catkin is in some cases useful. The position of the bract of the individual flower of the median, not basal, flowers along the catkin, seems to be important. This bract may be located: (1) at the base of the pedicel, therefore along the rachis of the catkin; (2) at the middle of the pedicel; (3) at the apex of the pedicel, hence at the base of the floral receptacle; or (4) essentially at the apex of the flower on its dorsal side just back of the two bracteoles (see illustration in Manning, 1948, *figs. 10, 11*). The term "at back of flower" is sometimes misleading and should be used only for position 4, the common condition in most species. In many cases, as explained by Manning (1948, p. 619), the position of the bract changes from the lower flowers to the median flowers of a catkin, so the lower flowers must not be used. The number of stamens seems to be a reliable feature, but there are cases where the number is higher than normal in individual flowers or plants.

In the leaves the number of leaflets is fairly constant for a species, though there may be a difference between the leaves on rapid and slow growth. The base of the leaflet is a very important feature, whether truncate or rounded as opposed to cuneate or narrowed in some way toward the base. This feature is obscured by the oblique condition of many leaflets, and does not show well on poorly pressed specimens. In some species the leaflets are decidedly stalked.

Hairiness of twig, rachis, upper surface of leaflet, and especially of the lower surface of the leaflet are important, each species having a definite limit of hairiness. It is necessary to define terms used for pubescence. There are two basic types of hairs: solitary, gland-tipped, multicellular pale or colored hairs, and pointed, non-glandular, one-celled pale hairs. On the rachis the former may be extremely short, consisting of essentially stalked glands so that the rachis having these numerous hairs may appear glabrous unless a strong lens is used, and the rachis may be described as minutely puberulent or even glabrate; or the hairs may be medium in length so that the hairs are evident but not conspicuous without a lens, and the rachis may be described as pubescent; or the hairs may be long and conspicu-

MAP 1. Distribution of the taxa which are treated in this paper. The dots indicate localities recorded in this paper, except where distributions overlap; some of these localities are indicated by "X"; the "X" for *J. mollis* is near Monterrey, just below "2".

ous, so that the rachis may be described as villous or even hirsute. Students, of course, will vary in their interpretation, and young leaves with undeveloped hairs will be misleading. The pointed hairs, common on the lower surfaces of the leaflets, may be solitary, in pairs, or in fascicles of three or more, these, of course, representing a branched condition of one true hair. To a certain extent all young leaves of *Juglans* may have fascicled hairs on the lower surfaces of the leaflets, but only in certain species are the leaflets fascicled-hairy, or tomentose, at maturity. In *J. mollis*, and frequently also in *J. hirsuta*, the permanent fascicle of hairs seems to be growing out of a short, yellow, glandular, basal cell. Some of the fascicled hairs present on young leaves, on the rachis or lower leaflet surface, are extremely short, and are evanescent types, which must be distinguished from the permanent type, if possible.

The shapes and measurements of leaflets are, as in all such cases, of importance within certain limits, but there is some variability. A terminal leaflet appears to be present in some leaves, but not in others. A careful examination of the apparent terminal leaflet will often reveal a small stub at its base, such as one finds frequently in *J. nigra* between the two uppermost leaflets; this may be the remains of a true terminal leaflet or of the other member of the uppermost pair of lateral leaflets, only one of which persists.

The color and stoutness of the twig (youngest growth) are undoubtedly of value, but to use these characters would require extensive field studies at different times of year. In almost all members of the Mexican and Central American species the terminal bud appears to be more slender (elongate?) than that of *J. nigra*.

The writer wishes to thank the American Philosophical Society for valuable assistance in collecting material in Mexico. He also wishes to thank the curators of the various herbaria for their generosity in lending specimens and sending photographs; especially Dr. O. Hagerup, Botanisk Museum, Copenhagen, Denmark; Dr. H. Humbert and Dr. J. F. Leroy, Muséum National d'Histoire Naturelle, Paris, France; Dr. M. Martinez and Dr. R. Llamas, Instituto de Biologia, Chapultepec, Mexico; Dr. C. Baehni, Conservatoire et Jardin Botaniques, Geneva, Switzerland; Sir Edward Salisbury, Royal Botanic Garden, Kew, England; and Dr. T. E. Hasselrot, Naturhistoriska Riksmuseet, Stockholm, Sweden.

In addition to the native species listed in the key and in the descriptions below, the Persian or English walnut, *J. regia* L., is cultivated in various regions of Latin America. There are no definite records of this species escaping from cultivation. This species has 7–9, entire, essentially glabrous leaflets, elongate, subsessile staminate flowers, glabrate somewhat irregularly dehiscent husk, and rugose nut shell with strong lips.

The following key to the native Mexican and Central American species and varieties of *Juglans* is not absolute, as there are occasional variations in individual features on certain trees or branches; a combination of characters as given in the descriptions must sometimes be used.

1. Mature leaflets about 1–1.5 cm. wide; fruit 1.2–2.2 cm. in diameter; nut 1–1.7 cm. in diameter; plants mostly of shrubby growth (leaflets 17–31, narrowly lanceolate, elongate, curved); nw. Nuevo León, Coahuila, and ne. Chihuahua. . . . . 6. *J. microcarpa.*
1. Mature leaflets 2 cm. or more wide; fruit 2.3–5.5 cm. in diameter; nut 2–5 cm. in diameter; trees.
    2. Leaflets 9–15 (fruit not conspicuously verrucose; nut not sharply ridged).
        3. Leaflets and rachis both essentially glabrous (rachis with minute stalked glands visible with a strong lens); leaflets tapering at base; fruit glabrate; nut rather deeply furrowed; Mexico, Guerrero, Jalisco, Michoacan, Durango. . . . . 4. *J. major* var. *glabrata.*
        3. Leaflets beneath and rachis both strongly fascicled-hairy or glandular-pubescent; fruit mostly pubescent; nut striate.
            4. Rachis whitish-pubescent; leaflets pubescent beneath with solitary hairs or rarely in part fascicled-hairy, not fascicled-hairy above, tapering at base; terminal leaflet mostly present; nut 1.8–2.8(–3) cm. in diameter; Chihuahua, Sonora, Sinaloa, Durango. . . . . 4. *J. major.*
            4. Rachis fascicled-hairy or rarely brownish glandular-pubescent; leaflets fascicled-hairy beneath, and slightly so above, truncate at base, though often oblique; terminal leaflet mostly absent; nut 2.5–4.5 cm. in diameter; Nuevo León, San Luis Potosí, Hidalgo, Tamaulipas, Guanajuato, Puebla. . . . . 3. *J. mollis.*
    2. Leaflets on larger leaves (16–)17–31; (fruit in some species conspicuously verrucose with open flat-topped warts; nut deeply furrowed or sharply ridged).
        3. Leaflets truncate at base, essentially sessile.
            4. Leaflets fascicled hairy beneath; nut sharply ridged, blackish; staminate catkins 6–10 cm. long; (leaflets 16–21); Nuevo León. . . . . 2. *J. hirsuta.*
            4. Leaflets glabrate, or pubescent beneath with solitary or paired hairs; nut deeply furrowed with flat-topped broad or rarely narrow ridges, dark brown; staminate catkins 18–22 cm. long (unknown in *J. steyermarkii*).
                5. Leaflets (19–)21–31, lanceolate or oblong-lanceolate, glabrate beneath; lateral veins mostly leading directly to sinuses, and then sending a branch to the tooth; husk strongly verrucose with open, flat-topped warts, glabrous; Vera Cruz. . . . . 1. *J. pyriformis.*
                5. Leaflets 16–18, ovate, strongly whitish-pubescent beneath; lateral veins mostly leading directly to the teeth; husk not strongly verrucose, pubescent; n. Guatemala. . . . . 7. *J. steyermarkii.*
        3. Leaflets strongly tapering at base or decidedly stalked; (fruit strongly verrucose with open warts; leaflets 17–23; staminate catkins (15–) 18–30, the bract on the pedicel).
            4. Leaflets and rachis appearing glabrous (but with strong lens rachis appearing covered with stalked glands); leaflets inconspicuously lepidote, decidedly stalked; Guatemala and Honduras. . . . . 6. *J. olanchana.*

4. Leaflets beneath strikingly fascicled-hairy, conspicuously lepidote under the hairs, subsessile; rachis whitish-villous; Colima and w. Jalisco. . . . . 6. *J. olanchana* var. *standleyi*.

A list of collections is recorded for each species to validate the distribution. In each state the localities are arranged in general from north to south. Also recorded are the herbaria wherein the specimen may be found. Whenever staminate flowers, pistillate flowers, immature fruit, or mature fruit as well as leaves are present, indication is made by the abbreviations "stam.," "pist.," "im. fr.," or "fr." respectively; "fr. only" indicates that no leaves are present. When the material is sterile no symbol is given. The following are the herbaria and their abbreviations as used in this paper: AA — Arnold Arboretum; AMH — Amherst College; BH — Bailey Hortorium; BPI — fruit collection, Bureau of Plant Industry, U.S.D.A.; CAL — University of California; CM — Chicago Museum of Natural History; CU — Cornell University; GH — Gray Herbarium; ILL — University of Illinois; MICH — University of Michigan; MO — Missouri Botanical Garden; MS — Michigan State College; NC — University of North Carolina; NY — New York Botanical Garden; OKLA — University of Oklahoma; P — Philadelphia Academy of Sciences; REY — H. C. Reynolds; TENN — University of Tennessee; TEX — University of Texas; US — U. S. National Herbarium; USDA — U. S. Department of Agriculture; USFS — U. S. Forest Service; Y — Yale University; WEM — the writer's personal herbarium, Bucknell University; COP — Botanisk Museum, Copenhagen, Denmark; GEN — Conservatoire et Jardin Botaniques, Geneva, Switzerland; HON — Escuela Agricola Panamericana, Tegucigalpa, Honduras; K — Royal Botanic Garden, Kew, England; MEX — Instituto de Biologia, Chapultepec, Mexico; PAR — Muséum National d'Histoire Naturelle, Paris, France; ST — Naturhistoriska Riksmuseet, Botaniska Avdelningen, Stockholm, Sweden.

The vernacular name for all species of *Juglans* throughout Latin America is *nogal;* for small walnuts, such as *J. microcarpa*, as well as for hickories, the name is *nogalillo*. The nut is usually called *nuez*, or *nuez encarcelado*. There are undoubtedly other names, but most of these are not recorded. Martinez (1937) lists alphabetically the vernacular names of plants including walnuts in different states, but there is some uncertainty as to which species they apply.

1. **Juglans pyriformis** Liebmann, Vid. Med. Naturh. Copenhagen **1850**: 78–80. — Dode, Bull. Soc. Dendrol. France **1909**: 198–199. — Standley, Contrib. U. S. Nat. Herb. **23**: 165. 1920, pro parte.

Tree tall, deciduous; twigs quite stout, chocolate-brown to gray-brown, conspicuously lenticellate, glandular-pubescent on hairy-leaved plants, soon becoming glabrate, or glabrous or nearly so on glabrate-leaved branches; pith light brown; terminal bud elongate, slender, light brown; lateral buds superposed, brown and glabrate or some of them grayish-pubescent; leaves large, 40–60 cm. long, up to 30 cm. broad, unequally or sometimes equally pinnate; rachis brownish-villous or -pubescent on some trees, minutely glandular-puberulent or with scattered minute appressed fascicled hairs on others, or even glabrous; leaflets 18–31, alternate, subopposite, or opposite, lanceolate or oblong-lanceolate, the principal ones 10–15 cm. long and 3–4.5 cm. wide (12 × 3; 15 × 4.5), sessile or subsessile, somewhat cordate to sub-truncate to rounded, rather oblique at the base, tapering to a long-acuminate tip, the margin slightly reflexed-falcate, serrulate, glabrous or apparently so on the upper surface (though on some specimens with minute scattered fascicles of hairs), on the lower surface brownish-pubescent on the main veins on leaves of some trees, on others nearly glabrous or sometimes with many scattered appressed fascicles of hairs on larger and some of the smaller ones; young leaflets densely dark-lepidote, especially on the lower surface, not tomentose, and usually without fascicled hairs, older leaflets inconspicuously lepidote with scattered minute dark glands; staminate catkins 18–22 cm. long (—37 cm. fide Dode), with rather large, distant flowers, the bract small (1 mm.), rounded, only slightly pubescent, at the apex of the pedicel (at base of the receptacle of the flower); stamens 43–58, the anthers glabrous; pistillate flowers unknown; fruit subglobose to pyriform-subglobose, 4.5–5 cm. long, 4.3–4.7 cm. in diameter, nearly glabrous, conspicuously verrucose with large open flat-topped grayish or light-brown warts; nut large, hard, thick-shelled, subglobose to depressed subglobose, compressed, 3.5–4 cm. long and 4 × 3.5 to 4.5 × 4 cm. in diameter, strongly longitudinally ridged, the ridges narrow but rounded at top (obtuse, fide Dode) to rather broad and flat, with sharp-angled edges, the furrows rather deep especially at the base of the nut, the whole often resembling a deep striate condition; dorsal partitions high; lacunae large, but otherwise much as in *J. nigra.*

VERNACULAR NAME: *Nogal,* though that name not recognized at Orizaba, where the tree was not well known.

VERA CRUZ: Coscomatepec, Gulf of Coscomatepec, near Mt. Orizaba, *F. Liebmann 3776* fr. (TYPE-NUMBER — COP, CM, K, GEN). — Coscomatepec, in village, alt. about 4200 ft., *W. E. & M. S. Manning 53808* fr., *53809, 53810* (WEM). — Orizaba, *Botteri 879* stam. (K, PAR). — Orizaba, mountain sides near town, *Witmer Stone 80* (P). — Santa Ana (about 10 miles north of Orizaba), *Borngeau 3032* fr. (PAR). — Trail up Cerro San Cristobal, Orizaba, alt. 4200 to 5000 ft., *W. E. & M. S. Manning 53736, 53745, 53773* fr., *53794, 53796, 53799* (WEM). — Cultivated in Alamda, Orizaba, *W. E. & M. S. Manning 53788* fr. (WEM). — East of San Andres Tuxtla, nw. of Catemaco, near Cerro Tapalcapan & C. Mastagaga, tropical evergreen forest, *Dressler & Q. Jones,* in 1953, nut only (WEM).

This species, the first to be described for Mexico, and the most distinctive, has not been well understood in the New World. This is probably because so few specimens have been collected — none between 1890 and 1953 — and because no specimens existed in the American herbaria until very recently. The description of Standley (1920) does not clearly indicate this species, as he lists a different number of leaflets and combines the features of various taxa. The writer fully understood the species only when he had collected from trees in the Orizaba and Coscomatepec region 112 years after Liebmann was there.

Liebmann clearly distinguished this species from *J. nigra*. *Juglans pyriformis* has more numerous, narrower, more finely serrate, less hairy leaflets and lighter colored, less sharply ridged nuts with more prominently verrucose husks. The internal structure of the nut is not distinctive, though Liebmann thought that the lacunae were larger. Dode (1909) also stressed the surface of the nut.

This species differs from all other Mexican species in the larger number of narrow leaflets and in its conspicuously verrucose husk, though there is some overlapping in the number of leaflets. The staminate catkins are longer than those found in all other species except *J. olanchana* var. *standleyi*. The large nut is typically more deeply grooved than that of *J. mollis* and *J. major*. In the type-collection of *J. pyriformis* the narrow, rounded ridges approach those of *J. hirsuta*; the nut of the latter species has a few or several broad ridges, but there are always more of the narrow, sharp, broken ridges present in the darker nut. In general. the features appear to combine features found in *J. hirsuta*, *J. mollis*, and *J. major* var. *glabrata*, with the differences noted above. Discussion of the relationship between *J. pyriformis* and the Central American species will be found under *J. olanchana*.

There is a variation in the hairiness of the rachis which is quite striking, and the writer at first thought that the two conditions represented two different species. The trees at Coscomatepec, as far as collected, have brown-villous rachises; some of the trees near Orizaba have villous rachises, while others have glabrous rachises; all have nearly identical shapes of leaflets and nearly identical fruits where collected.

It is surprising that this species appears to grow in such a limited area: within a range of less than 125 miles. Part of this seemingly limited range is due to a lack of collecting. Until the collection of Dressler and Jones in 1953 the range had been 40 miles. The species is so closely related to *J. olanchana* of Guatemala and Honduras that it must occur somewhere in the mountains of the isthmus of Tehuantepec and northwest, an area not well known botanically. It is significant that *Engelhardtia mexicana*, a member of the Juglandaceae which occurs with *Juglans pyriformis* on the same slope of Cerro San Cristobal close to Orizaba (see Miranda, 1946, where he at first considered *E. orizabensis* a distinct species), has been collected by Dr. A. J. Sharp and Dr. E. Hernandez X. on the isthmus northeast of Juchitan and north of Niltepec, on the divide of the Sierra del Sur near the headwaters of the Rio Coatzacoalcos.

2. **Juglans hirsuta** Manning, sp. nov.* (Amer. Jour. Bot. 35: 616. 1948, nomen subnudum).

* **Juglans hirsuta** Manning, sp. nov. Ramuli glanduloso-pubescentes; gemmis terminalibus gracilibus; foliis paripinnatis; rhachi valde rufescente-glanduloso-hirsuta; foliolis 16–22, 2.5–6 cm. latis, ovato-lanceolatis, sessilibus, basi truncatis venis supra glanduloso-pubescentibus, subtus pilis plerumque fasciculatis; fructibus 3–4.7 cm. dia-

Juglans mexicana sensu Sargent, Trees and Shrubs **1**: 1–2, *pl. 1.* 1902, pro parte.

Juglans mollis sensu Dode, Bull. Soc. Dendrol. France **1909**: 197, pro parte. — sensu Standley, Contrib. U. S. Nat. Herb. **23**: 165. 1920, pro parte.

Large, rather spreading deciduous tree; young twigs reddish brown, glandular-pubescent or -hirsute, sometimes partly fascicled-hairy, becoming gray-brown the second season; pith light brown; terminal bud slender, elongate, grayish-tomentose; leaves large, equally or sometimes unequally pinnately compound, true terminal leaflet usually absent; rachis strongly glandular-villous or hirsute, the hairs brown, with a few scattered fascicled hairs, the latter more prominent on younger leaves; leaflets mostly 16–21, rarely 14–23, opposite or subopposite, sometimes alternate, medium, rather thick, somewhat rugose, ovate to ovate-lanceolate to oblong-lanceolate, 2.5–6 cm. wide and up to 15 cm. long, the apex abruptly long-acuminate, the margin finely to coarsely serrate, the teeth often incurved, somewhat blunt, the lateral veins mostly leading directly to the sinuses and then sending a branch to the tooth; the middle leaflets sessile or nearly so, truncate to rounded at the base, commonly oblique, the upper surface commonly glandular-pubescent on the principal veins or over the whole surface, not fascicled-hairy, sometimes becoming glabrate, the lower surface inconspicuously lepidote, strongly tomentose with whitish fascicled hairs mixed with brown glandular hairs and with solitary and paired sharp-pointed whitish hairs (on surface and veins), the midrib and frequently the strong lateral veins densely brownish glandular-hairy; staminate catkins 6–10 cm. long, the flowers not especially crowded, with short (1–1.5 mm. long) ovate-lanceolate whitish-tomentose bract located on the back of the flower, the perianth consisting of the bract, 2 bracteoles, and 4 or sometimes 6 sepals; stamens 20–34; pistillate flowers few, tomentose with frequent to numerous glandular hairs appearing through the fascicled ones; fruit medium to large, 3–4.7 cm. in diameter, globose to somewhat pyriform-subglobose or oval, strongly glandular-pubescent or villous, especially when young, not conspicuously verrucose-punctate because of hairs but at complete maturity very finely and densely minutely verrucose, not so prominently so as in *J. nigra*; nut dark reddish brown or mostly blackish, somewhat compressed, about as high as broad, (2.5–)3–4 cm. in diameter with numerous interlacing irregular flat-topped to rather narrow-topped ridges or frequently a mixture of the two, the furrows rather deep, in general appearing sharp-ridged, and strongly resembling the nut of *J. nigra*; dorsal partition rather high; secondary wall cavities prominent, varying from 4–8 at different levels, as in *J. nigra*, the primary wall cavities absent.

VERNACULAR NAMES: *nogal, nogal encarcelado.*

NUEVO LEON: Potrero, Alamo, 5 miles south of Villaldama, at mouth of canyon and in narrow canyon in the mountain along stream with *Platanus*, *W. E. & M. S. Manning 53354* fr., *53358* fr., *53359* fr., *53366* fr., *53368* fr., *53369* fr.,

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metro, glanduloso-pubescentibus; nuce subfusca, 3–4 cm. diametro, extus rugosissima, rugis asperatis etiam subplanis.

53370 fr., *53371* fr., *53372* fr. (WEM). — Monterrey, canyons in Sierra Madre above city, alt. 2500 ft., *Canby, Sargent & Trelease 223* or *123a* stam., pist., fr. (AA, K, MO, US); *Pringle 10214* stam. (CAL, CM, COP, CU, GH, K, MEX, MO, MS, NY, P, ST, US); *Pringle 10374* fr. (TYPE-US; ISOTYPES-GH, MICH, Y); *Sargent*, in 1887, pist. (AA); unknown collector *18*, *"nogal encarcelado"*, fr. (P). — Monterrey, Sierra de la Silla, alt. 1700 ft., *Pringle 11178* fr. (CM, GH, K, MO, NY, US). — Monterrey, Canon Diente in Sierra Madre, *C. H. & M. T. Muller 63* fr. (AA, CM). — 3 miles west of Monterrey, Chipinque Mesa, base, alt. about 2000 ft., *W. E. & M. S. Manning 53336* fr. (WEM); same general locality, base to half way up to mesa, alt. 2000 to 3000 ft., *W. E. & M. S. Manning 53347*, *53341* (WEM). — 3 miles west of El Cercado (which is 2 miles south of Villa Santiago, 25 miles south of Monterrey), Hacienda Vista Hermosa, Horsetail Falls (Cola de Caballo), alt. about 2500 ft., *W. E. & M. S. Manning 53129a* fr., *53129b* fr. only, *53131* fr., *53132a*, *53132b*, *53132c*, *53132d*, *53132e* all fr. only (WEM); *A. Dyck*, Nov. 1954, fr. only (WEM); *Rowell & Barkley 16MS65* (TEX); *White 1633* (MICH); above Horsetail Falls, alt. 3000 to 4000 ft., *W. E. & M. S. Manning 53171a* fr., *53171b* fr. only (WEM). — Road from Linares to Galeana, along stream near base of canyon, alt. about 2000 ft., *W. E. & M. S. Manning 53187* (WEM).

Juglans hirsuta has been confused by various authors with *J. pyriformis*, *J. mollis* and *J. mexicana*, and yet it is probably more closely related to a very different species. The writer, at first confusing the Monterrey specimens collected by several botanists with *J. pyriformis*, and then with *J. mollis*, next decided that some of the specimens collected in the Jacala region of Hidalgo were conspecific with specimens from Monterrey because of the glandular-pubescent leaf rachises and fascicled-hairy lower leaflet-surfaces, though the nuts, where available, seemed somewhat different. Field studies by the writer of trees south of Monterrey, south of Galeana, and south of Jacala, showed at once that the nuts at Monterrey were quite different from those in the other regions. But abundant mature nuts of the Monterrey trees were not available until the fall of 1954 when, at the request of the writer, Miss Annabelle Dyck, of Monterrey, secured material from Horsetail Falls and sent it to the writer. These mature nuts are black, sharply ridged, and practically identical with those of *J. nigra*, although a few broad ridges are present on many of the nuts (this condition occasionally occurs on certain trees of *J. nigra*). It is possible that *J. hirsuta* may be a hybrid offspring of *J. nigra* and *J. mollis*, the ranges of which no longer overlap. Specimens collected by the writer at Potrero have small nuts similar to those of *J. hirsuta*, but the hairs on the rachises of the leaves of several of the trees are not as brown, and the fascicled hairs on the lower surfaces of the leaflets are rare. These trees, the leaves of which at first looked like those of *J. major*, are considered as variants of *J. hirsuta*, but they are similar to the small-fruited *J. nigra* of southern Texas. The features separating *J. hirsuta* from *J. nigra* are primarily vegetative ones: the striking brown-glandular hirsute leaf rachises, the fascicled hairs underneath the leaflets, the more nearly truncate leaflet-bases, the more slender terminal buds, and the less definitely verrucose husks of the fruits. The writer recognizes *J. hirsuta* until further studies can be made in Texas and Nuevo León to settle the relationship between the two taxa.

The sharply ridged nuts of *J. hirsuta* are different from those of all other species of Mexico and Central America, although immature nuts are confusing. Some of the nuts of *J. pyriformis* have, however, rather narrow ridges with rounded tops. The leaves are typically different from those of *J. mollis,* averaging more numerous leaflets and having villous instead of fascicled-hairy rachises with many of the pointed hairs beneath the leaflets solitary or paired instead of mostly in fascicles. However, the rachises of the leaves of certain specimens of *J. mollis*, especially those from near Jacala, Hidalgo, have glandular hairs, as in *J. hirsuta*, and these hairs are only slightly shorter than those of *J. hirsuta.* Leaflets of *J. hirsuta* do not seem to have fascicled hairs on the upper surface such as are found in *J. mollis*; the constancy of this feature will have to be studied (see note under *J. mollis*).

The distinctions between *J. hirsuta* and *J. pyriformis* have been discussed under the latter species. *Pringle 11178* has leaves which closely resemble those of *J. pyriformis* in shape of leaflets, but the leaflets are fascicled-hairy beneath, the husk is not strongly verrucose, and the nut is the smallest of all of the collections of *J. hirsuta*, hence much smaller than in *J. pyriformis.*

Some Mexicans told the writer that the nuts of *J. hirsuta* are not used as food by the natives. Farmers above Horsetail Falls, however, stated that the nuts are occasionally used. The trees are local, the nuts are hard to crack, and so the use as food is not significant. Good varieties of *J. nigra,* however, would probably grow where *J. hirsuta* is native. Whether these trees could compete under cultivation with the pecan, which, incidentally, was planted as an orchard tree in the exact region under discussion, is questionable.

3. **Juglans mollis** Engelm. in Hemsley, Diagnoses plantarum novarum vel minus cognitarum mexicanarum et centrali-americanum. Pars 3: 54. 1880. — Dode, Bull. Soc. Dendrol. France **1909**: 197, pro parte. — Standley, Contrib. U. S. Nat. Herb. **23**: 165. 1920, pro parte.

Juglans mexicana S. Watson, Proc. Amer. Acad. Arts and Sciences **26**: 152. 1891. — Sargent, Trees and Shrubs **1**: 1, *pl. 1.* 1902, pro parte.

Medium-sized tree; young twigs densely fascicled-pubescent or partly brown-glandular pubescent, very rarely brown glandular-pubescent, becoming glabrate, mostly dark brown, the second year's growth gray-brown with scattered prominent lenticels; terminal bud slender, brown- or gray-tomentose; pith light brown; leaves alternate, equally or sometimes unequally pinnately compound, terminal leaflet, when present, with stub of other leaflet at its base; rachis, usually tomentose with numerous persistent spreading fascicled hairs, especially beneath, in rare cases becoming glabrate or, in trees of some regions, densely pubescent with short brown glandular hairs, the fascicled hairs few; leaflets 10–14, rarely 8–16, opposite or alternate, sessile or subsessile, broadly ovate to ovate, occasionally ovate-lanceolate or elliptical-lanceolate, the larger ones 6 × 3, 8 × 3.5, 8.5 × 4, 10 × 4 or 15 × 5 cm. long and wide, truncate to rounded at the base, but frequently oblique, rather abruptly long-acuminate at the apex or tapering from the middle to the apex, finely or coarsely serrate, the upper surface glabrate, with minute appressed fascicled hairs along the midrib and principal side veins, lepidote on the lower surface with rather prominent golden glands and tomentose on the midrib, veins, and surface proper with fascicles of spreading hairs, each fascicle with a short yellowish glandular stalk, solitary pointed hairs apparently rare, the midrib fascicled-hairy or rarely in part brown-glandular pubescent; staminate catkins 8–10 (rarely 10–16, in *Salazar*) cm. long, slender, the flowers rather small, the individual floral bracts small, whitish tomentose, on the backs of the flowers; stamens 25–30 (rarely 87, in *Salazar*); pistillate flowers few, densely tomentose; fruit globose to subglobose, sometimes pyriform, the husk 3–4(–8?) mm. thick, at first usually covered with fascicled hairs, but in some cases with short brown-glandular hairs, becoming glabrate, usually very inconspicuously verrucose, 3–5 cm. in diameter, 3.5–5(–6, fide Sargent?) cm. long; nut globose to subglobose, somewhat compressed, 2.5–4.5 cm. in diameter, 2.8–4 cm. long, reddish brown, shallowly to deeply striate, that is, with broad flat to rounded longitudinal ridges, the grooves rather shallow, but strong, occasionally forked and interlacing, the nut very rarely with dorsal "lips" or "wings"; dorsal partition "rather low" to rather high; lacunae 8–4, depending upon the level, not especially large, the primary wall lacunae mostly absent, but present or indicated by dark areas in some of the larger nuts.

VERNACULAR NAMES: *nogal; nogal encarcelado; nuez meca* (fide Martinez).

NUEVO LEÓN: 3 miles west of Monterrey, near top of Chipinque Mesa, alt. about 4000 ft., *W. E. & M. S. Manning 53344, 53345* (WEM). — West of Galeana, at foot of Cerro Potosí, in arroyo near Ojo de Agua, alt. 5800 ft., *A. J. Sharp 45675* (TENN). — 15 mi. sw. of Galeana, Sierra Madre Oriental, *C. H. & M. T. Muller 428* stam., pist. (AA, CM, MEX, MICH, NY, US). — 15 mi. sw. of Galeana, Mesa de la Camisa, *C. H. & M. T. Muller 1156* im. fr. (AA, CM, MEX, MICH, NY, US). — near Tarey (e. of Pablillo, which is 20 mi. s. of Galeana), rainy area or fog belt, alt. about 7200 ft., *W. E. & M. S. Manning 53244, 53250* fr., *53268, 53331* (WEM). — Dulce Nombres and into Tamaulipas, just east of border, 24° N., 99.5°–100.5° W, Sierra Madre Oriental, *Meyer & Rogers 2642* im. fr. (MO, WEM). TAMAULIPAS: above Gomez Frias, Cerro del Tigre, Rancho del Cielo, alt. 1200m., *Sharp, Hernandez, Crum & Fox 50246* (NC, TENN, WEM). — SAN LUIS POTOSÍ: Mineral de Guadalcazar, *M. Villada* in 1892 (MEX). — Villar (40 mi. ne. of San Luis Potosí), alt. 5000 ft., *J. Graber 219* fr. (US). — San Luis Potosí (or Alvarez?, see *Carya illinoensis, Parry & Palmer 835 1/2*), *Parry & Palmer 835* fr. (TYPE-K; ISOTYPES-GH, MO, P, US). — *Alvarez, Palmer 68* fr. (AA, CM, GH, MEX, MO, NY, US, BPI, USDA). — San Jose Pass (near Villar?), *Pringle 3322* fr. (TYPE of *J. mexicana* Engelm.) (AA, AMH, CAL, CM, GH, MEX, MO, MS, NY, US, Y, GEN, K, BPI). — Minas de San Rafael, Sierra Tablon (near Cerritos?), *Purpus 5502* im. fr. (CAL, CM, GH, NY, US). — 16–18 mi. by road e. of Ciudad del Maiz, oak forest, alt. 3800 ft., *W. E. & M. S. Manning 53424, 53432* fr., *53426* (WEM). — 23 m. e. of Ciudad del Maiz, oak forest, alt. 2200 ft., *W. E. & M. S. Manning 53440* (WEM). — 4 mi. w. of Pendencia (about 10 mi. ne. of Ciudad del Maiz), alt. 4600 ft., *Graber 206* fr. (US). GUANAJUATO: Palmillas, Río Palmillas, 25 km. ne. of San Luis de La Paz, *Little 11093* (USFS, WEM). HIDALGO: n. of Jacala, *Clark 7029* (OKLA). — 6–10 mi. n. of Jacala, alt. 4900–5400 ft., *W. E. & M. S. Manning 53582* fr., *53594* fr., *53595* fr., *53600* (WEM). — Jacala, alt. 4400 ft. *Chase 7624* fr. (CM, GH, ILL, MO, NY, USDA); *Lyonnel 1304* fr. (US). — 6–7 mi. s. of Jacala, Sierra Madre Oriental, alt. 5000–5400 ft., *Reynolds 6826* fr. (REY, WEM); *W. E. & M. S. Manning 53641, 53643* fr., *53645, 53646, 53647* fr., *53648* fr. (WEM). — 13 mi. s. of Jacala, alt. 6200 ft., *W. E. & M. S. Manning 53636* (WEM). — SW. of Jacala on road to Zimapán, district Jacala, alt. 1500 m., *Moore & Wood 3946* fr. (BH, WEM). — La Majada, on route 1, 229 or 222 km. n. of Mexico City (about 20–29 mi. s. of Jacala), alt. 6400 ft., *Sharp, Hernandez X., Crum & Fox 5020* (NC, TENN, WEM); *W. E. & M. S. Manning 53623, 53624* (WEM). — Between Zacualtipán and Olatla, Río Panotlán, on road to Metzitlán, alt. 1600–2000 m., *Moore 5328* fr. (BH, CAL, WEM), *3241* im. fr. (BH, GH), *2386* stam. (BH, GH). — NE. of Molango, slopes below Chalma on trail from Molango to Calnali, *Moore 3013* im. fr. (BH, GH). — Sierra de la Mesa (probably w. of Ixmiquilpan), *Rose, Painter & Rose 9095* fr. (GH, NY, US). PUEBLA: Zacapoaxtla, *J. Salazar*, in 1913, stam. (MEX, US).

This species has a wide distribution and has been well known in Mexico ever since it was first described. It is difficult to separate it sharply from some of the other species. *Juglans mollis* differs from *J. pyriformis* in having fewer, broader, more fascicled-hairy leaflets, shorter staminate catkins, less verrucose husk and less deeply grooved nuts. Vegetatively, trees of this species in certain regions are similar to *J. hirsuta*, as discussed under that species and below, but the nuts are different. The nuts of *J. mollis* are rather similar in external markings to those of *J. pyriformis*, *J. major*, and *J. olanchana* var. *standleyi*, though there are differences in size and depth of grooves. Because of the extent of variation no single feature will hold throughout but two or more must be used in combination. The distinctions in nuts and vegetative features are discussed under the other species and are given in part in the key to the species.

The fascicled-hairy lower surface of the leaflets is rather constant in the species. The rachises found on the type-specimen are strongly fascicled-hairy, and are similarly hairy on many specimens. In southern Nuevo León and in Hidalgo the rachises on some of the trees are strongly glandular-pubescent as in *J. hirsuta* and, as discussed under that species, it is difficult to distinguish the two species except where fruiting.

The rather moldy specimen collected on the Mesa de la Camissa, 15 miles southwest of Galeana (*Muller 1156*), called *J. mollis* by the writer largely because of its range, resembles *J. major* var. *glabrata* in being much less hairy throughout (leaflets, rachis, fruit) and having essentially tapering leaflet bases but probably represents an aberrant collection from abnormal branches of *J. mollis*; mature fruit is lacking.

The original description of *J. mexicana* by Engelmann — "foliage as in *J. nigra*, but with the pubescence of *J. cinerea* —," i.e., with glandular-villous rachis and fascicled-hairy lower leaflet-surface, suggests *J. hirsuta*, not *J. mollis*. However, although the specimens of *Pringle 3322* (the type-collection of *J. mexicana*) in some herbaria have glandular-pubescent rachises, such as occur in *J. hirsuta* (also in *J. cinerea* and *J. nigra*), specimens in some other herbaria have fascicled-hairy rachises, and in others glabrate ones. The nut is clearly that of *J. mollis*, not *J. hirsuta*, though the lips on the nut are unusual for any species. This collection is the one illustrated by Dode for *J. mollis* (1909, p. 175). Sargent (1902), in his description and excellent illustration of *J. mexicana*, combines collections of *J. hirsuta* and *J. mollis*; in general, the flowers are *J. hirsuta* (*Pringle 10214*, Sargent), and the fruit is *J. mollis* (*Pringle 3322*); the figure of the leaves with the unusual leaflet-bases was made from an atypical specimen of *Pringle 3322*.

Two collections by the writer (*53250* and *53645*), presumably variants of *J. mollis* because all other trees in the region are that species, do not have fascicled hairs on the upper surfaces of the leaflets.

A collection of nuts at the Arnold Arboretum, marked *J. mexicana*, presumably sent by Newton Pierce, of U.S.D.A., who was stationed in California, are *J. mollis*, though two nuts do not belong to that species and may have been mixed in the herbarium from a collection from Colombia. Unfortunately the source in Mexico is not given.

The writer has not recorded *J. mollis* from Durango. However, certain specimens called by the writer *J. major* forma *stellata*, especially *Palmer 448* and *476*, appear similar to *J. mollis* in leaflet-base and hairiness; the rachis is glandular-pubescent as in *J. major* or certain trees of *J. mollis*. The nut is smaller than in *J. mollis*, and has surface markings closer to *J. major*. The trees of this region need further study.

Juglans mollis and *J. hirsuta* both grow in Nuevo León, but not together. The latter appears to grow at lower elevations (or possibly in different habitats: stream valleys instead of mountain fog belts). Thus at Chipinque Mesa, near Monterrey, *J. hirsuta* grows at the foot of the mesa at about 1800 ft. elevation and *J. mollis*, several miles away by winding road, grows near the top of the mesa at about 4000 ft. elevation, at the most northerly point in the range of the species. Unfortunately the trees of the latter collected by the writer were not fruiting, and the identification is not positive. A similar situation occurs with respect to the Linares (*J. hirsuta*) and Pablillo (*J. mollis*) collections.

4. **Juglans major** (Torr.) Heller, Muhlenbergia 1: 50. 1900. — Standley, Contrib. U. S. Nat. Herb. 23: 165. 1920. — Johnston, Jour. Arnold Arb. 25: 436. 1944.

Juglans rupestris Engelm. ex Torr. *β major* Torr. in Sitgreaves, Rep. Zuni & Colo. 171, *pl. 16.* 1853. — Sudworth, Poplars, Principal Tree Willows and Walnuts of the Rocky Mountain Region, U.S.D.A. Tech. Bul. **420**: 102. 1934.

Juglans elaeopyren Dode, Bull. de l'Herb. Boissier, II. 7: 247–284, *figs. 1–3.* 1907.

Juglans neomexicana Dode, Bull. Soc. Dendrol. France **1909**: 191. 1909.
Juglans arizonica Dode, loc. cit. 193.
Juglans torreyi Dode, loc. cit. 195.
Juglans microcarpa Berl. var. *major* (Torr.) Benson in Benson & Darrow, Trees and Shrubs of Southwestern Deserts, ed. 2, 110. 1954.

Small or large tree, sometimes with several trunks; young twigs light to dark brown, finely whitish glandular-pubescent or -puberulent, the second year's growth slender, usually ashy gray or sometimes yellowish brown, with rather prominent lenticels; terminal bud slender; leaves unequally or sometimes equally pinnately compound, the terminal leaflet usually present; rachis usually finely whitish glandular-pubescent, rarely glabrate, very rarely (on special branches: young growth?) glabrous; leaflets 9–15, rarely to 17, opposite or alternate, subsessile or short-stalked, oblong-lanceolate to ovate, the larger ones usually 2–3.4 cm. wide (or rarely 1.5–1.9 cm.), and 6–11.5 (rarely –13) cm. long, typically tapering at the base, characteristically oblique, acuminate at the apex, commonly tapering from the middle of the leaflet to the apex, definitely serrate, but varying from finely to coarsely serrate; youngest leaflets mostly glandular-puberulent, very rarely fascicled-hairy, the mature ones usually lightly puberulent above and densely whitish glandular-pubescent beneath as well as densely golden-glandular (lepidote), varying to partly fascicled-hairy (forma *stellata* below), very rarely glabrate; staminate catkins 7–17 cm. long, slender, the individual floral bracts small, whitish-tomentose, on the backs of the flowers; sepals, in addition to the bract and two bracteoles, 4–8; stamens 30–50; pistillate flowers solitary or few, glandular-pubescent; fruit globose to rather oval, the husk rather thin, finely glandular-pubescent, inconspicuously verrucose, usually 2.3–3 (rarely 1.9) cm. in diameter; nut 1.8–2.8 cm. in diameter, subglobose, slightly compressed, longitudinally striate, sometimes rather deeply so; dorsal partition varying from low to rather high, the lacunae 8–4, depending upon the level, typically well developed for the size of the nut, rarely reduced to barely more than a canal.

VERNACULAR NAMES: *nogal; nogal silvestre.*

SONORA: 5 mi. s. of Naco, San Jose Mts., alt. 6000 ft., *Wolf 2518* fr. (GH); *Mearns 1049* (NY). — Matiti (or Mababi, 10 mi. sw. of Fronteras), *Thurber 409* fr. (GH, NY). — 9 mi. e. of Imuris in canyon of Magdalena river, alt. 3100 ft., *Ferris 8778* stam., fr. (MICH, US). — NE. of Colonia Morelos, Cañon de la Mescalera, Sierra de la Caballera, alt. 4900 ft., *White 4704* (GH, NY). — Colonia Oaxaca (about 25 mi. n. of Bavispe, on Rio Bavispe), *White 464* (GH, MICH). — La Angostura, Cañon de los Otates, *White 3527* (GH, MICH, USDA). — NW. of Bavispe, Cañon International, *White 3496* (GH, MICH, USDA). — W. of Bavispe, Cañon de Bavispe, *White 2994* (GH, MICH, USDA). — Bavispe, Cañon de los Metates, *White 2824* (GH, MICH). — Bavispe, Río Bavispe, *White 2875* fr. (GH, MICH). — Santa Rosa Cañon (between Bavispe and S. Miguelito), *White 499* (MICH). — W. of Magdalena, Aqua Nuevo Arroya, El Alamo, *Kennedy 7040* fr. (CAL, CM, US). — Horconcitos, Rio Huachinera, n. of Huachinera, *White 2971* (GH, MICH, USDA). — La Chumata (a mine, e. of Sierra de San Antonio, probably in the vicinity of Banamichi), alt. 3400 ft., *Brown*, in 1905 (AA). — Between Granados and Bacadehuachi, Aguaje de

Bacatejaca, *White 2925* (GH, MICH). — Curohui, Río Mayo, *Gentry 3642* im. fr. (CM). CHIHUAHUA: Municipio de Janos, Carretas, border of Chihuahua and Sonora, alt. 4800 ft., *White 2616* (GH, MICH, USDA). — Casas Grandes, *Goldman 427* im. fr. (GH, US). — St. Diego, *Hartman 588* stam. (AA, GH, K, P). — W. of Chihuahua, mouth of Majalca Cañon, *Le Sueur 448* fr. (CAL, CM); *Le Sueur*, in June 1936, fr. (GH). — Chihuahua, alt. 1300 m., *Palmer 141* stam., pist., fr. (GH, K, MO, NY, ST). — Chihuahua, canyon near city, *Pringle 1596* stam., pist. (CAL, K, MEX, MS). — 7.5 mi. e. of Victoria, road from Jaco to Mestenas, *Stewart & Johnston 1999* fr. (GH). SINALOA: Quebrado de Platano, Sierra Monterrey, deep moist canyon in oak forest, alt. 3000 ft., *Gentry 5908* (USDA). DURANGO: Nombre de Dios, alt. 6500 ft., *W. E. & M. S. Manning 531291, 531293, 531294, 531296* fr., *531297* (WEM).

Sargent (1933) described the staminate catkins as 20–25 cm. (8–10 inches) long; the writer has examined specimens from Mexico and the United States and finds that the catkins are 7–17 cm. long as given in the description above.

Dode (1909, pp. 191–195) in his descriptions of *J. arizonica*, *J. neomexicana*, *J. elaeopyren*, and *J. torreyi* gave the number of leaflets as 8–24, 8–20, and 10–20, numbers intermediate between *J. major* and *J. microcarpa*. Studies by the writer of the isotypes of these species in the American herbaria show that the number of leaflets is 11–13 in *J. neomexicana* and *J. elaeopyren*. Isotypes of *J. arizonica* so far have not been located in the United States but most specimens of *J. major* from Arizona have 15 or fewer leaflets. *Juglans torreyi* is based on plants cultivated in France. It should also be noted that all fruits located of the isotypes of Dode's species have only immature fruits, and it is difficult to see how Dode could have described the structure of the nuts from specimens such as these.

Dode discarded the name *Juglans major* (Torr.) Heller, because in the description of the species Heller included both *J. rupestris* var. *major* Torr. and *J. californica* S. Wats. The name *J. major* (Torr.) Heller is, however, based definitely on *J. rupestris β major* Torr. which in turn is based on material from Arizona and New Mexico. Hence, the name *J. major* should be retained.

The writer is dividing *J. major* into two main races, the northern race being the well known typical taxon, ranging from Arizona and New Mexico to Sinaloa and Durango, and a southern race, the variety *glabrata* described below with larger, glabrate leaves and larger fruits.

The detailed description given above is for the typical species, based upon Mexican specimens, and the deviations within this taxon, considerable in extent, will be discussed first.

At the beginning should be mentioned the variation in hairiness on the lower surfaces of the leaflets. This is sufficient to make the basis for the description of a new form:

4a. **Juglans major** forma **stellata** Manning, forma nova.*

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* A *J. majore* differt foliolis subtus pilis saepe fasciculatis.

A plant differing from the species in having many of the hairs on the lower surfaces of the leaflets fascicled, so that these surfaces appear somewhat tomentose. The leaflets of this form are more frequently subtruncate at the base than in the species proper.

Several sheets of specimens intermediate between the species and forma *stellata*, with a few fascicled hairs, are listed under *J. major* itself.

This form approaches *J. mollis* somewhat in leaflet structure, but the leaflets are usually smaller, the fascicled hairs usually shorter, the short, glandular hairs on the lower leaflet-surface more common, the hairs on the rachis usually paler and typically not fascicled, and the fruit and nut smaller. The leaves of this form are similar in some ways to those of *J. hirsuta*.

SONORA: 1 mi. w. of El Tigre, La Matancita, alt. 4250 ft., *White 4161* (GH, MICH). — 8 mi. from Cucurpe, fork of road to El Tigre, *Wiggins 7161* fr. (AA, US). CHIHUAHUA: 3 mi. w. Ciudad Camargo, alt. 4000 ft., *White 2284* fr. (GH, MEX, MICH, USDA). — Beyond village of Cocomorachic, Río Papagochic, District Guerrero, *Mexia 2633* im. fr. (TYPE-AA; ISOTYPES-CAL, CM, GEN, GH, K, MICH, NY, P, ST). DURANGO: Tejamen (s. of Santiago Papasquiaro), *Palmer 476* fr. (CAL, CM, COP, GH, MO, NY, US). — Santiago Papasquiaro, *Palmer 448* fr. (AA, CAL, CM, COP, K, NY, ST, US); *Nelson 4670* (GH, US).

In addition to the deviation described above there are other critical variations in rachis, leaflets, and fruit in the typical species.

The rachises on a very few specimens are glabrate or nearly glabrous, instead of pubescent. It is significant that in *White 2616* and *3527* the rachises and the leaflets are essentially glabrous in specimens in some herbaria, strongly pubescent in specimens of the same number in other herbaria.

The leaflet is usually very short-stalked, and oblique with tapering base, but sometimes the stalk is well developed, and sometimes the bases appear almost truncate above an extremely short stalk (leaflet subsessile) or above a well developed stalk. The teeth are definite but range from coarse to rather fine, though the leaflets are never revolute along the margin as *J. microcarpa*. The larger leaflets in *White 3496*, *Thurber 409*, *Kennedy 7040*, *Stewart & Johnston 1999*, *Le Sueur* in June 1936, are small and narrow, 1.5–1.9 cm. in width on the specimens observed by the writer.

The number of leaflets in Mexican collections appears to be rather constant, 9–15, rarely 17. For this reason *J. major* var. *stewartii* Johnston has been transferred to *J. microcarpa*, as discussed under that species.

In the shape of the fruit and nut (subglobose) and the lacunae of the nut (well developed), the Mexican collections appear to be rather constant where fruit is present but, since *J. elaeopyren* Dode with oval fruit and nuts has been described from Arizona, one may expect this variation from Mexico (see also *J. major* var. *glabrata* below). Dode describes the lacunae of the nut of *J. arizonica* (nuts not located by the writer) as reduced to a canal, as in *J. microcarpa,* an unusual condition for *J. major* if fully substantiated.

The size of the fruit and nut varies within rather broad limits. Thus *Palmer 448, 476, Mearns 1049, Wolf 2518,* and *Stewart & Johnston 1999* have fruits less than 2.2 cm. in diameter, with nuts 1.5–1.9 cm. in diameter. Some of these collections, especially the first two, have fruits of two sizes, indicating the possibility that some of the small fruits might represent abnormal collections or immature fruits. *Stewart & Johnston 1999* is listed by Johnston (1944) under *J. microcarpa,* and although the leaflets are rather long drawn out and the bases not clearly oblique, the leaflets are 14(16?) in number. The extreme on the larger size of fruit in the northern race is represented by a collection by *C. R. Biederman* from Garces, Arizona, found in the fruit collection of Arnold Arboretum. The nuts are 3.1 cm. in diameter.

In general, in the typical *Juglans major* the leaflets are 9–15, relatively narrow, whitish-pubescent beneath, as is the rachis; the nuts are relatively small (but larger than in *J. microcarpa*), striate or longitudinally ridged, with rather large lacunae as seen in cross-section of the nut.

From southern Durango to Guerrero there are trees present in scattered localities in the mountains similar to the northern race of *J. major* in having 11–15 leaflets, these short-stalked, lanceolate to ovate-lanceolate, with tapering leaflet-bases, and staminate catkins 8–16 cm. long, but differing in certain important features. This taxon, the southern race of the species, is here described as a new variety:

4b. **Juglans major** (Torr.) Heller var. **glabrata** Manning, var. nov.*

Juglans pyriformis Liebm. sensu Standley, Contrib. U. S. Nat. Herb. **23**: 165. 1920, pro parte.

Juglans glabrata Manning, Amer. Jour. Bot. **35**: 616. 1948, nomen subnudum.

Trees of this variety differ from typical *J. major* in having the leaflets and leaves commonly larger, the twig, the rachis and the leaflets appearing glabrous, the stamens 60–75, the fruit and nut larger, and the pith frequently not chambered.

Leaves 30–45 cm. long, and up to 25 cm. wide, the rachis appearing glabrous, but under a strong lens minutely and densely puberulent with extremely short-stalked brown glands, and with scattered evanescent small appressed fascicled hairs in addition to the typical sessile yellow glands, rarely completely glabrous; leaflets 2.3–3.4 cm. wide, 8–11.5 cm. long, occasionally 5.5 × 15 cm., the margin finely serrate, the lateral veins 13–22 pairs, some of them ending in the teeth, the youngest leaflets (1 cm. wide) drying dark, the lower surface grayish tomentose, soon becoming glabrate, the older leaflets with scattered, minute, brown, appressed, evanescent fascicled hairs (appearing to the naked eye as pinpoints) on the largest veins, appearing glabrous except under a very

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* A *J. majore* differt foliolis et foliis plerumque majoribus, rhachi et foliolis glabris, staminibus 60–75, fructu et nuce majore.

strong lens, not at all tomentose, the fascicled hairs without glandular bases, the surface lepidote with many pale glands, rarely completely free of hairs; upper surface of mature leaflets glabrous or with scattered minute appressed fascicles of hairs along the veins; sepals of staminate flowers, in addition to bract and two bracteoles, commonly 6–8, or even 14; young pistillate flowers whitish-tomentose; immature fruit pyriform, densely to lightly fascicled hairy, the hairs minute, evanescent, to rather glabrate, about 2 flowers on each peduncle, the peduncle proper 2 cm. long, peduncle and rachis together 2.5–3 cm. long; mature fruit about 3.6 cm. in diameter, 4 cm. long, with thin husk, wrinkled when dry, very inconspicuously verrucose, subglobose to broadly ovate, with some scattered glandular pubescence; nut dark brown, subglobose to ovate, 3–3.4 cm. in diameter, 3–4 cm. long, with broad, flat-topped to rounded fairly high to shallow broken ridges, the general appearance essentially strongly longitudinally striate; secondary partition rather high, the primary wall lacunae absent.

Vernacular names: *nogal; nogal de Uriqui* (Jalisco, fide Martinez).

DURANGO: San Ramon (80 mi. w. of Tepehuanes, nw. Durango), *Palmer 104* im. fr. (GH, K, NY, US). — Sianori, alt. 800 m., *Ortega 5350* stam. (K, MEX, US). JALISCO: Guadalajara, *Rose & Hough 4805* im. fr. (US). MICHOACAN: Coalcomán, Sierra Naranjillo, alt. 1350 m., *Hinton 13759* stam. (GH, US). MEXICO: Naranjo, district Temascaltepec, *Hinton 3807* stam., pist. (K, NY, ST, US). — Luvianos, district Temascaltepec, *Hinton 3973* im. fr. (TYPE-AA, K, US). GUERRERO: Acamixtla, n. of Taxco, *Martinez* in 1942 fr. (WEM). — 7 mi. ne. of Taxco, ravine by stream, alt. 6000 ft., *W. E. & M. S. Manning 531005* fr., *531020, 531021, 531023* fr. (WEM). — Chilapa, *Hernandez X. X3167* fr. only (WEM).

This variety may, upon further study, prove to be a distinct species. The writer was unable to locate trees of this taxon in the Guadalajara region. Nuts from the original collection at Guadalajara were planted in California, and fruiting trees are now found at Davis and Riverside. These trees are used as the source of understock for buddings of *J. regia*; they are reported to be subevergreen there, being without leaves for less than a month. In Taxco, wood presumably of this taxon is used locally to make fine furniture.

This taxon is similar to *J. mollis* in having 11–15 leaflets and rather large fruits. The bases of the leaflets are typically tapering in *J. major* var. *glabrata*, and rounded or truncate in *J. mollis*, but as the leaflets are commonly oblique in most species this distinction is not always evident. The lower surface of the leaflets is glabrate or with a few appressed fascicled hairs in *J. major* var. *glabrata* and tomentose in *J. mollis*. The rachis of *J. mollis* is much hairier, with either fascicled hairs or brown, glandular ones. The nuts of *J. major* var. *glabrata* are typically more deeply grooved than in *J. mollis*. As mentioned under *J. mollis*, *Muller 1156* from Nuevo León may be *J. major* var. *glabrata*; this would represent a tremendous extension of range.

The differences between *J. major* forma *stellata* and the members of the northern race of *J. major* closest to *J. mollis,* are given under the description of that form.

The true distinctions between *J. major* and *J. microcarpa* have always been problematic and many authors consider *J. major* a variety of *J. microcarpa* (or of *J. rupestris*) since they seem to intergrade in their features. One reason for this in the United States may be that *J. microcarpa* and *J. nigra* may hybridize in certain regions, such as Oklahoma, and the resulting hybrids appear to be *J. major.*

Sudworth (1934) gave in his key (prepared by W. A. Dayton) the main distinctions separating *J. rupestris* and var. *major.* In addition, Johnston (1944, p. 437) states that the leaflets of *J. major* are evidently short-petiolulate, with the bases of the leaflets strongly oblique, with one side of the blade decurrent on the petiolule for at least a millimeter, while the curved, more elongate leaflets of *J. microcarpa* are subsessile with the blade decurrent only very obscurely, if at all. The writer agrees with Johnston, in general, but believes there is some deviation in both species. Scott (1954, Plate 15, figs. 17, 18, 20, 21) illustrates the seeds of *J. major* and *J. microcarpa* as quite different and he believes that these features will always separate the two species. Preliminary observations by the writer, however, indicate that the embryo of *J. major* as figured by Scott is not typical of the species and that most of the seeds are closer to the illustration of *J. microcarpa.* Consequently, Scott's distinction does not hold. This feature, however, is worth further study. Scott made his study by filling the seed-cavities of the nut with soft metal, after which he removed the woody pericarp with strong sulphuric acid, leaving a metallic cast of the seed. The writer has cut nuts in half, then painted the seed cavity with latex, and finally removed the mold of the upper half of the seed.

Since the writer's key to the species brings out only one or two distinctions between *J. microcarpa* and *J. major,* species which grow not far from each other and which are often confused, Sudworth's key is repeated here with some changes and additions. This key applies primarily to the northern race of *J. major,* as this taxon is closer to *J. microcarpa* than the southern race.

1. Leaflets 17–23, rarely to 31, lanceolate, mostly narrowly so, about 1–1.5 cm. broad, usually falcate, finely serrate or nearly entire, subsessile, mostly rounded at the base, long tapering at the apex; fruit 12–20 mm. in diameter; nut 10–17 mm. in diameter, the lacunae of the wall much reduced; stamens about 20–30; much-branched, round-headed shrub or small tree, ranging from Texas to western Oklahoma and southeastern New Mexico into nw. Nuevo León, Coahuila, and ne. Chihuahua. . . . . *J. microcarpa.*

1. Leaflets 9–15, rarely 17, oblong-lanceolate to ovate, 1.7–3.4 cm. broad, acuminate, usually coarsely serrate but sometimes finely serrate, usually short-stalked, strongly oblique, with one side of the blade decurrent on the stalk for at least a millimeter; fruit mostly 23–35 mm. thick; nut 18–30 mm. in diameter, the lacunae of the wall prominent; stamens about 30–50;

medium-sized tree, occasionally 50–60 feet high, with well-defined trunk and narrow crown, ranging from central and southern New Mexico and Arizona to Chihuahua, Sonora, Sinaloa, and Durango. . . . . *J. major.*

The range of typical *J. major* is shown in the key above. Details of the range in the United States will be found in Sargent (1933), Sudworth (1934), and Benson (1944). The distribution as shown on the map in Sudworth is not accurate for Mexico. The distributions in Mexico of *J. major*, its one variety and one form is shown on Map 1 of this paper.

5. **Juglans microcarpa** Berlandier in Berl. & Choval, Diario Viage Comision de Limites baja Mier y Teran 276. 1850; Johnston, Jour. Arnold Arb. **25**: 436. 1944.

Juglans nana Engelm. Proc. Amer. Assoc. Adv. Sci. **5**: 226. 1851.

Juglans rupestris Engelm. ex Torr. in Sitgreaves, Rep. Exped. Zuni & Colorado Rivers 171, *t. 15.* 1853; Dode, Bull. Soc. Dendrol. France **1909**: 189. 1909; Standley, Contrib. U. S. Nat. Herb. **23**: 165. 1920; Sudworth, Poplars, Principal Tree Willows and Walnuts of the Rocky Mountain Region, U.S.D.A. Tech. Bull. **420**: 98. 1934.

Juglans subrupestris Dode, Bull. Soc. Dendrol. France **1909**: 191. 1909.

Much-branched, round-headed shrub or small tree; young twigs slender, orange-red and strongly lenticellate, finely whitish glandular-pubescent or -puberulent during their first winter, the second year slender, ashy gray, often puberulent; terminal bud slender; leaves moderate or small, usually unequally pinnately compound; rachis usually finely whitish-puberulent; leaflets usually 19–23, rarely 17 or more, opposite or alternate, subsessile, lanceolate or narrowly lanceolate, usually 1–1.5 cm. wide (or to 1.9 cm. in var. *stewartii*), and 5–8(–11?) cm. long, typically rounded at the base, but occasionally oblique, acuminate and long-tapering at the apex, usually falcate, finely serrate or frequently revolute and almost entire, finely pubescent beneath or rarely glabrate; staminate catkins 7–11 cm. long, very slender, the individual floral bracts small, whitish-tomentose, on the backs of the flowers; stamens 20–30; pistillate flowers solitary or few, whitish- or reddish-puberulent; fruit globose or subglobose, pubescent or puberulent, 1.2–2.1 cm. in diameter; nut 1–1.7 cm. in diameter, subglobose, longitudinally ridged or striate, sometimes with definite dorsal lips; dorsal partition rather low, lacunae typically reduced to canals or almost points.

Vernacular names: *nogal; nogalillo.*

NUEVO LEON: Lampazos, Rancho Resendez, *Mary T. Edwards 420* fr. (CAL, MEX). COAHUILA: Cañon de San Enrique, east side of Sierra de la Encantado, nw. Coahuila, *Stewart 1390.* — Cañon del Indio Felipe, Sierra Hechiceros, close to Chihuahuan border, lat. 28° 33′, *Stewart 134A* (GH). — 6 mi. e. of El Tule, 24 km. n. of Castillon, and close to Chihuahuan border, southern foothills of igneous Sierra Hechiceros, *Stewart 482* fr. (GH). — Sabinas, *Nelson 6787* (or *6187?*) fr. (COP, ST, US). — Musquiz, Hacienda Mariposa, near Puerto Santa Ana, *Wynd & Muller 283* (GH, ILL, K, MEX, US). — Musquiz, Flores Pasture, Hac. Mariposa, *Marsh 313* fr. (GH). — Vicinity of La Noria, Sierra del Pino, *Johnston & Muller 509* fr. (GH). — Municipio de Castanos, cañon Bocatoche, *Muller 3120* fr. (CAL, GH, USDA, WEM). — 9 mi n. of Hipolito, *Johnston 7229* fr. (GH). — Guadeloupe, *Aguirre* in 1942, pist. (NY, WEM).

This species is the smallest in stature and has the smallest fruit of any known walnut. It is easily distinguished from all other species of *Juglans* of Mexico, with the possible exception of *J. major*, by the narrow leaflets and small fruit. The differences between *J. microcarpa* and *J. major* are discussed above under the latter species and in the key given there is the range of the species in Mexico and the United States. The distribution in Mexico as shown on the map in Sudworth (1934) is not accurate.

In northwestern Coahuila and northeastern Chihuahua there are shrubs or trees intermediate in certain respects between *J. microcarpa* and *J. major*. This taxon, possibly a hybrid race, has been called *J. major* var. *stewartii* by Johnston, but because the number of leaflets is within the range of *J. microcarpa*, this variety is here transferred to that species:

5a. **Juglans microcarpa** Berlandier var. **stewartii** (Johnston) Manning, comb. nov.

Juglans major (Torr.) Heller var. *stewartii* Johnston, Jour. Arnold Arb. **25**: 437. 1944.

COAHUILA: Sierra Hechiceros, Cañon del Indio Felipe, nw. Coahuila, *Johnston & Muller 1358* fr. (TYPE-GH); *Stewart 134* fr. (GH). — CHIHUAHUA: Cañon de la Madera, southeastern flank of Sierra Rica, north of Rancho de la Madera, oak pinon belt, (west of Manuel Benavides or San Carlos), tree or shrub, *Stewart 2557* (GH).

This variety has the number of leaflets 17–21 (or to 32 in *Stewart 2557*), these with long drawn out tips, as in *J. microcarpa*, but the leaflets are frequently broader (1.1–1.9 cm. wide), usually with an oblique base; the fruits average larger (1.8–2.5 cm. in diameter). In the single, probably atypical specimen of *Stewart 134* there are only 17 leaflets, but the other collections given above have higher numbers. The writer believes that *Muller 7968*, from Chisos Mts., Brewster Co., Big Bend National Park, Texas belongs to this variety; in the nuts of this specimen the lacunae are rather large.

Johnston (1944), in discussing the variety, states "A plant agreeing with the western *J. major* in its arborescent habit, large fruits, and oblique leaflet-bases, and resembling *J. microcarpa* in its numerous elongate leaflets."

6. **Juglans olanchana** Standley & Williams, Ceiba 1: 76. 1950.

Juglans guatemalensis Manning, Amer. Jour. Bot. **35**: 616. 1948, nomen subnudum; in Standley & Steyermark, Flora of Guatemala, Fieldiana: Botany **24**(3): 356. 1952.

Medium-sized or large tree the bark dark and deeply furrowed; twigs dark brown, appearing glabrate, but minutely glandular-puberulent, the lenticels prominent; leaves large, mostly 45–65 cm. long and 30–35 cm.

wide, the terminal leaflet usually present; leaflets large, distant, chiefly 17–21, each 14–17 cm. long and 5–6 cm. wide, decidedly stalked, the stalk 2–4 mm. long; leaflets finely to strongly serrate, oblong-elliptic to ovate, obliquely truncate or rounded at the base above the stalk, commonly cuneate on the lower side, long-acuminate at apex, the lowest leaflets frequently small; lower surfaces of leaflets glabrate, with only a few stalked glands and a few minute fascicled hairs on midrib and a few on larger lateral nerves, inconspicuously lepidote, young leaflets with whitish pointed hairs on the smallest veins; very young leaflets drying green, with almost no fascicled hairs beneath; upper surface of leaflets glabrate; rachis glabrous or glabrate, but under a strong lens appearing densely puberulent with minute stalked glands; staminate catkins (15–)22–30 cm. long, the bracts, small, 1 mm. long, obtuse, short-hairy, essentially on the catkin-rachis at the base of the flower-stalk throughout the catkin; flower-stalk well developed, 4–5 mm. long; the bracteole-sepal ring frequently with 8 organs; stamens 61–102; pistillate flowers and immature fruits unknown; peduncle and rachis of fruiting spike together 8 cm. long; mature fruit large, subglobose-pyriform, 4.3–4.5(–5.5) cm. thick and 4.7–4.8(–5.8) cm. long, to essentially glabrous, shining greenish brown, strongly and conspicuously white punctate-verrucose (warty), with the punctations open and lenticel-like, not wrinkled in drying, the husk thick; nut reddish brown, subglobose, slightly flattened, 3.4–4.5 cm. thick and 3.2–4.2 cm. long, strongly ridged, the ridges broad, flat-topped, interrupted, rather rounded in cross-section, the furrows comparatively shallow except at the depressed base of the nut, where the ridges are sharp and the furrows deep; primary wall cavities usually well developed at all levels, frequently united with tertiary wall cavities, and at the very base of the nut uniting also with secondary wall cavities; secondary wall-cavity ridges strongly projecting into the loculus at the one-celled level and at least in one collection at the 2-celled level; secondary septa rather low.

VERNACULAR NAMES: *nogal; nuez.*

GUATEMALA: Alta Verapaz: Tucuru, *Popenoe 265a* nuts only (AA, BPI). Baja Verapaz: Finca Chejel, *Popenoe 180a* nuts only (AA, BPI). Quiche: Finca San Francisco, Cotzal, alt. 3800 ft., *Skutch 1866* fr. (AA: TYPE of *J. guatemalensis*; CM, NY). Huehuetenango: 5 mi. se. of Barillas, Sierra de los Cuchumatane, cafetal of Finca Soledad, alt. 1150 m., *Steyermark 49544* fr. (CM, WEM). — Above Democracia on trail towards Jutal, alt. 1000 m., *Steyermark 51072* (CM). Guatemala: Antigua, cultivated in finca, Standley, in 1939, nuts only (CM). — Guatemala, cultivated, *Lewis 1125* stam. (CM); *Morales 624* stam. (US).

HONDURAS: Olancho: Catacamas, common in moist forest along rio de Catacamas, alt. 450 m., *Standley 18159* fr. (TYPE-CM, HON). — *Standley 18149* stam. (CM, HON). Morazan: Mont. de la Flor., Rio Guarabuqui, *Molina A-3009* fr. (CM). — Along river, alt. 2600 ft., *C. & W. Von Hagen 1271* (CM, NY).

SALVADOR: cultivated: San Salvador, *Standley 22637* (GH, NY, US). — *Calderon 1528* stam. (GH, US). — Finca San Nicolas, *Calderon 1570* im. fr. (US). — Playa Santiago de Maria, Dept. Usulutan, alt. 150 m., *Carlson 656* (CM). —

Dept. Sonsonate, brush slope south of headquarters of Hacienda Las Tablas, near Rio Acachapa, Balsam Range, alt. 660 m., *Tucker 1364* fr. (CAL, GEN, NY).

NICARAGUA: cultivated: Dept. Managua, vicinity of Casa Colorado near El Crucero & summit of Sierra de Managua, planted in hedge of finca, *Standley 8209* (CM).

The description above seems to differ radically from the original description by Standley & Williams of *J. olanchana.* Their description reads, in part: "folia magna, 10–12-foliolata, petiolata, rhachi dense puberula; — amenta mascula — 13–17 cm. longa." The writer has studied the two sheets cited by these authors, and believes that the leaflets, some of which have fallen off, are more numerous than stated in the description; the difference in the description of the pubescence is merely a matter of interpretation.

As stated in the Flora of Guatemala, "The collections of Popenoe and of Standley (in Guatemala) are represented only by nuts, and there is some uncertainty about the identification; the collection of Steyermark has the internal cavities absent at the end of the primary partition in the nut. This may be the species reported by Rene Guerin (as *nogal, Juglans nigra*), in Catalogue des products presentes par la Republique de Guatemala a l'exposition universalle de Paris, 1900, from Coban, Alta Verapaz; Cuilapa, Santa Rosa; Chimaltenango, Zacapa, and Chiquimula."

This native walnut (*J. olanchana*) of Guatemala and Honduras has been called for many years *Juglans pyriformis* and is undoubtedly closely related to it. The fruit of *J. olanchana* is quite similar to the fruit of *J. pyriformis,* but the leaves are entirely different, with the leaflets mostly 17–21, strongly stalked, frequently cuneate at least on the lower side at the base, as opposed to leaflets 19–31, sessile, truncate. The cross section of the nut of *J. olanchana* resembles that illustrated by Dode (1909) for *J. peruviana* (*J. boliviana,* according to the writer).

The identification of *Steyermark 51072* is uncertain, as the young leaves have 17–25 leaflets, which are slightly more hairy than in typical *J. olanchana* with colorless pointed hairs beneath.

Certain specimens cultivated in Salvador (i.e. *Calderon 1570*) are quite different from what the writer considers typical *J. olanchana* and closely resemble *J. major* var. *glabrata* in having smaller leaves, fewer (13–15), narrower (2.5–3.5 cm. wide by 8–11.5 cm. long) leaflets whose bases are strongly cuneate on both sides. In *Calderon 1528,* which has about 19 leaflets but small and narrow as in *Calderon 1570,* the staminate catkin is only 9 cm. long. *C. & W. Von Hagen 1271,* from Honduras, is similar to these specimens, although it should be noted that *Molina A3009,* from the same general region, has leaves characteristic of *J. olanchana.* Mature fruits are lacking on these specimens. Whether these atypical specimens are variants of *J. olanchana,* poorly collected specimens of *J. olanchana* (such as young shoots), true *J. major* var. *glabrata,* or a different species is uncertain. These plants need further study. It should be pointed out that Standley & Calderon, in Lista Preliminar de las Plantas de El Salvador, in 1935, stated that *Juglans pyriformis* Liebm., *nogal*, planted in many places in Salvador, was introduced from Mexico. The writer believes that all walnuts in Salvador and Nicaragua have been planted, and most specimens from these countries are so marked; no statement, however, is made on the labels of *Carlson 656* and *Tucker 1364*.

Skutch states, in a note concerning his specimen, that near Cotzal "there were a number of huge trees standing in the cleared lands near the river, 175 feet high. From the size and appearance of the trees, coupled with what I heard of the relatively recent date of the clearing, I had no doubt that they were relics of what must have been an extraordinarily magnificent forest. They were associated with a sycamore which here also seemed to be near the southern limit of its range." Popenoe, concerning his No. *180a* states that "the tree, seen occasionally on mountain sides and along water courses, at elevations of 1500–4500 ft. . . . . is only moderately large, rarely reaching a greater height than 40–45 feet."

Record & Hess (1943) state that a wood, *Yale 300*, probably a walnut, called "Cedro Nogal" has been obtained in Copare, Honduras. In a recent letter William L. Stern, of the Yale School of Forestry, has informed the writer that *Yale 300* is called "Cedro Negro" and came from the Comya district, Dept. of Copan, Honduras. This wood was exhibited at the 1904 St. Louis Exposition.

Two collections from western Mexico are similar to *J. olanchana* in having large leaves with 17–20 large, lanceolate to oblong-lanceolate leaflets, staminate catkins 23–29 cm. long, the bracts of the large flowers short, located on the rachis or the very base of the pedicel, large light brown nuts strongly longitudinally furrowed with broad flat ridges. These are here described as a new variety:

6a. **Juglans olanchana** Williams & Standley var. **standleyi** Manning, var. nov.*

This differs from typical *J. olanchana* in having the twigs, rachis, and leaflets conspicuously hairy, and the leaflets essentially sessile or with a short broad stalk, tapering somewhat on both sides at the base but especially on the lower side.

Twigs densely glandular-villous with whitish hairs, gummy (fide Ynes Mexia); rachis stout, densely and strongly pale-brown glandular-villous; leaflets 12 cm. long and 4–4.5 cm. wide, conspicuously and densely finely whitish tomentose with fascicles of long hairs beneath, each fascicle lacking a bulbous base, with strong tufts of hairs at bases of side veins, very finely and remotely serrate, appearing nearly entire, possibly because of the subrevolute margin, lepidote under the hairs with golden glands, the midrib with glandular hairs; upper surface of leaflets with most of strong veins glandular-pubescent, some fascicled hairs being present toward base of midrib; pistillate flowers unknown; husk of fruit unknown; nuts subglobose, 3.2–3.5 cm. in diameter, 3.2 cm. long, somewhat compressed.

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* A *J. olanchana* differt ramulis, rhachibus et foliolis conspicue pilosis, foliolis subsessilibus, basi angustatis.

COLIMA: San Antonio, *Reiche*, in 1913, stam. (MEX). JALISCO: San Sebastian, Sierra Madre Occidental (Sierra Madre del Sur?), *Ynes Mexia 1438* fr. (TYPE-NY; ISOTYPES–AA, CAL, CM, GH, GEN, MICH, MO, US, BPI).

Husks which might correlate this variety more fully with *J. olanchana* have not been collected. This taxon may prove, upon further study, to be a distinct species.

The hairs are somewhat similar to those of *J. mollis* or *J. hirsuta,* but are extraordinarily developed; the leaflet base, the length of the staminate catkin, the position of the staminate bract, and the nuts are quite different.

7. **Juglans steyermarkii** Manning in Standley & Steyermark, Flora of Guatemala, Fieldiana: Botany **24**(3): 358. 1952; in Amer. Jour. Bot. **35**: 616. 1948, nom. subnud.

Tree about 50 feet tall, the bark gray and furrowed; twigs densely glandular pubescent; terminal bud elongate, densely grayish tomentose; leaf-scar only slightly notched; leaves large, up to 60 cm. long and 30 cm. wide, the terminal leaflet usually absent; rachis conspicuously pubescent with reddish glandular hairs; leaflets large, distant, mostly 16–18, each 14–17 cm. long and 5–8 cm. wide, essentially sessile or very short-stalked, ovate or ovate-lanceolate, typically finely but rather remotely serrate with the serrations shallow and turned outward, and with most of the small veins terminating in the teeth rather than the sinus; upper surface of leaflets pubescent with minute glandular hairs, the lower surface pubescent with reddish glandular hairs on larger and smaller veins and especially on the midrib and with solitary or paired whitish pointed hairs on the surface and smaller veins; base of leaflet usually truncate to broadly rounded, the apex acute or abruptly acuminate, the lowest leaflet somewhat reduced; flowers unknown; nearly mature fruit wrinkled, subglobose-pyriform, truncate at the base, 4 cm. in diameter and 4.5 cm. high, strongly pubescent with reddish glandular hairs; punctations numerous, drying brown, very inconspicuous; husk not very thick; nut apparently deeply grooved, with rounded ridges, but nut immature; cavities present in the wall at each end of the primary partition.

VERNACULAR NAME: *nogal.*

GUATEMALA: Huehuetenango: Paso del Boqueron, along Rio Trapichillo, below La Libertad (west of Jacaltenango, almost on Mexican border), alt. 1200–1300 m., *Steyermark 51140* fr. (CM, WEM).

This species is completely different vegetatively from *J. olanchana*; the husk is different, also. Unfortunately the nut is immature, so that it is impossible to compare the nuts of the two Central American species.

Although *J. olanchana* has a fruit similar to that of *J. pyriformis* of eastern Mexico, it is similar to the species of western Mexico in its narrow leaflet bases and type of hairiness. *Juglans steyermarkii,* on the other hand, is similar vegetatively to the eastern Mexican species with truncate leaflet bases and brownish pubescent rachises. The differences between *J. steyermarkii* and the eastern Mexican species are given in the main key to species.

Both *J. olanchana* and *J. steyermarkii* occur within a few miles of the border of Chiapas, Mexico, and it is very probable that one or both species may occur in that state of Mexico.

INTERRELATIONSHIPS OF SPECIES OF THE NEW WORLD

With the exception of *Juglans cinerea,* all species of the New World are closely related and have probably evolved from one or two common ancestors.

Juglans boliviana (C. DC.) Dode and *J. columbiensis* Dode, of South America, are similar in vegetative features to *J. olanchana* and *J. major* var. *glabrata. Juglans neotropica* Diels, of northern South America, has truncate leaflet-bases as in *J. mollis. Juglans australis* Griseb. of Argentina and Brazil is similar to *J. major.*

The one (two?) species of *Juglans* of the West Indies is similar vegetatively to *J. olanchana* and *J. pyriformis* but is also similar to *J. columbiensis* Dode of Venezuela.

The nuts of all species of Latin America are very similar, most of them having rather flat-topped ridges. It is almost impossible to identify positively any nut of this area by itself. Dode (1909) has natural-size drawings of the nuts of many species, showing for each nut the external appearance, a cross-section at the middle, and a longitudinal section along the dorsal partition. These illustrations include not only the Mexican species but also the species from South America and the West Indies. The Mexican species illustrated are *J. pyriformis* Liebm., *J. mollis* Engelm. (represented by *Pringle 3322* which is unusual in having dorsal lips), *J. major* (Torr.) Heller (as *J. arizonica* Dode, *J. neomexicana* Dode, *J. torreyi* Dode, *J. elaeopyren* Dode) and *J. microcarpa* Berlandier (as *J. rupestris* Engelm. and *J. subrupestris* Dode). The nuts of some species not illustrated by Dode, such as *J. hirsuta* Manning and an unnamed species of South America, with sharply ridged nuts, as in *J. nigra* L., are different.

The species of *Juglans* of South America and the West Indies will be treated by the writer in a later paper.

The species of *Juglans* of Central America probably gave rise to those of Mexico and the United States. There seem to have been three principal lines of evolution, an eastern, a western, and a central branching one. In the east *J. pyriformis* has arisen from *J. olanchana,* though the leaflet-bases are similar to those of *J. steyermarkii. Juglans olanchana* is represented in extreme western Mexico by its variety *standleyi.* In central Mexico *J. major* var. *glabrata* is similar in many ways to *J. olanchana* and has, in turn, evolved into the more eastern *J. mollis* and into the more western *J. major, J. microcarpa,* and *J. californica. Juglans mollis* has the truncate leaflet bases of *J. steyermarkii* and *J. pyriformis* and there may have been some cross breeding; *J. mollis* and *J. major* have fewer leaflets than typical *J. olanchana. Juglans hirsuta* seems to be a combination of *J. mollis* and *J. pyriformis*, though it might have evolved directly from *J. pyriformis*; *J. hirsuta* has in turn evolved into *J. nigra*.

McVaugh (1952) on page 332 (Map 10) shows the locations of many areas in northern Mexico and western United States where *Juglans* is found; he considers *Juglans* in that area to be one species, *J. microcarpa* Berl.

The map in this paper shows the localities where the seven species, three varieties and one form of *Juglans* treated in this paper have been collected. The legend on the map is self-explanatory.

A study of future collections may affect the concepts of taxa in this paper.

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VEGETATION ON BAUXITIC SOILS IN JAMAICA, II

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THE FIRST PART OF THIS PAPER (Jour. Arnold Arb. **38**: 1–41. 1957) described the vegetation of Jamaica in areas of commercial accumulations of bauxite ores and considered the relationship of this vegetation to the aluminum ions in the soils. Also considered were the effects of the mining operations on the vegetation as well as the terrain. The surveys of the vegetation made by the authors on lands to be mined and on lands adjacent to the mined-out areas where seed trees could contribute to the revegetation of abandoned mine pits were described. Certain pits from which the available bauxitic ore has been removed were designated as control pits to observe the invasion, succession and competition of natural reseeding. Other mined-out pits have been resurfaced or recontoured and planted to pasture grasses, stands of forest trees, or agricultural crops of vegetables and fruits. We have commented on the success of these rehabilitation attempts to the present.

Throughout their study of the vegetation on bauxite soils in Jamaica both authors have searched for undisturbed areas of vegetation in which could be found indications of a selection through survival of plants tolerant to or requiring aluminum ions for their persistence. Such plants they felt might be considered as indicators of aluminum concentrations and therefore of further aid in both an interpretation of vegetation types in other parts of Jamaica as well as being a valuable aid in the search for additional aluminum deposits. They have indicated that in neither the parish of St. Ann near the operations of the Reynolds Jamaica Mines nor in the parish of St. Elizabeth near the mining operations of Kaiser Bauxite Company could they find undisturbed areas of forest, shrub or herbaceous vegetation. All have shown the effects of man's long occupancy of the respective areas through gardening, pasturage or forest utilization. Mining operations are to the present being conducted on lands with a long history of agricultural usage. Further development in the parishes of Trelawny and Portland should reveal less disturbed vegetation associated with bauxite.

The following tabulation is a summary of our findings to date. Listed are the species which we have found by a careful study of the existing vegetation in the two principal areas of commercial bauxite mining in Jamaica. Species are listed according to the genera and families of their relationship and, for the sake of convenience, are alphabetical. The ferns and allied non-flowering plants have been grouped together. The monocotyledons are listed before the dicotyledons. Species lists are presented for the area of Reynolds Jamaica Mines operations in the parish of St. Ann and for the area of mining operations of the Kaiser Bauxite Company in the parish of St. Elizabeth. We have tabulated the species as they occurred in three arbitrary divisions for each area. Representatives of both the Reynolds Jamaica Mines and the Kaiser Bauxite Company were willing to indicate for us those areas which were to be mined immediately or in the near future. Our prime efforts were to obtain records, supported in most cases by herbarium vouchers, of the vegetative components on lands to be mined. Such areas comprised bauxite deposits at least five feet deep. They varied in surface area from two to nearly sixty acres. Many of these areas have since been mined out and of these some have been replanted. The species listed under the heading "To be Mined" were collected in such areas. Photographs document the original vegetation and subsequent stages of rehabilitation. Other areas too small or too shallow for commercial mining operations may have comparable concentrations of aluminum ions in the bauxitic soils. These were examined by us, but failed to yield any species not listed in the tabulation under "To be Mined."

Adjacent to, or intermingled with the bauxite ore bodies were limestone outcrops in the mining areas in both St. Ann and St. Elizabeth. The limit of bauxite soils in many cases was defined by the outcrop of limestone rock. Such areas of limestone rock will not be altered by mining operations. The vegetation on these outcrops has been studied and reported in the first part of this paper. One undisturbed, or at most slightly disturbed, unit of forest vegetation was found on such an outcrop in St. Elizabeth. In St. Ann every forest unit studied appears to have been cut selectively some time in the past. Nevertheless, one source of natural seeding in the mined-out pits will be from mature trees or shrubs located in the vegetation currently found on the limestone outcrops. The species we have collected in such areas are listed under the heading "Adjacent" for both St. Ann and St. Elizabeth. The vegetation of the limestone outcrops is perhaps the most typical expression of the native vegetation of each area. The differences between the native vegetation of the drier area in St. Elizabeth parish and that of the more moist area in St. Ann can be seen in these tabulations which are more complete than the quadrat and transect studies of PART I. We have listed the epiphytes and parasites for a complete record, even though the distribution of these cannot be attributed to the occurrence of bauxite soil.

A third tabulation under the heading of "Invaders" lists those species which have been observed in the control pits where only natural seeding and invasion has occurred as well as mined-out and rehabilitated pits where some species have been planted and others have appeared spontaneously. It is to be expected that this category will show additions as time goes by and some deletions as early invaders succumb to competition. All listings are based on field observations between December 1953 and September 1956. Specimens validating the species listed are filed in the herbarium of the Institute of Jamaica in Kingston, Jamaica, B.W.I., and in the Harvard University Herbarium in Cambridge, Massachusetts.

	REYNOLDS			KAISER		
	To be Mined	Adjacent	Invaders	To be Mined	Adjacent	Invaders
FERNS & FERN ALLIES						
Adiantum fragile			X			
Adiantum latifolium		X				
Adiantum pulverulentum		X				
Adiantum tenerum		X				
Aneimia adiantifolia		X				
Asplenium auritum		X				
Asplenium dentatum		X				
Asplenium jamaicense		X				
Cheilanthes microphylla		X			X	
Ctenitis effusa		X				
Dennstaedtia cicutaria			X			
Lomariopsis underwoodii		X				
Lycopodium linifolium		X				
Maxonia apiifolia		X				
Nephrolepis biserrata	X	X				
Nephrolepis exaltata	X	X		X		
Ophioglossum palmatum		X				
Paltonium lanceolatum		X				
Pityrogramma calomelanos		X				
Polypodium angustifolium		X				
Polypodium astrolepis		X				
Polypodium aureum		X				
Polypodium crassifolium		X				
Polypodium heterophyllum		X				
Polypodium lycopodioides		X				
Polypodium pectinatum		X				
Polypodium phyllitidis		X			X	
Polypodium phyllitidis f. latum		X				
Polypodium piloselloides		X				
Polypodium plumula		X			X	
Polypodium polypodioides		X			X	
Polystichum christianae		X				
Polystichum echinatum		X	X			
Psilotum nudum		X				
Pteridium caudatum		X	X			
Pteris grandifolia	X	X				
Pteris longifolia	X	X	X			
Tectaria apiifolia		X				
Tectaria heracleifolia		X				
Thelypteris asterothrix		X				
Thelypteris guadalupensis		X				
Thelypteris normalis		X				
Thelypteris oligophylla		X				
Thelypteris reptans		X				
Thelypteris serra		X				
Thelypteris serrulata		X				

	REYNOLDS			KAISER		
	TO BE MINED	AD-JACENT	IN-VADERS	TO BE MINED	AD-JACENT	IN-VADERS
Thelypteris tetragona		X	X			
Vittaria lineata		X				
MONOCOTYLEDONEAE						
Amaryllidaceae						
Agave sisalana					X	
Hypoxis decumbens			X			
Araceae						
Anthurium grandifolium		X				
Anthurium scandens		X				
Colocasia esculenta						P*
Philodendron lacerum	X		X		X	
Syngonium auritum					X	
Bromeliaceae						
Aechmea paniculigera		X				
Catopsis berteroniana		X				
Catopsis nutans		X				
Guzmania lingulata		X				
Guzmania monostachya		X				
Hohenbergia polycephala		X				
Hohenbergia spinulosa					X	
Tillandsia balbisiana		X			X	
Tillandsia compressa		X				
Tillandsia festucoides		X				
Tillandsia flexuosa					X	
Tillandsia recurvata		X			X	
Tillandsia schiedeana					X	
Tillandsia tenuifolia		X			X	
Tillandsia usenoides					X	
Tillandsia utriculata					X	
Tillandsia valenzuelana		X				
Commelinaceae						
Campelia zanonia		X				
Commelina elegans			X	X		
Tradescantia multiflora		X				
Cyperaceae						
Cyperus filiformis				X		
Cyperus ligularis		X				
Dichromena ciliata	X		X			
Fimbristylis annua			X			
Rhynchospora pusilla		X	X			
Scleria lithosperma		X			X	X
Scleria pterota			X			

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* Species deliberately planted for cultivation are indicated with a "P". Cultigens occurring spontaneously as invaders are recorded with an "X".

	REYNOLDS			KAISER		
	TO BE MINED	AD-JACENT	IN-VADERS	TO BE MINED	AD-JACENT	IN-VADERS
Dioscoreaceae						
Dioscorea alata		X				
Dioscorea polygonoides		X				
Gramineae						
Andropogon glomeratus	X		X	X		
Andropogon virginicus				X		
Anthephora hermaphrodita						X
Axonopus compressus			X	X		
Bambusa vulgaris	X					
Cenchrus brownii			X			
Cenchrus echinatus				X		X
Cenchrus gracillimus				X		
Chloris petraea				X		X
Chloris radiata			X			
Digitaria decumbens (Pangola Grass)	P					
Digitaria sanguinalis			X	X		X
Eleusine indica	X		X	X		X
Eragrostis ciliaris				X		
Ichnanthus pallens		X	X			
Lasiacis divaricata		X			X	
Lasiacis sloanei					X	
Lasiacis sorghoidea					X	
Leptochloa domingensis				X		
Melinis minutiflora (Wynne Grass)			P			P
Panicum adspersum				X		
Panicum maximum (Guinea Grass)			P			P
Panicum purpurascens (Para Grass)			P			P
Paspalum blodgettii	X		X			
Paspalum caespitosum				X	X	
Paspalum conjugatum	X		X			
Paspalum fimbriatum			X	X		X
Paspalum notatum	X		X	X		
Paspalum paniculatum	X	X				
Paspalum propinquum			X	X		
Pennisetum purpureum			X	X		
Pharus glaber					X	
Setaria geniculata	X		X	X		X
Sorghum bicolor			X			
Sporobolus indicus				X		X
Stenotaphrum secundatum	X	X	X	X		
Trichachne insularis		X	X	X		X
Zea mays			X			

	REYNOLDS			KAISER		
	To be Mined	Adjacent	Invaders	To be Mined	Adjacent	Invaders
Iridaceae						
Trimezia martinicensis	X					
Lemnaceae						
Wolffia columbiana		X				
Liliaceae						
Smilax balbisiana		X				
Musaceae						
Musa sapientum			X			
Orchidaceae						
Bletia florida		X				
Brassia caudata		X				
Broughtonia sanguinea					X	
Campylocentrum barrettiae		X				
Centrogenium setaceum		X			X	
Dendrophylax funalis		X				
Elleanthus longibracteatus		X				
Epidendrum anceps		X				
Epidendrum difforme		X				
Epidendrum diffusum		X				
Epidendrum fragrans		X				
Epidendrum nutans var. *obtusifolium*		X				
Epidendrum polybulbon		X				
Galeandra beyrichii		X				
Govenia utriculata		X				
Habenaria alata		X				
Habenaria quinqueseta		X				
Ionopsis utricularioides		X				
Jacquiniella globosa		X				
Liparis elata		X				
Malaxis spicata		X				
Oncidium luridum		X				
Oncidium tetrapetalum					X	
Oncidium triquetrum		X				
Pleurothallis tribuloides		X				
Polystachya foliosa		X				
Ponthieva ventricosa		X				
Schomburgkia lyonsii		X				
Spiranthes adnata		X				
Spiranthes tortilis		X				
Palmae						
Cocos nucifera				X		
Thrinax parviflora					X	
Thrinax sp.		X				

	REYNOLDS			KAISER		
	To be Mined	Adjacent	Invaders	To be Mined	Adjacent	Invaders
DICOTYLEDONEAE						
Acanthaceae						
Anthacanthus armatus		X			X	
Blechum brownei			X			
Dicliptera assurgens				X		
Salpixantha coccinea		X				
Thunbergia alata	X		X			
Thunbergia fragrans	X	X				
Amaranthaceae						
Achyranthes indica			X			
Amaranthus dubius			X			
Amaranthus polygonoides				X		
Amaranthus spinosus			X			
Celosia nitida					X	
Iresine paniculata		X				
Anacardiaceae						
Anacardium occidentale				X		
Comocladia pinnatifolia		X			X	
Mangifera indica				X		P
Metopium brownei					X	
Spondias purpurea	X					
Annonaceae						
Annona jamaicensis		X			X	
Annona muricata				X		
Xylopia muricata		X			X	
Apocynaceae						
Catharanthus roseus				X		X
Echites umbellata						X
Forsteronia floribunda		X				
Mandevilla torosa					X	
Plumeria obtusa		X	X	X	X	
Rauvolfia tetraphylla					X	
Urechites lutea	X	X	X	X		X
Aquifoliaceae						
Ilex uniflora		X				
Araliaceae						
Dendropanax arboreus		X			X	
Oreopanax capitatum		X				
Asclepiadaceae						
Asclepias curassavica	X		X	X		X
Asclepias nivea	X	X				
Metastelma ephedroides		X			X	
Metastelma filiforme		X				

	REYNOLDS			KAISER		
	To be Mined	Adjacent	Invaders	To be Mined	Adjacent	Invaders
Balanophoraceae						
Scybalium jamaicense		X				
Begoniaceae						
Begonia glabra		X				
Begonia purpurea		X				
Bignoniaceae						
Crescentia cujete	X			X		
Schlegelia parasitica		X			X	
Spathodia nilotica	X			X	X	
Tabebuia angustata		X			X	
Tabebuia riparia					X	
Tecoma stans	X	X		X	X	
Bombacaceae						
Ceiba pentandra	X	X	X	X	X	X
Ochroma pyramidale			X			
Boraginaceae						
Bourreria succulentata					X	
Cordia asperrima					X	
Cordia gerascanthus		X				
Cordia globosa	X	X	X	X	X	
Cordia jamaicensis				X	X	
Cordia macrophylla		X				
Cordia martinicensis				X		
Cordia nitida					X	
Ehretia tinifolia				X	X	
Heliotropium angiospermum				X		X
Heliotropium hirsutissimum	X	X		X	X	
Tournefortia hirsutissima	X	X	X			
Tournefortia volubilis				X	X	
Burseraceae						
Bursera simaruba				X	X	
Cactaceae						
Rhipsalis cassytha		X				
Rhipsalis jamaicensis	X	X				
Cereus swartzii					X	
Cereus triangularis					X	
Capparidaceae						
Capparis cynophallophora		X			X	
Capparis ferruginea				X	X	
Cleome gynandra		X	X			
Caprifoliaceae						
Viburnum alpinum		X				
Viburnum villosum		X				

	REYNOLDS			KAISER		
	To be Mined	Adjacent	Invaders	To be Mined	Adjacent	Invaders
Caryophyllaceae						
Drymaria cordata	X					
Celastraceae						
Elaeodendron dioecum		X				
Maytenus jamaicensis		X				
Schaefferia frutescens					X	
Combretaceae						
Terminalia latifolia		X	X			
Compositae						
Ageratum conyzoides			X			
Ambrosia paniculata	X	X	X			
Aster exilis			X			
Bidens cynapiifolia			X			
Bidens pilosa	X		X	X		X
Crepis japonica			X			
Eclipta alba			X			
Elephantopus mollis	X					
Eleutheranthera ruderalis			X			
Emilia sagittata	X		X			
Emilia sonchifolia	X		X	X		
Erechtites hieracifolia			X			X
Erigeron canadensis	X		X	X		X
Eupatorium dalea					X	
Eupatorium macrophyllum		X				
Eupatorium odoratum	X	X	X	X		
Eupatorium parviflorum		X				
Eupatorium villosum	X	X	X	X		X
Lactuca jamaicensis			X			X
Lagascea mollis				X		
Melanthera aspera						X
Mikania cordifolia		X				
Mikania micrantha	X	X	X			
Notoptera hirsuta		X				
Parthenium hysterophorus				X		
Pluchea odorata		X	X			
Porophyllum ellipticum			X			
Pseudelephantopus spicatus		X				
Salmea scandens		X			X	
Sonchus oleraceus			X			
Synedrella nodiflora			X			
Verbesina alata	X		X			X
Verbesina pinnatifida			X			
Vernonia acuminata		X	X			
Vernonia cinerea		X	X			X
Wedelia gracilis	X		X			

	REYNOLDS			KAISER		
	To be Mined	Adjacent	Invaders	To be Mined	Adjacent	Invaders
Connaraceae						
Rourea paucifoliata		X				
Convolvulaceae						
Dichondra repens			X			X
Ipomoea cathartica	X	X	X			
Ipomoea dissecta				X		X
Ipomoea grisebachii		X			X	
Ipomoea ternata		X				
Ipomoea tiliacea	X		X			
Ipomoea triloba						X
Jacquemontia jamaicensis			X			
Crassulaceae						
Bryophyllum pinnatum				X	X	
Cruciferae						
Lepidium virginicum			X			
Cucurbitaceae						
Cionosicys pomiformis		X		X		
Cucumis anguria		X				
Momordica charantia	X					
Ebenaceae						
Diospyros tetrasperma		X			X	
Elaeocarpaceae						
Sloanea jamaicensis		X				
Erythroxylaceae						
Erythroxylum areolatum					X	
Erythroxylum confusum					X	
Erythroxylum incrassatum		X				
Erythroxylum rotundifolium					X	
Euphorbiaceae						
Acidoton urens	X	X			X	
Alchornea latifolia		X				
Bernardia carpinifolia				X	X	
Croton glabellus					X	X
Croton humilis				X	X	
Croton linearis					X	X
Croton lucidus				X		
Croton wilsonii					X	
Drypetes alba					X	
Drypetes lateriflora		X			X	
Euphorbia geniculata				X		
Euphorbia heterophylla	X			X		X
Euphorbia hirta var. *hirta*	X		X	X		X

	REYNOLDS			KAISER		
	To be Mined	Adjacent	Invaders	To be Mined	Adjacent	Invaders
Euphorbia hirta var. *procumbens*	X		X			X
Euphorbia hypericifolia					X	
Euphorbia hyssopifolia	X		X		X	X
Euphorbia punicea		X				
Gymnanthes lucida					X	
Manihot utilissima						P
Omphalea triandra		X			X	
Pedilanthus tithymaloides				X		
Phyllanthus coxianus		X				
Phyllanthus inaequalifolius		X				
Phyllanthus montanus					X	
Phyllanthus nutans					X	
Ricinus communis	X		X	X		X
Tragia volubilis					X	
Flacourtiaceae						
Casearia aculeata		X		X	X	
Casearia guianensis	X	X			X	
Casearia hirsuta		X				
Casearia odorata		X				
Casearia sylvestris		X			X	
Laetia thamnia		X			X	
Xylosma fawcettii		X				
Gesneriaceae						
Columnea fawcettii		X				
Columnea sp.					X	
Gesneria acaulis		X				
Rhytidophyllum tomentosum	X	X				
Guttiferae						
Clusia flava		X			X	
Rheedia sessiliflora		X				
Labiatae						
Hyptis capitata	X	X	X			
Hyptis pectinata			X	X		
Leonurus sibiricus		X	X	X		
Ocimum micranthum				X		X
Salvia coccinea					X	X
Salvia micrantha	X				X	
Teucrium vesicarium	X		X			
Lauraceae						
Nectandra antillana		X	X			
Nectandra coriacea		X			X	
Nectandra patens		X				

	REYNOLDS			KAISER		
	To be Mined	Adjacent	Invaders	To be Mined	Adjacent	Invaders
Ocotea floribunda		X				
Ocotea staminea		X			X	
Persea americana			P			
Leguminosae						
Abrus precatorius		X			X	
Adenanthera pavonina		X				
Aeschynomene americana	X	X				
Albizzia berteriana					X	
Andira inermis		X				
Arachis hypogaea						P
Bauhinia divaricata	X	X		X	X	
Caesalpinia sepiaria		X				
Cajanus cajan				X		P
Calliandra portoricensis				X	X	X
Canavalia ensiformis		X				
Cassia ligustrina	X	X	X	X		X
Cassia occidentalis	X		X			X
Cassia siamea			P			P
Cassia uniflora	X			X		X
Centrosema virginianum	X			X		X
Crotalaria incana	X		X			X
Crotalaria retusa						X
Crotalaria verrucosa				X		X
Desmodium axillare var. *acutifolium*	X	X	X			
Desmodium canum	X		X	X		X
Desmodium scorpiurus				X		X
Desmodium tortuosum				X		
Flemingia strobilifera	X	X				
Galactia pendula					X	
Galactia striata				X		
Haematoxylon campechianum	X	X		X	X	X
Indigofera suffruticosa	X		X	X		X
Leucaena glauca				X	X	
Lonchocarpus domingensis					X	
Mimosa pudica	X		X	X		X
Peltophorum brasiliense		X				
Phaseolus lathyroides	X					
Pueraria lobata			P			
Piscidia piscipula	X	X		X	X	
Pithecellobium alexandri					X	
Pithecellobium arboreum		X			X	
Rhynchosia minima						X
Rhynchosia phaseoloides		X				
Sophora tomentosa						X
Stylosanthes hamata				X		X
Tamarindus indicus				X		

	REYNOLDS			KAISER		
	TO BE MINED	AD-JACENT	IN-VADERS	TO BE MINED	AD-JACENT	IN-VADERS
Lobeliaceae						
Lobelia viridiflora	X	X	X			
Loganiaceae						
Spigelia anthelmia		X	X			X
Loranthaceae						
Phoradendron latifolium		X				
Oryctanthus occidentalis		X				
Lythraceae						
Cuphea parsonsia			X			
Malpighiaceae						
Bunchosia jamaicensis		X				
Bunchosia media					X	
Bunchosia swartziana		X		X	X	X
Byrsonima coriacea					X	
Malpighia glabra	X	X			X	
Malpighia urens		X				
Mascagnia hiraea					X	
Stigmaphyllon emarginatum				X		
Malvaceae						
Abutilon crispum					X	
Gossypium hirsutum			X			
Hibiscus clypeatus		X			X	
Hibiscus elatus			P			P
Malvastrum spicatum		X				
Malvaviscus arboreus		X				
Pavonia rosea		X				
Pavonia spinifex	X					
Sida acuta			X	X		X
Sida cordifolia				X	X	X
Sida glabra				X		
Sida rhombifolia	X		X			
Sida spinosa				X	X	
Sida urens	X		X			
Urena lobata	X		X			X
Wissadula amplissima		X		X	X	X
Wissadula fadyenii					X	
Melastomataceae						
Blakea trinervia		X				
Miconia laevigata		X	X			
Ossaea microphylla	X					
Tetrazygia hispida		X				
Tetrazygia pallens		X				
Meliaceae						
Cedrela odorata		X			X	P

	REYNOLDS			KAISER		
	To be Mined	Adjacent	Invaders	To be Mined	Adjacent	Invaders
Guarea glabra	X	X			X	
Melia composita						P
Swietenia mahagoni					X	
Trichilia glabra					X	
Trichilia moschata					X	
Menispermaceae						
Cissampelos pareira	X	X		X	X	
Hyperbaena domingensis		X			X	
Hyperbaena laurifolia		X				
Moraceae						
Artocarpus communis	X			X		P
Artocarpus integrifolia	X	X				
Cecropia peltata	X	X	X		X	
Chlorophora tinctoria		X			X	
Ficus harrisii		X				
Ficus ochroleuca	X	X				
Ficus populnea		X			X	
Ficus suffocans		X	X	X	X	
Ficus wilsoni	X	X				
Trophis racemosa		X				
Myrsinaceae						
Rapanea guianensis					X	
Wallenia grisebachii					X	
Wallenia laurifolia		X		X	X	
Myristicaceae						
Myristica fragrans			P			
Myrtaceae						
Calyptranthes chytraculia		X			X	
Calyptranthes pallens		X			X	
Eugenia axillaris	X	X			X	
Eugenia biflora					X	
Eugenia disticha		X				
Eugenia eperforata		X				
Eugenia isosticta					X	
Eugenia monticola					X	
Pimenta dioica		X	P		X	
Psidium guajava	X	X		X		X
Nyctaginaceae						
Boerhavia diffusa				X		
Boerhavia erecta				X		
Pisonia aculeata					X	
Pisonia discolor					X	
Torrubia fragrans		X			X	

	REYNOLDS			KAISER		
	To be Mined	Adjacent	Invaders	To be Mined	Adjacent	Invaders
Olacaceae						
Schoepfia multiflora		X				
Oxalidaceae						
Oxalis corniculata	X		X			
Oxalis martiana		X				
Papaveraceae						
Bocconia frutescens		X	X			
Passifloraceae						
Passiflora foetida var. *hispida*	X		X			
Peperomia clusiaefolia					X	
Passiflora perfoliata		X			X	
Passiflora rubra	X	X	X	X	X	
Passiflora suberosa	X	X	X	X		
Phytolaccaceae						
Phytolacca icosandra			X			
Rivina humilis					X	
Trichostigma octandrum		X			X	
Piperaceae						
Peperomia amplexicaulis		X			X	
Peperomia clusiaefolia					X	
Peperomia glabella		X				
Peperomia rotundifolia	X					
Peperomia serpens		X				
Piper aduncum	X	X	X			
Piper amalago			X	X		
Piper arboreum		X				
Piper jamaicense		X	X			
Piper umbellatum	X		X			
Plumbaginaceae						
Plumbago scandens				X		
Polygalaceae						
Polygala paniculata	X		X			
Securidaca brownei		X				
Polygonaceae						
Coccoloba diversifolia					X	
Coccoloba longifolia		X				
Coccoloba plumieri		X				
Coccoloba proctori					X	
Coccoloba swartzii		X			X	
Coccoloba tenuifolia					X	
Coccoloba uvifera			X	X		
Polygonum glabrum	X	X				

	REYNOLDS			KAISER		
	To be Mined	Adjacent	Invaders	To be Mined	Adjacent	Invaders
Portulacaceae						
Talinum triangulare				X		
Ranunculaceae						
Clematis dioica		X	X		X	
Rhamnaceae						
Colubrina ferruginosa		X		X	X	
Gouania lupuloides			X			
Krugiodendron ferreum					X	
Rhamnus sphaerosperma		X	X			
Sarcomphalus laurinus				X	X	
Zizyphus chloroxylon		X				
Rosaceae						
Prunus myrtifolia		X			X	
Rubus jamaicensis	X		X			
Rubiaceae						
Antirrhoea jamaicensis		X				
Borreria laevis	X		X	X		X
Borreria verticillata	X	X	X	X		X
Casasia longipes				X	X	
Casasia piricarpa		X				
Chiococca alba		X			X	
Chiococca parvifolia		X			X	
Coffea arabica	X					
Erithalis quadrangularis		X				
Exostema caribaeum					X	
Guettarda argentea		X				
Guettarda elliptica					X	
Hamelia chrysantha		X			X	
Hamelia cuprea		X				
Hamelia patens		X				
Hamelia ventricosa		X				
Hillia tetrandra		X				
Palicourea domingensis		X				
Portlandia grandiflora					X	
Portlandia microsepala		X				
Psychotria balbisiana					X	
Psychotria dura		X				
Psychotria fadyenii		X				
Psychotria myrstiphyllum					X	
Psychotria nervosa	X	X				
Psychotria patens		X				
Psychotria pedunculata	X	X				
Psychotria pubescens	X	X				
Richardia brasiliensis						X
Rondeletia polita		X				

	REYNOLDS			KAISER		
	To be Mined	Adjacent	Invaders	To be Mined	Adjacent	Invaders
Rondeletia trifolia					X	
Schradera involucrata		X				
Rutaceae						
Amyris elemifera				X		
Amyris plumieri					X	
Citrus aurantifolia				X		P
Citrus vulgaris	X	X		X	X	
Esenbeckia pentaphylla		X		X	X	
Spathelia sorbifolia					X	
Zanthoxylum elephantiasis		X				
Zanthoxylum flavum				X	X	X
Zanthoxylum insulare		X			X	
Zanthoxylum martinicense	X	X	X	X		
Sapindaceae						
Allophylus cominia	X	X			X	
Allophylus jamaicensis		X				
Blighia sapida				X		
Cardiospermum grandiflorum	X	X				
Cardiospermum microcarpum		X				
Cupania glabra		X	X	X	X	
Dodonaea viscosa				X		
Exothea paniculata		X		X	X	
Hypelate trifoliata					X	
Paullinia jamaicensis		X	X			
Sapotaceae						
Chrysophyllum cainito	X					
Dipholis nigra		X			X	
Dipholis salicifolia		X		X	X	X
Manilkara zapotilla		X		X		
Pouteria multiflora		X				
Simarubaceae						
Picramnia antidesma		X		X	X	
Picramnia pentandra					X	
Picrasma excelsa					X	
Simaruba glauca		X		X	X	
Solanaceae						
Brunfelsia americana		X				
Brunfelsia jamaicensis		X			X	
Capsicum baccatum	X				X	
Capsicum frutescens		X				
Cestrum diurnum		X	X			
Physalis pubescens	X		X			
Solandra grandiflora		X				

	REYNOLDS			KAISER		
	To be Mined	Ad-jacent	In-vaders	To be Mined	Ad-jacent	In-vaders
Solanum bahamensis var. *subarmata*				X	X	
Solanum ciliatum			X			
Solanum havanense					X	
Solanum jamaicense			X			
Solanum mammosum	X					
Solanum nigrum	X		X			
Solanum stellatum	X		X			
Solanum torvum	X		X	X	X	X
Solanum verbascifolium	X		X	X		
Sterculiaceae						
Ayenia pusilla				X		
Cola acuminata	X					
Guazuma ulmifolia				X	X	
Helicteres jamaicensis					X	X
Melochia pyramidata				X		X
Theobroma cacao	X				X	
Waltheria americana			X	X		X
Theaceae						
Ternstroemia hartii		X				
Thymelaeaceae						
Daphnopsis americana	X	X			X	
Tiliaceae						
Corchorus siliquosus		X	X			X
Muntingia calabura		X				
Triumfetta hispida	X		X			
Triumfetta lappula	X			X		
Turneraceae						
Piriqueta cistoides						X
Ulmaceae						
Celtis swartzii		X		X	X	X
Celtis trinervia		X				
Umbelliferae						
Apium leptophyllum	X					
Eryngium foetidum	X	X				
Hydrocotyle asiatica	X	X	X			
Urticaceae						
Boehmeria jamaicensis		X				
Pilea brevistipula		X				
Pilea crassifolia		X				
Pilea hollickii		X				

	REYNOLDS			KAISER		
	To be Mined	Adjacent	Invaders	To be Mined	Adjacent	Invaders
Pilea microphylla	X	X	X			
Urera expansa		X				
Verbenaceae						
Citharexylum spinosum	X	X		X	X	
Lantana angustifolia					X	
Lantana camara	X	X	X	X		
Lantana reticulata				X	X	X
Lantana trifolia	X		X			
Petitia domingensis	X	X	X			
Phyla nodiflora	X		X			
Phyla stoechadifolia	X					
Priva lappulacea	X		X	X		X
Stachytarpheta cayennensis			X			
Stachytarpheta jamaicensis	X	X	X	X		X
Tectona grandis						P
Vitaceae						
Cissus microcarpa	X	X				
Cissus sicyoides	X	X	X			
Zygophyllaceae						
Kallstroemia maxima						X

Arnold Arboretum
and
The Institute of Jamaica

A MONOGRAPHIC STUDY OF THE WEST INDIAN SPECIES OF PHYLLANTHUS *

GRADY L. WEBSTER

With three plates

Subgenus IV. **Phyllanthus.**

Herbs or undershrubs with phyllanthoid branching and relatively small leaves. Monoecious or dioecious; female flowers solitary, male flowers solitary or in axillary cymules. Male flower: calyx-lobes 5 or 6; disk of 5 or 6 segments; stamens 2 or 3, free or united; anthers dehiscing vertically to horizontally; pollen grains various. Female flower: calyx-lobes 5 or 6; disk cupuliform or divided into 5 or more segments; ovary of 3 carpels, smooth or roughened; styles bifid, mostly free. Fruit capsular, often explosively dehiscent; seeds trigonous, 2 in each locule, mostly ribbed or verruculose.

This subgenus, as here defined, comprises a part of sections *Paraphyllanthus* and *Euphyllanthus* sensu Mueller, and includes the majority of the herbaceous species in the genus. It is certainly a heterogeneous group and possibly a polyphyletic one, the various herbaceous representatives perhaps having evolved from different shrubby ancestors; but in the absence of any pertinent evidence to the contrary, the following four West Indian sections seem best grouped together.

It must be admitted that the demarcation of this, the typical subgenus, is the most unsatisfactory of any of the subgeneric divisions of *Phyllanthus*. At present it is most difficult to decide whether a number of puzzling Old World groups, such as the Indo-Chinese species of sections *Emblica* and *Paraphyllanthus* (sensu Beille, Fl. Gen. Indo-Ch. **5**: 572–573. 1927), should be included or not. These plants, being mostly trees and shrubs, do not clearly fit into subg. ***Phyllanthus***, but there does not appear to be any other very satisfactory place to put them. In the West Indies, however, members of subg. ***Phyllanthus*** can be easily recognized by their herbaceous habit and reduced male flowers.

KEY TO THE SECTIONS

1. Ovary smooth or papillose; seeds mostly verruculose or longitudinally ribbed, never transversely ribbed or foveolate; leaf-blades never hispidulous (margins crenulate in sect. *Callitrichoides*).
   2. Disk or calyx purplish-tinged, or else ovary papillose; flowers entirely solitary; pollen grains not colporate.
      3. Stamens connate by the filaments but anthers free; leaves crisply succulent; pollen grains banded . . . . 8. **Callitrichoides**

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* Continued from volume XXVIII, p. 80.

3. Stamens completely connate into a circumscissile synandrium; leaves not succulent; pollen grains foveolate .... 9. **Cyclanthera**

2. Disk or calyx never purplish, sometimes reddish-tinged; ovary smooth; male flowers not solitary (except in *P. mimicus*, which has free stamens); pollen grains colporate .... 11. **Phyllanthus**

1. Ovary bullate-rugose; seeds transversely ribbed and often foveolate on the sides; leaf-blades hispidulous beneath near the margins .... 10. **Urinaria**

Sect. 8. **Callitrichoides** Webster, Contr. Gray Herb. **176**: 51. 1955.

Small herbs with the habit of species of *Callitriche* and *Peperomia*, tissues crisp-succulent; branching phyllanthoid, the primary axis short, bearing crowded, spreading branchlets, these often rooting at the nodes; leaves of branchlets distichous, with crenate-cartilaginous margins. Monoecious; flowers solitary, most branchlets with 1–4 male flowers and a single distal female flower near the tip. Male flower: calyx-lobes 5, obovate, acute; disk-segments 5, reniform, purplish; stamens 2, filaments completely united, anthers discrete but sessile atop the column, dehiscing horizontally; pollen grains spheroidal, appearing banded due to the transversely elongated areoles.[13] Female flower: calyx-lobes 6, oblong or spathulate; disk-segments 6, narrowly cuneate, purplish; ovary densely scabridulous; styles ascending, emarginate or bifid. Capsule small, densely scabridulous; seeds brownish, verruculose with scattered dark points.

TYPE SPECIES: *Phyllanthus carnosulus* Muell. Arg.

The type species, a rare plant endemic to eastern Cuba, is the sole representative of this interesting monotypic section. Its unique habit at once distinguishes it from all its North American congeners. Although Mueller placed it in the alliance of *P. heliotropus*, *P. hyssopifolioides*, et al. (now in sect. *Loxopodium*), it is not at all closely related to these. Its nearest affinity is undoubtedly with the species of sect. *Cyclanthera*, which (as pointed out below) have either been derived from sect. *Callitrichoides* or from some common ancestor.

Although there can be little doubt that sects. *Callitrichoides* and *Cyclanthera* are closely allied (so closely, in fact, that the two could perhaps be treated as subsections of a common section), it is not at all clear from what other group in the genus these two highly specialized sections might have been derived. The ancestral group certainly was not any of the taxa in sect. *Phyllanthus*, none of which shows a close relationship. The peculiar pollen of sect. *Callitrichoides* is found nowhere else in the genus and has a counterpart only in *Andrachne brittonii*. The latter also has very small somewhat succulent leaves; but it differs in many important details, such as its woody xerophytic habit with spiny branch-tips and its petaliferous flowers, so that its resemblance to *P. carnosulus* must be ascribed to an interesting case of parallelism.

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[13] See Plate IX, fig. 39.

Perhaps sect. *Loxopodium* comes closest to being a likely progenitor, so that Mueller's placement of *P. carnosulus* among the species of that group was not entirely without merit. The leaves and stipules of sect. *Callitrichoides* are certainly similar to those of various representatives of *Loxopodium*, and the free cuneate disk-segments of the female flower — as well as several other floral details — are suggestively alike in both groups. However, to suggest that sect. *Callitrichoides* did evolve from some representative of sect. *Loxopodium* involves the assumption that the phyllanthoid branching of this section has evolved independently of that in sect. *Phyllanthus*. Since a similar assumption appears necessary in the case of sect. *Urinaria*, it thus is quite possible that phyllanthoid branching has originated independently three times within subg. *Phyllanthus*.

11. **Phyllanthus carnosulus** Muell. Arg. Linnaea **32**: 30. 1863; DC. Prodr. **15**(2): 388. 1866. (PLATE XVI, *figs. A–E*).

Diasperus carnosulus (Muell. Arg.) O. Ktze. Rev. Gen. **2**: 598. 1891.
Phyllanthus haplocladus Urb. Repert. Sp. Nov. **28**: 214. 1930.

Low perennial herb with crisply and slightly succulent branches and leaves, the habit like that of a small *Peperomia* or *Pilea*; primary axis becoming a slender dark brown rootstock c. 0.5–1 cm. long and 1.5–4 mm. thick, bearing stubs of old branches below. Cataphylls scarious, brownish; stipules triangular-ovate, denticulate or lacerate towards the acute or acuminate tip, up to 0.8 mm. long and 0.6 mm. broad; blade narrower. Deciduous branchlets crowded at apex of rootstock, spreading or prostrate, sometimes rooting at the nodes, (3–) 5–8 (–15) cm. long, 0.2–0.6 mm. thick, stramineous, minutely papillate-scabridulous, angled, furrowed when dried, with c. (10–) 25–40 (–50) leaves; first internode usually 1 cm. long or more, median internodes mostly 1–3.5 (–6) mm. long. Leaves: stipules ovate-triangular to lanceolate, acute or acuminate, somewhat dilated at the basal corners but not distinctly auriculate, denticulate or nearly entire, at first thin and olivaceous or reddish-tinged, at length firmer, the midrib dark brownish, the margins scarious, 0.5–0.9 mm. long, 0.3–0.6 (–0.7) mm. broad. Petioles 0.2–0.4 mm. long, flattened, smooth. Blade obovate to elliptic or oblong, rounded or obtuse and apiculate at the tip, acute to obtuse at the base, (2–) 3.5–6 (–7) mm. long, 1.5–4 mm. broad; above olivaceous, rugulose-reticulate, the midrib, laterals and anastomosing tertiary veinlets slightly raised; beneath pallid, dull reddish, obscurely scabridulous, the midrib prominent but second-

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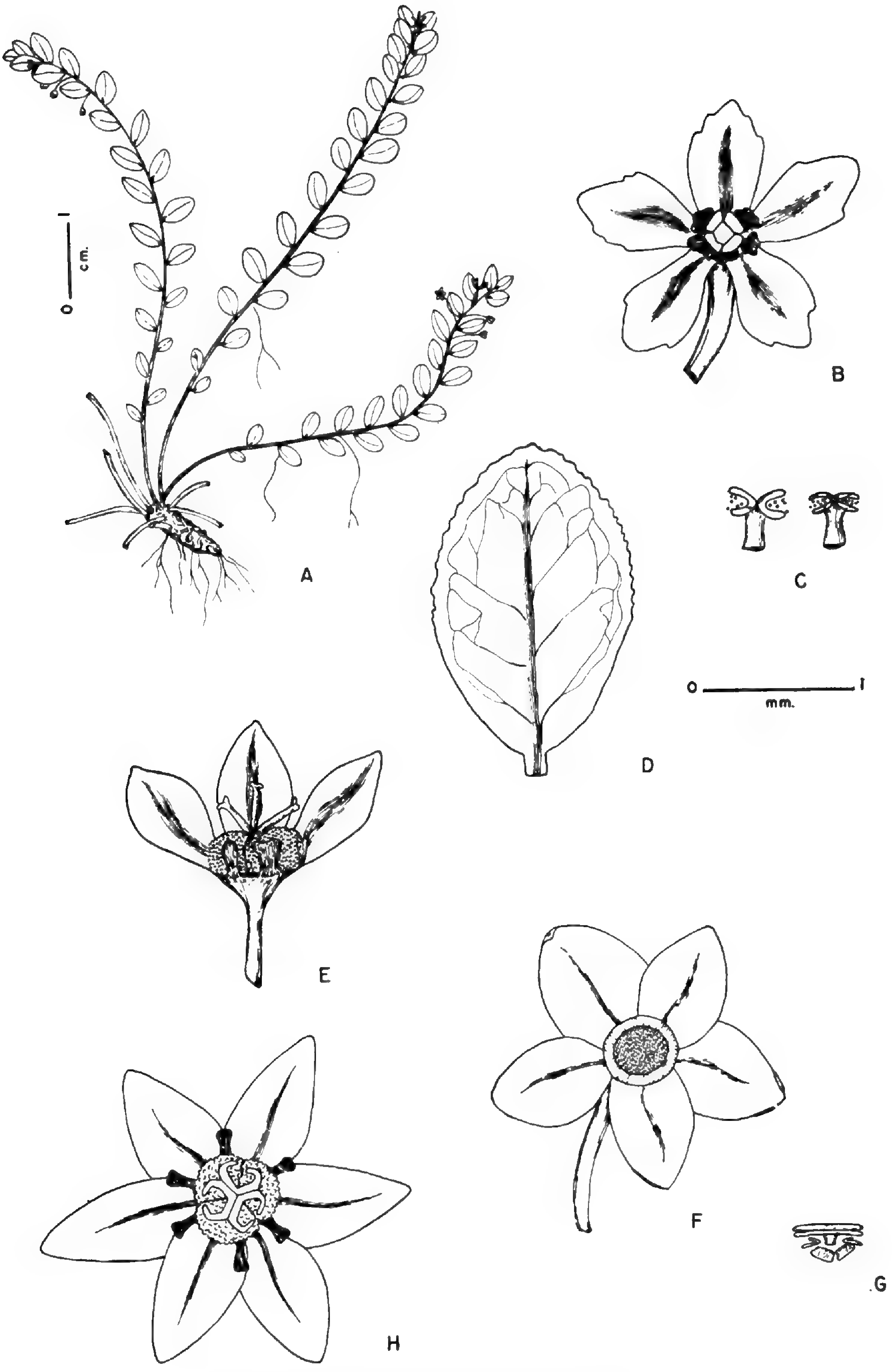
PLATE XVI. Sections *Callitrichoides* and *Cyclanthera*.

FIGS. A–E. *Phyllanthus carnosulus* Muell. Arg. A. habit (*Ekman 16090* [S]); B, male flower; C, androecium seen from one side (left) and facing an anther (right); D, leaf; E, female flower with three calyx-lobes removed (*Wright* "714" [GOET]).

FIGS. F–H. *Phyllanthus tenuicaulis* Muell. Arg. (*Wright 1675*). F, male flower; G, androecium and disk seen from the side; H, female flower. (Figs. B–H drawn to the same scale.)

Plate XVI



Webster, West Indian Phyllanthus

ary veins obscure; margin usually unevenly cartilaginous-thickened, or more less regularly cartilaginous-toothed beyond the middle.

Monoecious, but male flowers readily deciduous and specimens thus sometimes appearing entirely female. Flowers strictly solitary in the distal axils of the branchlet; most often the males 2–4 on a branchlet and the single female flower distal to them (but female flower sometimes proximal).

Male flower: pedicel capillary, mostly 2.5–5 mm. long. Calyx-lobes 5, narrowly elliptic to obovate, c. 0.7–0.8 mm. long, 0.4–0.5 mm. broad, acute, entire or obscurely denticulate, membranous, yellowish with a scarious margin, thin, the midrib somewhat raised without but plane within, unbranched. Disk-segments 5, more or less reniform, c. 0.25–0.35 mm. broad and 0.15–0.2 mm. long, distinctly purple, subentire, smooth and not evidently pitted. Stamens 2; filaments completed fused into a column c. 0.2–0.3 mm. high; anthers sessile atop the column and contiguous but discrete, 0.25–0.3 mm. broad, dehiscing horizontally, the anther-sacs not confluent; pollen grains spherical, c. 15 μ in diameter, banded by ribbon-shaped areoles.

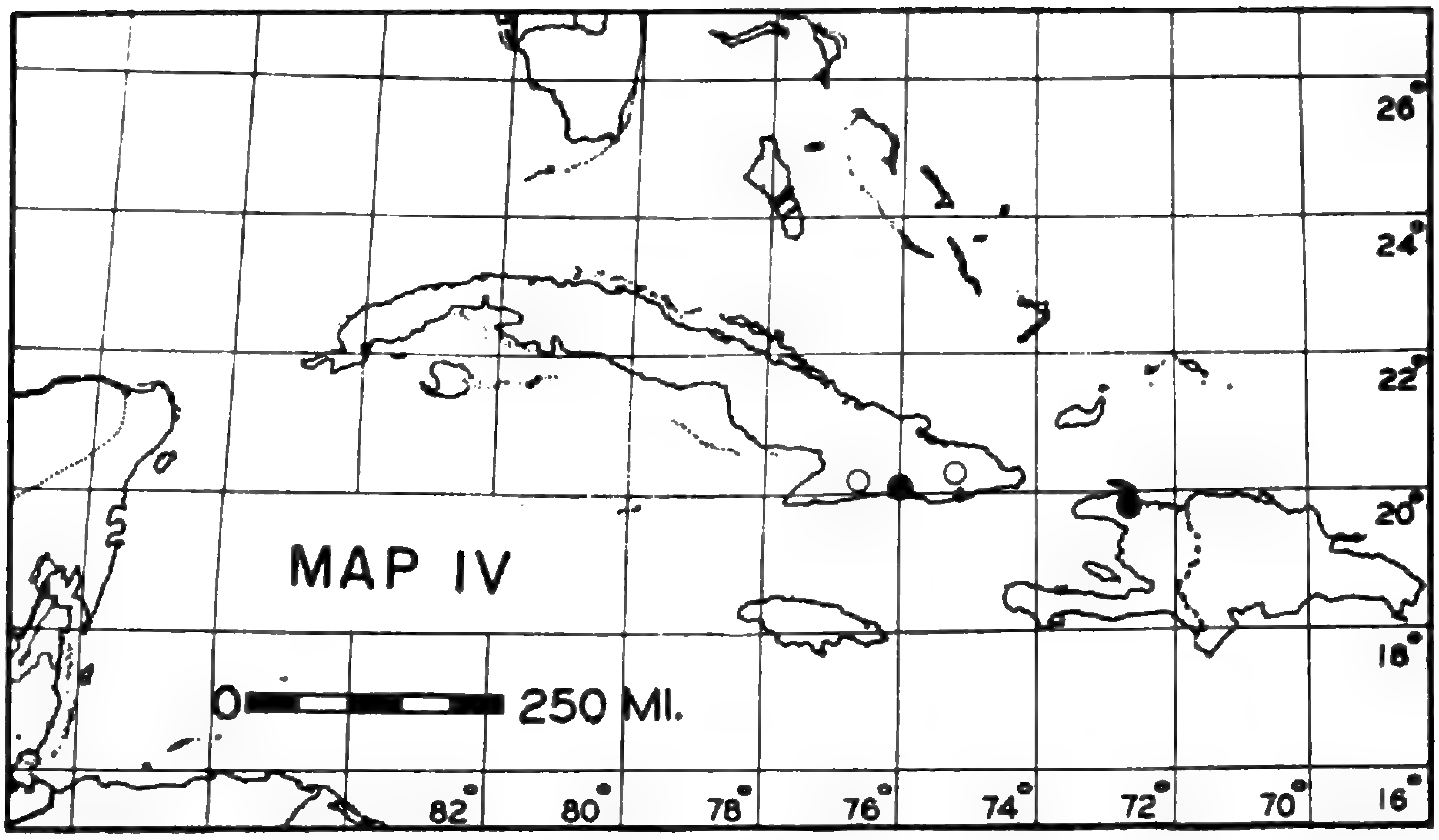
Female flower: pedicel straight, terete, smooth, c. 1–1.7 mm. long. Calyx-lobes 6, narrowly oblong to spathulate, 0.8–0.9 mm. increasing to 1–1.4 mm. long, 0.35–0.7 mm. broad, acute or obtuse, olivaceous with scarious margins; midrib slightly raised without and (at the base) within, unbranched. Disk-segments 6, completely separate, c. 0.2–0.25 mm. long, cuneate (often narrowly so) from a stipitate base, expanded to a truncate, emarginate, or bifurcate tip, distinctly purplish, subcarnose, smooth and entire. Ovary oblate, c. 0.3 mm. high and twice as broad, densely but minutely papillate-scabridulous. Styles free, erect or ascending, c. 0.3 mm. long, emarginate to shortly bifid, slender, the tips spreading to recurved.

Capsule c. 1.5 mm. in diameter when mature, breaking up readily, the thin valves yellowish brown, scurfy-roughened, not nervose. Seeds 0.7–0.75 mm. long, 0.55–0.6 mm. radially, 0.6–0.7 mm. tangentially, fuscous, plumply trigonous, granulate with evenly spaced raised dark points.

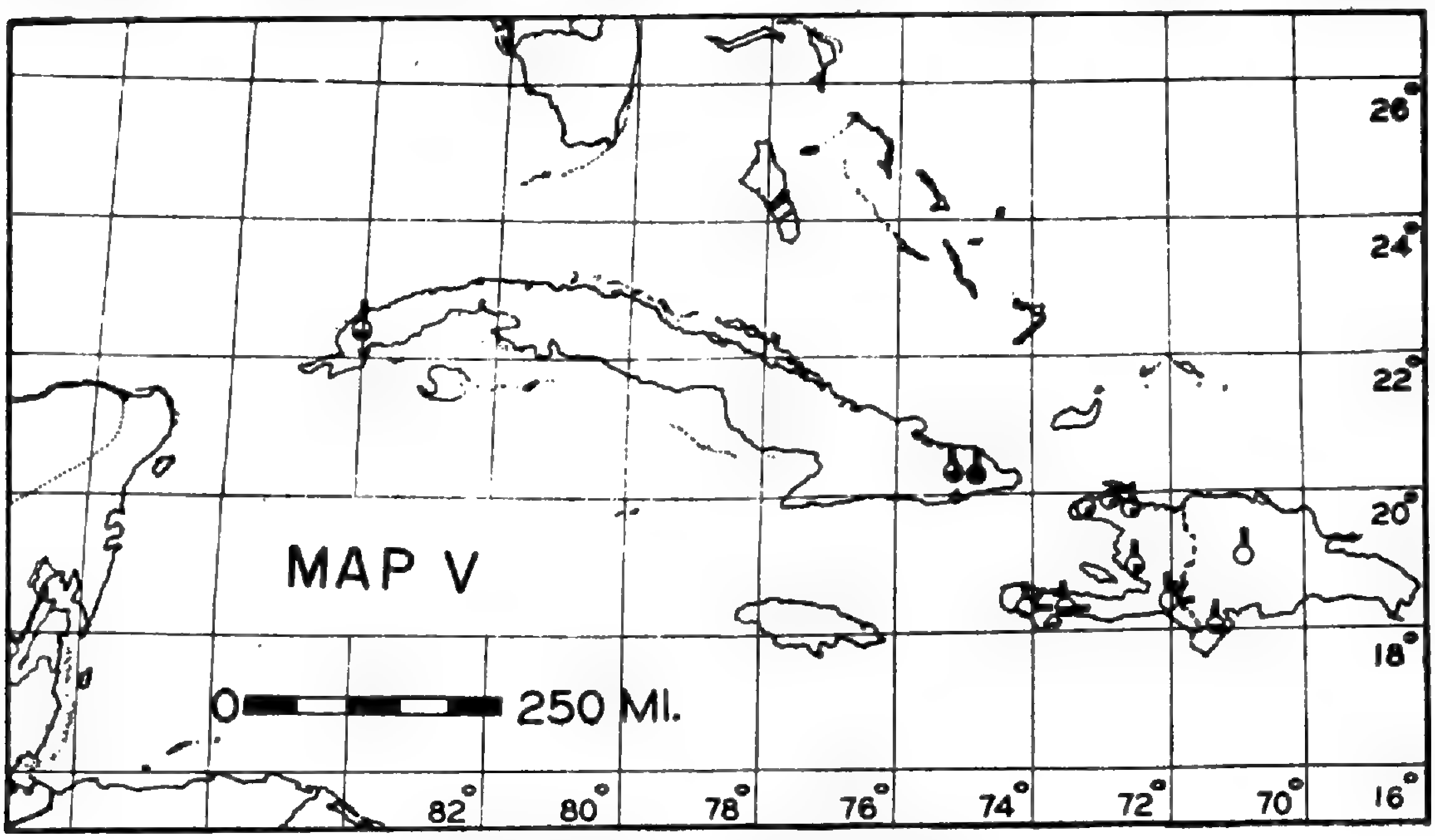
MAP IV. Distribution of *Phyllanthus carnosulus* Muell. Arg. (open circles) and *Phyllanthus tenuicaulis* Muell. Arg. (solid circles).

MAP V. Distribution of certain taxonomic characters among the populations of *Phyllanthus lindenianus* Baill. Open circles indicate plants completely smooth; scabridulosity is indicated by blackening portions of circles as follows: southeast quadrant, female pedicel; southwest quadrant, stem; northwest quadrant, female calyx; northeast quadrant, leaf. Erect bar indicates presence of iterative axes on branchlets (at least in part); oblique bar signifies marked inequality of leaf size; horizontal bar denotes perennial habit.

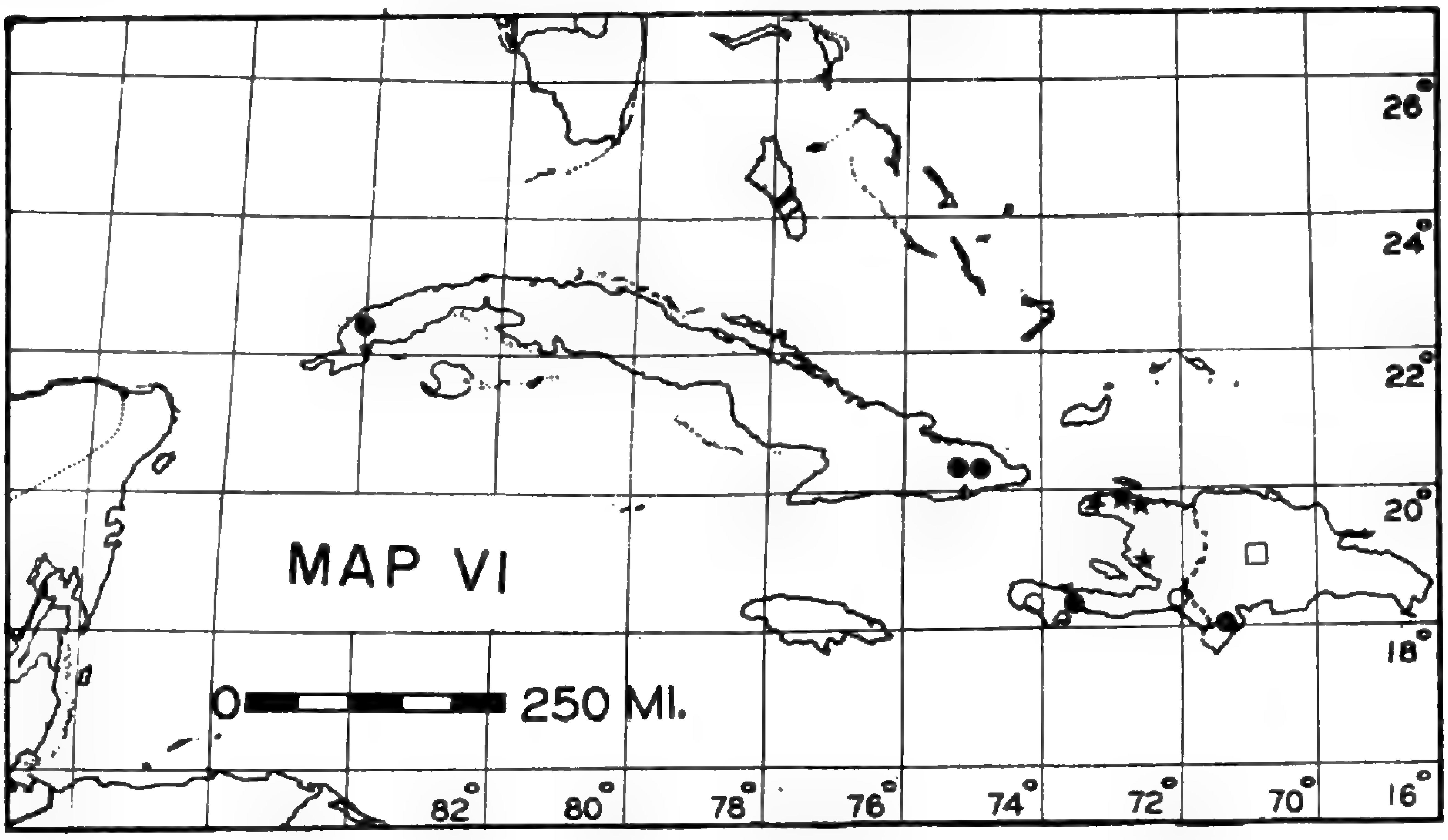
MAP VI. Distribution of the varieties recognized within *Phyllanthus lindenianus*: var. *inaequifolius*, open circles; var. *jimenezii*, square; var. *leonardorum*, stars; var. *lindenianus*, solid circles.



MAP IV



MAP V



MAP VI

TYPE: "Cuba orientali," *Wright 591* (G, HOLOTYPE). According to the data associated with the isotype specimen in the New York Botanical Garden Herbarium, this number was collected at Monte Toro. In the packet of the Gray Herbarium sheet on which *Wright 591* is mounted are three labels with the localities: "La Luisa in Monte Toro," "Potosí Mt. Liban," and "Potosí Monte Toro"; however, it is not clear whether these belong with no. *591* or with *Wright 1939*, which is also mounted on the sheet.

DISTRIBUTION: endemic to the mountainous parts of Oriente Province, Cuba (MAP IV).

CUBA. ORIENTE: Sierra Maestra, southeast of Bayamo, in the rocky shrub forest at the base of an enormous stone ("El diente del Gigante"), on top of Loma del Gigante, alt. c. 1200 m., *Ekman 16090* (NY, S; type collection of *P. haplocladus*). "Cuba orientali" [i.e., Sagua-Baracoa range], *Wright 591* (G, HOLOTYPE; BR, GH, NY, ISOTYPES), *1939* (G, GH, GOET, MO, S, W), "530", "714", (GOET, these being field numbers and presumably corresponding to either *591* or *1939*).

This remarkable little plant, though apparently quite rare, may be encountered by future collectors in the wetter parts of both the Sierra Maestra and the Sagua-Baracoa range. On his manuscript notes quoted above, Wright gave the habitat data for the species as "base of cliffs," "margins of mountain-rivulets," and "dense woods," respectively. The habit of the plant leaves no doubt that it is quite hydrophilic, and from the debris clinging to the specimens one can infer that it grows in rain-forest areas on marly banks, often associated with mosses and liverworts. Dr. Howard Crum kindly identified the moss associated with *Ekman 16090* as *Phyllogonium fulgens,* and the two with *Wright 591* and "714" as *Trichostomum jamaicense* and *Thuidium urceolatum*, respectively.

As far as can be judged from examination of the relatively few collections, *P. carnosulus* is a rather homogeneous species. Although there is some variation in length and number of leaves per branchlet, as well as in other respects, there is no evidence that the Sierra Maestra population deserves any special subspecific designation. Urban, in fact, appears to have overlooked the fact that Mueller had already described the species, for when proposing *P. haplocladus* as a new species he said nothing about its relationships. Urban's description is misleading in that he reported the plant to be annual and probably dioecious. However, several of the plants of the type collection (*Ekman 16090*) are obviously more than one year old; evidently the species is a perennial which may flower the first year. Nor is it likely that plants of *P. carnosulus* are ever dioecious; but the male flowers are readily deciduous, so that older specimens sometimes give the appearance of bearing only female flowers.

The slightly succulent leaves with cartilaginous "toothing," the adventitious roots, the solitary flowers with purplish disk-segments (described as "dark red" in the living condition by Wright), and the unique pollen grains distinguish *P. carnosulus* from all its congeners. However, it is clearly more closely related to *P. tenuicaulis* of the following section than to any other species; the two plants show a near affinity through the common possession of a very small papillose capsule, in addition to the several characters that the other species of sect. *Cyclanthera* share with *P. carnosulus.* It appears reasonable to conclude, therefore, that the species of sect. *Cyclanthera* have been derived from sect. *Callitrichoides* via *P. tenuicaulis* or some very similar form.

Sect. 9. **Cyllanthera** Webster, Contr. Gray Herb. **176**: 47. 1955.

Annual or perennial herbs or low subshrubs, with phyllanthoid branching; deciduous branchlets often with a smaller iterative axis [14] from the first node, and leaves of upper branchlets often much smaller than those below. Monoecious or dioecious; flowers entirely solitary, in axils on both axes of branchlet. Male flower: calyx-lobes 5 or 6; disk-segments 5 or 6, purplish; stamens 3, filaments connate into a column, anthers completely coalescent into a disciform circumscissile synandrium; pollen grains globose, foveolate.[15] Female flower: calyx-lobes 6; disk of 3–8 lobes, usually purplish; ovary smooth or scabridulous; styles bifid, free or united. Capsule smooth or scabridulous; seeds verruculose.

TYPE SPECIES: *Phyllanthus lindenianus* Baill.

This very distinctive section of eight specific and subspecific taxa is endemic to Cuba and Hispaniola. As pointed out in the original description, the section is strongly characterized by the remarkable modification of the androecium, the unique pollen grains somewhat resembling those of *Polygonum* sect. *Persicaria,* and the common production of an extra ("iterative") leafy axis from the first node of the deciduous branchlet. The only clearly related group, sect. *Callitrichoides,* is believed to be ancestral to the present section because of its less specialized androecium. If this is correct, then the "foveolate" ornamentation of the pollen grains of *Cyclanthera* has presumably been derived through modification of the "banded" pollen grain of *Callitrichoides* (cf. Plate IX, figs. 39 and 40).

The vegetative peculiarities of sections *Callitrichoides* and *Cyclanthera* are of particular interest in considerations of both phylogeny and the origin of phyllanthoid branching. In sects. *Urinaria* and *Phyllanthus* the branchlets produce at the nodes only flowers or floral axes; but in sect. *Callitrichoides* roots can be formed at branchlet nodes, and in sect. *Cyclanthera* all of the species except *P. berteroanus* produce a second leafy axis (iterative branchlet) from the first node of each branchlet. Furthermore, in sect. *Cyclanthera* the leaves of the upper part of the stem are often strikingly smaller than those of the lower part. These specializations provide evidence favorable to the hypothesis that phyllanthoid branching has originated independently in three different lines within subg. *Phyllanthus.*

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[14] See Plate XVII, fig. A.

[15] See Plate IX, fig. 40.

From a phytogeographic point of view, sect. *Cyclanthera* is noteworthy in having its center of distribution in Hispaniola. Of the eight named taxa of the section, seven occur in Hispaniola and six are endemic there, while only two taxa are found in Cuba, and only the typical variety of *P. tenuicaulis* is endemic there. However, when one considers the origin of the section, Cuba assumes a relatively more important position, since the ancestral sect. *Callitrichoides* is confined to Oriente Province. Perhaps the origin of sect. *Cyclanthera* may be referred to that period in the Cenozoic when eastern Cuba and Hispaniola formed a single landmass.

The following treatment of the eight constituent taxa of sect. *Cyclanthera* must be considered only provisional, and the lack of field observations is keenly felt. A satisfactory treatment does not appear possible until further collecting is done and the possibility of hybridization taken into account.

KEY TO THE SPECIES

1. Leaves of main axis not reduced to cataphylls except at uppermost nodes, mostly coriaceous; deciduous branchlets never with iterative axes; disk-segments petaloid, extending far outside the margins of the synandrium; pedicel of female flower mostly 6–10 mm. long or more; seeds 1.8–2.3 mm. long; northern Hispaniola . . . . 14. *P. berteroanus*

1. Leaves of main axis reduced to cataphylls; deciduous branchlets often with iterative axes; disk-segments inconspicuous, not projecting far beyond the synandrium; pedicel of female flower 5 mm. long or less; seeds not over 1.4 mm. long.

    2. Capsule minutely scabridulous, c. 1.5 mm. in diameter; calyces greenish white or purplish only at the base; slender annual with nearly smooth, greenish (never purplish) branchlets; Cuba and northern Haiti . . . . 11. *P. tenuicaulis*

    2. Capsule smooth, 2 mm. or more in diameter; calyces usually purplish-stained.

        3. Synandrium subsessile, the column less than 0.3 mm. high; calyx-lobes of male flower free to the base; styles free; habit various; Cuba and Hispaniola . . . . 12. *P. lindenianus*

        3. Column of synandrium c. 0.7 mm. high; calyx-lobes of male flower united into a turbinate cup; styles united into a column 0.15–0.2 mm. high; subshrub with clustered stems and membranous leaves; southwestern Haiti . . . . 13. *P. abditus*

11. **Phyllanthus tenuicaulis** Muell. Arg. Linnaea **32**: 44. 1863; DC. Prodr. **15**(2): 409. 1866. (PLATE XVI, *figs. F–H*).

Diasperus tenuicaulis (Muell. Arg.) O. Ktze. Rev. Gen. **2**: 601. 1891.

A very slender herb with an erect simple or sparingly branched stem 1–3 dm. high, 1 mm. thick or less, stramineous or greenish, terete, nearly smooth. Cataphylls thin and scarious, greenish white with an olivaceous tinge; stipules lanceolate, acute or acuminate, more or less obliquely attached but not auriculate, entire, 0.4–0.6 mm. long, 0.2–0.3 mm. broad; blade linear-lanceolate, entire, 0.4–0.7 mm. long, c. 0.15 mm. broad. Permanent branches mostly suppressed. Deciduous branchlets simple or producing an iterative axis from the first node, 1–3.5 cm. long, 0.1–0.2 mm. thick, stramineous, smooth or very obscurely scabridulous proximally, terete or somewhat angled, with 7–20 leaves; first internode 3–7 (–9) mm. long, median ones c. 1.5–3 (–4) mm. long. Leaves: stipules ovate to lanceolate, 0.4–0.5 mm. long, 0.2–0.25 mm. broad, acuminate, truncate at the base, entire, olivaceous with pale scarious margins. Petioles smooth, 0.3–0.5 mm. long. Leaf-blades membranous, obovate to elliptic or suborbicular, (3–) 4–8 (–11) mm. long, (1.5–) 2–4 mm. broad, mostly subtruncate or rounded and apiculate at the tip, acute at the base; above deep green, the nerves rather obscure; beneath pruinose, smooth or appearing roughened when young, the midrib slightly raised, the laterals obscure or visible and anastomosing; margin not thickened, smooth or sometimes crinkled.

Monoecious; flowers solitary, branchlets often with 1 to 2 female flowers toward the tip, the male flowers proximal or sometimes also distal to them; sometimes male and female flowers apparently on separate branchlets (due to the fugaciousness of the male flowers).

Male flower: pedicel capillary, 1.7–3.3 mm. long. Calyx-lobes 5 (rarely 6), ovate or triangular, 0.5–0.9 mm. long, 0.3–0.8 mm. broad, sharply acute, entire, thin, scarious-hyaline, entirely yellowish white or sometimes purplish-blotched at the base (never with purplish midrib or scattered flecks). Disk-segments 5, cuneate, c. 0.2–0.25 mm. broad, with a rather fleshy fold at the base but thin and subpetaloid distally, more or less hidden under the nearly sessile synandrium. Synandrium disciform, 0.3 mm. broad across the connective; pollen grains c. 13–14 μ in diameter.

Female flower: pedicel slender, straight or slightly curved, smooth, olivaceous, 1–2.2 mm. long. Calyx-lobes 6, elliptic to ovate, 0.9–1 mm. long, 0.45–0.6 mm. broad, acute, entire, olivaceous with broad yellowish white scarious margins, sometimes purple-blotched at the base (never purple-flecked all over). Disk-segments 6, thin, hyaline, c. 0.25 mm. long, cuneate, smooth, entire. Ovary closely and minutely scabridulous. Styles free, horizontally spreading, 0.15–0.2 mm. long, bifid or c. 2/3-parted, the branches spreading, the unthickened tips recurved.

Capsule scabridulous, c. 1.5 mm. in diameter, the valves thin, stramineous, nervation obscure. Seeds [all those observed immature] c. 0.75 mm. long, 0.5 mm. radially, marked with dark raised points.

The species comprises two vicarious populations, one Cuban and one Haitian, which differ in the characters mentioned in the following synopsis:

11a. **Phyllanthus tenuicaulis** var. **tenuicaulis.**

Deciduous branchlets c. 1–3.5 cm. long, with 7–11 leaves; leaves obovate, (3–) 4–7 (–11) mm. long; calyx-lobes of male flower 0.5–0.7 mm. long; pedicel of female flower c. 1–1.2 mm. long.

TYPE: "Cuba Orientali," *Wright 1675 ex p.*

DISTRIBUTION: endemic to eastern Cuba (Map IV).

CUBA. ORIENTE: Sierra Maestra. La Madelena, on banks, Dec. 9, 1859, *Wright 1675 ex p.* (G, HOLOTYPE; GH, GOET, NY, W, ISOTYPES); Sierra Maestra, Loma del Gato, *Clemente 597* (NY), *2065* (MICH).

11b. **Phyllanthus tenuicaulis** var. **haitiensis** Webster, Contr. Gray Herb. **176**: 48. 1955.

Deciduous branchlets usually 3–5 cm. long, with 13–20 leaves; leaves elliptic or broadly obovate, or nearly orbicular, 4–8 mm. long, 2.5–4 mm. broad; calyx-lobes of male flower c. 0.9 mm. long; pedicel of female flower c. 2 mm. long.

TYPE: Haiti, *Ekman H4417.*

DISTRIBUTION: endemic to northern Haiti (MAP IV).

HAITI. NORD-OUEST: Massif du Nord, Anse-à-Foleur, Morne Cheneau, highest part of ridge, c. 800 m. alt., 25 June 1925, *Ekman H4417* (S, HOLOTYPE); Riv. Côte de Fer, vicinity of Jean Rabel, in crevice of rock, *E. C. & G. M. Leonard 12630* (US).

The specimen of the Leonards is referred to this variety and indeed to the species with some doubt. The ovary appears not to be scabridulous, and judging from the calyx-lobes, the plant resembles *P. lindenianus* var. *leonardorum.* At the present time it is impossible to tell whether the variability present in the five known collections of *P. tenuicaulis* is due to hybridization or to other factors.

Among the species of sect. *Cyclanthera, P. tenuicaulis* is of especial interest because it undoubtedly is the species most closely related to sect. *Callitrichoides*; the small scabridulous capsule common to both *P. tenuicaulis* and *P. carnosulus* appears to be an unmistakable mark of affinity. On the other hand, however, the androecium of *P. tenuicaulis* is quite typical for sect. *Cyclanthera,* and the species shows several points of resemblance to some of the varieties of *P. lindenianus.*

12. **Phyllanthus lindenianus** Baill. Adansonia **2**: 13. 1861.

Phyllanthus cyclanthera sensu Mueller in DC. Prodr. **15** (2): 408. 1866.

Variable annual or perennial herb, sometimes suffruticose, 0.5–7 dm. high, with a single main stem or with several stems clustered at the base; stems terete, smooth or scabridulous, olivaceous and more or less purplish-tinged, internodes mostly 8–20 mm. long. Leaves of stems and permanent branches reduced to cataphylls: stipules triangular or lanceolate, usually acuminate, truncate at the base, entire, thin and scarious, purple or purplish brown, 0.4–1 mm. long, 0.2–0.5 mm. broad; blade narrower, acuminate, 0.5–1 mm. long, 0.1–0.2 mm. broad. Permanent branches often developed. Deciduous branchlets simple or often producing an iterative axis from the first node, (2–) 4–10 cm. long, 0.2–0.4 (–0.7) mm. thick, stramineous or greenish and usually purplish-tinged, smooth or scabridulous, terete or angled, with (5–) 10–30 nodes; first internode mostly 5–15 mm. long, median internodes c. 2–6 mm. long. Leaves: stipules triangular to lanceolate, 0.3–1 mm. long, 0.15–0.5 mm. broad, acuminate, truncate at the base, entire, purplish-flecked with a whitish scarious margin. Petioles 0.3–0.7 mm. long. Leaf-blades membranous, elliptic to obovate or sometimes suborbicular, mostly 5–15 mm. long and 2–10 mm. broad, acute or obtuse and apiculate at the tip, acute or obtuse and sometimes inequilateral at the base, sometimes somewhat falcate in outline; above light or dark green, often purplish-stained, smooth or sometimes scabridulous, the nerves inconspicuous; beneath pallid, often purplish-speckled, smooth or scabridulous, the midrib raised and prominent, the laterals (c. 4–6 on a side) straight, anastomosing intramarginally, obscure or purplish and conspicuous; margins smooth, plane.

Deciduous branchlets mostly floriferous; flowers solitary, the male either proximal or distal to the female (male flowers fugacious and branchlets sometimes thus appearing entirely female).

Male flower: pedicel c. 1–5 (–6) mm. long. Calyx-lobes 5 (rarely 6), equal or unequal, ovate to elliptic or sometimes obovate, 0.5–1.5 (–1.7) mm. long, 0.4–1 (–1.4) mm. broad, obtuse or acute, entire, usually greenish white densely flecked or stained with purple, the purplish midrib unbranched. Disk-segments 5 (6), cuneate, subentire, small and inconspicuous, scarcely if at all protruding from beneath the synandrium. Synandrium subsessile, c. 0.5–0.8 (–0.9) mm. across, c. 0.15 mm. high; connective 0.25–0.5 (–0.75) mm. in diameter, concave or plane, often with a central rounded knob c. 0.1 mm. across; pollen grains c. 17.5–21 μ in diameter.

Female flower: pedicel 1.5–4 (–5) mm. long, greenish or more often purplish, smooth or scabridulous, terete, gradually broadening upwards. Calyx-lobes 6 (rarely 5), ovate (in flower) becoming elliptic to obovate (in fruit), 0.9–2 mm. long, 0.4–1.3 mm. broad, obtuse or rounded to acute, more or less purplish-stained, the midrib unbranched. Disk irregularly cut into (5–) 7–9 cuneate, thin, purple-flecked segments, these sometimes more or less connate. Ovary smooth; styles free, ascending or horizontally spreading, rather thick and fleshy, purple-flecked, 0.2–0.4 mm. long, 1/3- to 2/3-parted, the branches divergent, the narrowed obtuse tips recurved.

Capsule obtusely trigonous, smooth, 2–26 mm. in diameter, stramineous, the nerves not apparent. Seeds when mature 0.9–1.4 mm. long, 0.7–1

(–1.2) mm. radially and tangentially, dark greyish brown, with fine slightly raised closely arranged dark points in longitudinal rows; hilum triangular, brownish, c. 0.2 mm. across.

As pointed out earlier (Contr. Gray Herb. 176: 48–50. 1955), this widespread and variable species must take the name *Phyllanthus lindenianus*, since the earlier *P. cyclanthera* Baill. is a *nomen confusum* incapable of typification. At the time of that nomenclatural discussion, three distinct species were recognized within the *P. lindenianus* complex, but since then further study (including the examination of additional material) has led to a reevaluation. It has become apparent that the relative amount of scabridulousness on various organs is not as valuable a diagnostic character as had been thought. A comparison of MAP VI, which shows the specimens of *P. lindenianus* distributed by variety, with MAP V, in which the same specimens are scored as to scabridulousness and habit, shows that the variation pattern in these characters is not perfectly correlated with the recognized subspecific taxa. The fluctuation of characters appears so extensive, in fact, that one might think the recognition of varieties within this species is an artificial procedure which cuts across natural, random patterns of variation. However, although the available specimens constitute an admittedly incomplete sampling of the populations, the present classification seems justified for at least two reasons. In the first place, with the exception of var. *lindenianus* and var. *inaequifolius*, the varieties are allopatric, with well-defined ranges. Furthermore, the various populations include representatives with such divergent features — as the suffruticose habit of var. *inaequifolius* or the seed size of var. *leonardorum* — that it would be definitely misleading to obscure this geographically localized diversity by recognizing no subspecific entities.

A previously neglected feature which appears to be of some importance is the spatial relationship of the sexes. In var. *lindenianus* the male flowers are at the proximal nodes of the branchlet and the female flowers are distal, while in the other varieties this is reversed, the female being proximal to the male. This inflorescence character has been used with some misgiving, since it is very difficult to determine the disposition of the sexes in many specimens and since further study may perhaps demonstrate more variation in this respect than there now appears to be. A careful inspection of the relative positions of the male and female flowers is commended to those who may have occasion to encounter this species in the field.

KEY TO THE VARIETIES

1. Seeds 0.9–1 mm. long; female calyx-lobes acute; slender annual with smooth stems but scabridulous female pedicel; iterative axes typically lacking; northern Haiti .... var. *leonardorum* (12c)
1. Seeds 1.2–1.4 mm. long; female calyx-lobes obtuse

or rounded; at least some branchlets on every plant with iterative axes.

2. Male flowers proximal and female distal on the main or iterative axis of branchlet; stem, and usually the female pedicel, scabridulous; stems usually unbranched at base; Cuba, southern Hispaniola . . . . var. *lindenianus* (12a)
2. Male flowers distal and female proximal; stem, and usually the female pedicel, smooth.
   3. Perennial, with several stems clustered at the base; leaves of upper branchlets often conspicuously smaller than those below; southern Hispaniola . . . . var. *inaequifolius* (12d)
   3. Annual, with a single unbranched main stem; leaves all approximately the same size; central Hispaniola . . . . var. *jimenezii* (12b)

12a. **Phyllanthus lindenianus** var. **lindenianus** (PLATE XVIII, *fig. A*).

Phyllanthus lindenianus Baill. Adansonia **2:** 13. 1861.
Phyllanthus gracilissimus Baill. op. cit. 14.
Phyllanthus cyclanthera β scabrellus Muell. Arg. Linnaea **32:** 44. 1863.
Phyllanthus cyclanthera γ gracillimus Muell. Arg. ibid.
Phyllanthus cyclanthera α lindenianus (Baill.) Muell. Arg. in DC. Prodr. **15**(2): 408. 1866.

Annual, or possibly sometimes perennial, but with a single main stem unbranched at base; stem 1–4 dm. high, 1.5–3 mm. thick, stramineous to purplish and rather sparsely scabridulous or almost whitish due to densely compacted papillae. Cataphylls: stipules 0.7–1 mm. long, 0.3–0.5 mm. broad; blade 0.5–1 mm. long. Deciduous branchlets usually with an iterative axis from the first node; main axis (4–) 5–8 (–10) cm. long, greenish or purplish, sparsely to densely papillate or scabridulous, with mostly 10–20 nodes. Leaves: stipules 0.5–0.8 (–1) mm. long, 0.2–0.5 mm. broad; blades mostly 5–15 mm. long, 2–10 mm. broad, elliptic to obovate, above smooth or conspicuously scabridulous, beneath nearly smooth to conspicuously scabridulous. Branchlets typically with proximal male flowers and 1–6 distal female flowers on both main and iterative axes, or sometimes remaining entirely male. Male flower: pedicel 1.5–3.5 (–6) mm. long; calyx-lobes elliptic to obovate or less commonly ovate, 0.8–1.5 (–1.7) mm. long, (0.6–) 0.7–1 (–1.4) mm. broad; synandrium 0.5–0.8 (–0.9) mm. across; connective purple-flecked, 0.3–0.6 (–0.75) mm. in diameter. Female flower: pedicel 1.7–3.5 (–5) mm. long, purplish at least above, scabridulous (rarely almost smooth); calyx-lobes elliptic to obovate, mostly 1.5–2 mm. long, (0.7–) 0.9–1.3 mm. broad, obtuse or rounded at the tip; styles 0.35–0.4 mm. long. Capsule c. 2.5–2.6 mm. in diameter; seeds 1.2–1.4 mm. long, c. 1 mm. radially and tangentially.

TYPE: Cuba, Monte Libano, *Linden 1827* ex p.

DISTRIBUTION: Cuba and western Hispaniola (MAP VI).

CUBA. PINAR DEL RIO: Sierra de las Animas, 15 Mar. 1920, *Ekman 10508* (S). ORIENTE: Monte Libano, May 1844, *Linden 1827* ex p. (P, HOLOTYPE; G, ISOTYPE); Loma de Jagüey, alt. 600 m., among rocks, Mar. 1889, *Eggers 4928* (P, SV); Monte Verde, on rocks in dense woods, 7 July 1859, *Wright 1935* (G, GH, GOET, MO, W).

HAITI. SUD: Massif de la Hotte, central group, St.-Louis du Sud, Bonnet-Carre, limestone, c. 1150 m., 2 Nov. 1927, *Ekman H9229* (S).

DOMINICAN REPUBLIC. BARAHONA: Nochebuena Berge, alt. 1200 m., Sept. 1910, *Fuertes 345* (C, F, G, GH, MO, P, S, US); Las Filipinas, 1200 m. alt., Apr. 1912, *Fuertes 1470* (C, F, G, GH, P, S, US).

The somewhat aberrant form described as *P. gracilissimus* is represented by the following two specimens:

CUBA. ORIENTE: Monte Liban, *Linden 1827* ex p. (P, HOLOTYPE of *P. gracilissimus*); "entree des cavernes du Mt. Liban", *Linden 1827* ex p. (BR, ISOTYPE).

Baillon published *P. lindenianus* and *P. gracilissimus* at the same time, basing the two species on different plants from the same collection. Although Baillon considered the two species as very distinct, one must agree with Mueller (DC. Prodr. **15**[2]: 408. 1866) that neither Baillon's descriptions nor the specimens furnish any convincing distinguishing characters. The type specimen of *P. gracilissimus* is indeed peculiar in several points: the flowers are small, the sharply acute male calyx-lobes are merely purple-striped down the center instead of being diffusely purplish-tinged, the disk of the female flower is 3-lobed, and the plant has a slenderer more fragile aspect which well justifies Baillon's specific epithet. In gross appearance the plant bears a striking resemblance to var. *leonardorum*, but it does not agree in technical characters; on the other hand, in its habit and male flowers the type specimen of *P. gracilissimus* is almost exactly intermediate between var. *lindenianus* and *P. tenuicaulis*. Serious consideration must therefore be given to the possibility that it represents a hybrid between *P. lindenianus* and *P. tenuicaulis*, especially since intermediates between *P. lindenianus* var. *leonardorum* and *P. tenuicaulis* have been collected in northern Haiti. However, thus far *P. tenuicaulis* has not been found in the Monte Libano region in Oriente, the two known localities both being in the Sierra Maestra. The exact status of the plant referred to *P. gracilissimus* by Baillon must therefore remain in doubt.

Even if *P. gracilissimus* is excluded from consideration, var. *lindenianus* remains a polymorphic entity which is rather difficult to delimit. The Cuban plants, which have a tendency to greater scabridulousness (particularly on the leaves), evidently belong together; but some of the specimens from Hispaniola, where the range of the variety overlaps that of var. *inaequifolius*, are somewhat discordant. *Ekman H9229* from the Massif de la Hotte appears to be perennial like var. *inaequifolius* and has unusually large synandria up to 0.9 mm. in diameter, but because of its uniform leaves and scabridulous stems must be classified with the present variety.

12b. **Phyllanthus lindenianus** var. **jimenezii**, var. nov.[16]

Herb with a single main stem, apparently annual, decumbent at the base but erect above, up to 8 dm. high (ex coll.); stems smooth, purplish-tinged. Cataphylls: stipules c. 0.6–0.7 mm. long, blade about as long. Deciduous branchlets either with or without an iterative axis from the first node; main axis 6–10 cm. long, purplish, smooth, with c. 15–30 leaves. Leaves: stipules 0.8–1 mm. long, c. 0.3–0.4 mm. broad; blades broadly elliptic, mostly 6–10 mm. long, 3–5.5 mm. broad, obtuse or rounded and apiculate at the tip, smooth on both sides. Branchlets with proximal female and distal male flowers, whether or not main axis is branched. Male flower: pedicel c. 1.5 mm. long; calyx-lobes ovate to elliptic, 0.8–0.9 mm. long, 0.6–0.75 mm. broad, obtuse or subacute; synandrium c. 0.75 mm. across, connective c. 0.5 mm. in diameter. Female flower: pedicel becoming 4–5 mm. long, purplish, smooth or obscurely roughened; calyx-lobes oblong-ovate to elliptic, 1.2–1.5 mm. long, 0.7–0.9 mm. broad, obtuse or rounded at the tip; styles c. 0.35 mm. long. Mature capsule not seen entire; seeds c. 1.4 mm. long, 1.2 mm. radially and tangentially.

DOMINICAN REPUBLIC: Constanza, El Salto de Constanza, alt. 1200 m., 15 July 1955, *Jiménez 2972* (US 2114149, HOLOTYPE).

DISTRIBUTION: known only from the type (MAP VI).

This variety is still poorly known, and the description may have to be modified when additional material becomes available. In general aspect var. *jimenezii* approaches more closely to var. *lindenianus* than to either of the other varieties, but it differs sharply in its completely smooth parts and apparently in its inflorescence. The fact that the Jiménez specimen represents a geographically isolated population which cannot be accommodated within any of the three previously known varieties makes it seem advisable to designate it as the type of a new variety. However, since var. *jimenezii* combines some of the features of var. *inaequifolius* and var. *lindenianus*, its discovery has not only been influential in the decision not to recognize those two taxa as independent species, but has also raised the possibility that the present four varieties of *P. lindenianus* may be merely arbitrary concepts which mask a complex and random pattern of variation. Although this seems unlikely, only future collecting can settle the question.

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[16] **Phyllanthus lindenianus** var. **jimenezii**, var. nov.

Verisimiliter annuus, omnino laevis; foliis membranaceis, ellipticis, plusminusve inter se aequalibus, 6–10 mm. longis; lobis calycis florum masculorum c. 0.8–0.9 mm. longis, florum femineorum c. 1.2–1.5 mm. longis; seminibus c. 1.4 mm. longis.

12c. **Phyllanthus lindenianus** var. **leonardorum** (Webster), stat. nov.

Phyllanthus leonardorum Webster, Contr. Gray Herb. **176**: 50. 1955.

Slender erect annual; stem unbranched except above, 0.5–2.5 dm. high, 0.4–1.3 mm. thick, usually pale stramineous-whitish or greenish below, purplish and more or less pruinose above, smooth or very obscurely and remotely scabridulous. Cataphylls: stipules 0.4–0.8 mm. long, 0.15–0.25 mm. broad; blade 0.5–0.7 mm. long, 0.1–0.2 mm. broad. Deciduous branchlets with a female flower at the first node or less commonly producing an iterative axis there, (2–) 4–6 (–7) cm. long, purplish, smooth, with 5–25 leaves. Leaves: stipules 0.3–0.6 mm. long, 0.2–0.3 mm. broad, blades obovate or elliptic, (2–) 4–9 mm. long, (1.5–) 2–5 mm. broad, smooth on both sides. Branchlets very often with a female flower at the first node, the succeeding two nodes typically bearing male flowers; this arrangement repeated with more or less regularity the entire length. Male flower: pedicel 0.75–2 mm. long; calyx-lobes usually ovate-triangular and sharply acute (sometimes obovate and obtuse), 0.5–0.8 mm. long, 0.4–0.8 mm. broad; synandrium 0.45–0.5 mm. across, connective 0.25–0.3 mm. in diameter, yellowish white. Female flower: pedicel 1.6–3.5 mm. long, greenish or purplish, scabridulous; calyx-lobes ovate in flower, tending to become obovate in fruit, 1–1.4 mm. long, 0.3–0.6 mm. broad, narrowed to an acute tip; styles 0.2–0.35 mm. long. Capsule c. 2–2.2 mm. in diameter; seeds c. 0.9–1.1 mm. long, 0.7–0.9 mm. broad.

TYPE: Haiti, *E. C. & G. M. Leonard 12624.*

DISTRIBUTION: dry calcareous areas, central and northern Haiti (MAP VI).

HAITI. NORD-OUEST: Presqu'ile du Nord-Ouest, Port-de-Paix, cultivated place in Prosopis thickets south of Saline-Michel, 12 Apr. 1925, ***Ekman H3756*** (S); west of Saline-Michel, 15 Mar. 1928, ***Ekman H9702*** (S); vicinity of Jean Rabel, Môle Road, 27 Jan. to 9 Feb. 1929, ***E. C. & G. M. Leonard 12624*** (GH, HOLOTYPE; MICH, MO, NY, US, ISOTYPES). ARTIBONITE: Massif des Matheux, l'Archaie, Trou-Forban, in Bayahonde thickets, 10 Oct. 1926, ***Ekman H7092*** (S, US).

Variety ***leonardorum*** is perhaps the most xerophytic population of ***P. lindenianus***; and it is so well characterized by its depauperate habit, small fruit and seeds, and usually unramified branchlets, that it was originally described as a distinct species. However, further analysis of the variation within the *P. lindenianus* complex has led to the conclusion that it is preferable to regard *P. leonardorum* as a geographically and ecologically isolated variety of the inclusive species ***P. lindenianus***.

In aspect var. ***leonardorum*** strongly resembles ***P. tenuicaulis,*** which also occurs in northern Haiti; the latter, however, may be easily distinguished by its lack of purplish coloration. It is difficult to decide whether the resemblance between the two taxa is due to close affinity (var. ***leonardorum*** possibly representing the group through which ***P. lindenianus*** evolved from *P. tenuicaulis*), or to hybridization between them, or to both of these factors. An intermediate specimen possibly of hybrid origin (*Leonard & Leonard 12630*) has already been discussed under *P. tenuicaulis.*

The Ekman collection from the Massif de Matheux differs from the other collections of var. *leonardorum* in aspect, blunter lobes of the male calyx, and shorter fruiting pedicels. However, until other collections are available from the area it is impossible to tell whether it represents anything more than a local variant.

12d. **Phyllanthus lindenianus** var. **inaequifolius** (Webster), stat. nov. (PLATE XVII, *figs. A–C*; PLATE XVIII, *fig. B*).

Phyllanthus inaequifolius Webster, Contr. Gray Herb. **176:** 48. 1955.

Suffruticose perennial 3–7 dm. high with few to several main stems diverging from the base; stems subsimple above, smooth, brownish below, above olivaceous and more or less purplish-tinged. Cataphylls: stipules 0.7–1 mm. long, mostly 0.3–0.4 mm. broad; blade 0.7–1 mm. long, c. 0.15–0.2 mm. broad, commonly adnate to the stipules in the lower half. Deciduous branchlets, at least those above, usually with an iterative axis from the first node; main axis 5–10 cm. long, green or purplish, smooth, with mostly 15–30 leaves; leaves of lower branchlets usually conspicuously larger than those of the upper branchlets, the transition more or less abrupt, or sometimes leaves not noticeably unequal. Leaves: stipules 0.7–1 mm. long, c. 0.3 mm. broad; blades membranous to chartaceous, elliptic to obovate, usually obtuse and apiculate at the tip, smooth on both sides, the smaller c. 2–5 mm. long and 1–2.5 mm. broad, the larger c. 5–15 mm. long and 3–8 mm. broad. Branchlets ordinarily not producing female flowers on the main axis (unless it is unramified), but often with distal male flowers; iterative axis with (1–) 3 proximal female flowers, succeeded distally by several males. Male flower: pedicel 1.7–3.7 mm. long; calyx-lobes mostly ovate, 0.7–1 (–1.2) mm. long, 0.5–0.9 mm. broad, acute or subacute; synandrium 0.5–0.75 mm. across, connective 0.3–0.5 mm. in diameter. Female flower: pedicel 1.7–4 mm. long, purplish, smooth; calyx-lobes ovate to obovate, 0.9–1.3 mm. long, 0.6–0.9 mm. broad, obtuse at the tip; styles 0.35–0.4 mm. long. Capsule c. 2.2–2.3 mm. in diameter; seeds 1.2–1.4 mm. long, 1–1.1 mm. radially and tangentially.

TYPE: Haiti, *Ekman H1344.*

DISTRIBUTION: limestone areas, southern Haiti (MAP VI).

HAITI. SUD: slopes of limestone hills near Randelle, at roadside, not far from Port-à-Piment, 12 Aug. 1917, *Ekman H674* (S). OUEST: Massif de la Selle, Morne Brouet, on dry ridges, alt. 1700 m., 6 Aug. 1924, *Ekman H1344* (S, HOLOTYPE; US, ISOTYPE); Mornes des Commissaires, in open pine forest, alt. 1600 m., 17 Oct. 1941, *Holdridge 859* (MICH, NY, US); vicinity of Mission, Fonds Varettes, alt. 1000 m. and above, 17 Apr. to 4 May 1920, *Leonard 3985* (NY, US); vicinity of Furcy, Morne de Wegan, cliff, alt. c.

1300 m., *Leonard 4600* (US); Mornes des Commissaires, on mossy limestone boulders, alt. 5560 ft., 17 Sept. 1955, *Proctor 10865* (A).

The plant of the type collection, *Ekman H1344*, has such a distinctive aspect due to its perennial habit with the leaves abruptly smaller above that it was originally described as a species distinct from *P. lindenianus*. However, the examination of additional material has shown that only the two Ekman collections have a marked difference in leaf size; furthermore, the population typified by *Ekman H1344* agrees in essential details of leaf, flower, and seed with typical *P. lindenianus*. As MAP V demonstrates, the scabridulous character of stem, female pedicel, and calyx is too fluctuating to serve for the delimitation of distinct species. The difference in disposition of the sexes may prove to hold even when more material becomes available, but even so it does not appear to outweigh the many apparent similarities. Consequently, the preferable course is to recognize this population of southern Haiti as a variety of the widespread *P. lindenianus*.

A difficulty raised by the adoption of the present concept is that at least one collection of var. *lindenianus* (*Ekman H9229*) lies within the known range of var. *inaequifolius*. If further collecting should make it apparent that the two entities occur sympatrically over much of southern Haiti without intergradation, the possibility of specific status for var. *inaequifolius* might have to be re-examined. However, *Ekman H9229* is itself such an aberrant representative of var. *lindenianus* that it can hardly be taken as evidence for the sympatric distribution of the two varieties.

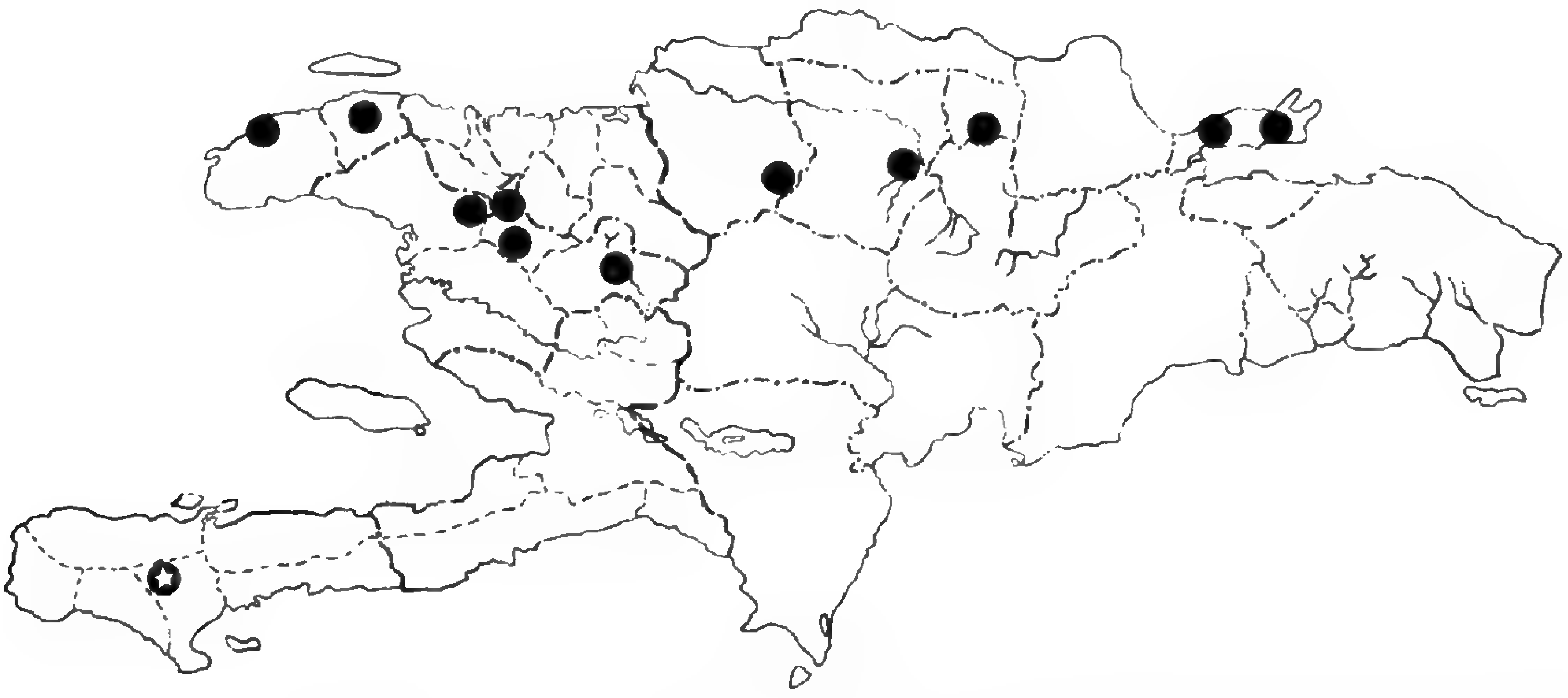
13. **Phyllanthus abditus** Webster, Contr. Gray Herb. **176**: 50. 1955. (PLATE XVII, *figs. D–E*; PLATE XVIII, *fig. C*).

Suffruticose perennial c. 4 dm. high with several erect stems clustered on a caudex; stems terete, smooth, greenish, somewhat zigzag above, c. 1.5 mm. thick; internodes c. 10–25 mm. long. Leaves of main stems reduced to cataphylls: stipules lanceolate, c. 1 mm. long, 0.3–0.4 mm. broad, acuminate, purplish-flecked, entire; blade narrower, more or less adnate to the stipules in the lower half. Deciduous branchlets simple below but upper ones producing an iterative axis from the first node; main axis 6–9 cm. long, 0.2–0.4 mm. thick, green, smooth, terete or somewhat angled below, with c. 25–35 leaves; first internode 5–7 mm. long, median internodes 2–6 mm. long. Leaves: stipules lanceolate, 0.8–0.9 mm. long, 0.2–0.3 mm. broad, acuminate, purplish. Petioles 0.5–0.75 mm. long. Leaf-blades membranous, elliptic or obovate, c. 5–12 mm. long, 3–6 mm. broad, broadly obtuse or rounded and apiculate at the tip, cuneate or obtuse at the base, smooth on both sides; above bright green, the nerves (except the midrib) obscure; beneath pallid, the laterals forming a delicate reticulum; margins smooth, unthickened.

Deciduous branchlets never with a female flower at the first node (an iterative axis produced instead), the female flowers 1 (or sometimes 2?)

per branchlet, produced on the proximal part of either the main or iterative axis, the several male flowers distal.

Male flower: pedicel 1.4–1.8 mm. long. Calyx 1.7–1.8 mm. long; calyx-lobes 5, purple-flecked, 1-nerved, fused in the lower third into a turbinate cup c. 0.6–0.7 mm. high which is constricted at the juncture with the lobes; free portion of lobes broadly ovate or suborbicular, 1–1.2 mm. long, 0.8–1.2 mm. broad, obtuse or rounded, purple-flecked, the midrib unbranched, entire with an extremely narrow thickened margin. Disk-segments 5, suborbicular, fleshy, rather thick, whitish, concealed in the calycine cup at the base of the synandrial column. Synandrium on a column c. 0.7 mm. high, c. 0.15–0.2 mm. thick, tapering slightly upwards, lightly purplish-tinged; synandrium circular or elliptic in outline, c. 0.7–0.8 mm. across; connective c. 0.45–0.5 mm. in diameter, purplish-flecked, with a conspicuous central knob; pollen grains c. 17–21 μ in diameter.



MAP VII. Distribution of *Phyllanthus abditus* Webster (starred circle) and *Phyllanthus berteroanus* Muell. Arg. (solid circles).

Female flower: pedicel 3.3–3.7 mm. long, purplish, smooth, tapering upwards from the slender lower half. Calyx-lobes 6, separate essentially to the base, obovate, 1.4–1.6 mm. long, 0.75–0.9 mm. broad, rounded at the tip, entire, purplish-flecked or nearly immaculate, midrib unbranched. Disk divided as in *P. lindenianus* into c. 7 or 8 thin, cuneate segments up to 0.2 mm. long. Ovary smooth; styles united at the base into a short but definite column 0.15–0.2 mm. high, steeply and divergently ascending, 0.5–0.6 mm. long, 2/5-parted to bifid, slender, the branches diverging, the acute tips recurved.

Capsules not seen entire; valves olivaceous, nerveless. Seeds c. 1.25 mm. long, 1 mm. radially and tangentially, dark brown, with longitudinal rows of dark raised points; hilum triangular, c. 0.25 mm. across.

TYPE: Haiti, Dépt. Sud, Massif de la Hotte, western group, Camp Perrin, northern slope of Morne Vandervelde, on rocks at Source Mare Blanche, c. 700 m., 30 Nov. 1925, *Ekman H5197* (S, HOLOTYPE; associated on the sheet with *Lygodium volubile* Sw.).

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

This restrictedly endemic species resembles *P. lindenianus* var. *inaequifolius* in a number of ways, and perhaps is most closely related to it. Vegetatively the present species could hardly be distinguished from forms of *P. lindenianus*, but the floral characters are so distinctive that *Ekman H5917* surely must represent a distinct species rather than a mere aberrant state of *P. lindenianus*. However, there is little doubt that *P. abditus* is closely related to that species and does not stand as isolated in the section as does *P. berteroanus*.

14. **Phyllanthus berteroanus** Muell. Arg. Linnaea **32**: 44. 1863; DC. Prodr. **15**(2): 408. 1866.

(PLATE XVII, *figs. F–G*; PLATE XVIII, *fig. D*).

Diasperus berteroanus (Muell. Arg.) O. Ktze. Rev. Gen. **2**: 598. 1891.
Phyllanthus anisophyllus Urb. Repert. Sp. Nov. **18**: 364. 1922.

Perennial herb c. 3–8 dm. high, with one to several terete erect stems from a woody base; all parts completely smooth and glabrous. Lowermost c. 15–20 nodes on main stems bearing large leaves and no branchlets, the subsequent leaves (subtending branchlets) on the main stem and those on the branchlets more or less abruptly reduced in size. Leaves of main axis, though reduced above, mostly not completely scale-like: stipules lanceolate, c. (0.7–) 1.2–2 mm. long, 0.4–0.8 mm. broad, acuminate, entire, olivaceous or brownish, scarious. Petioles of lower leaves up to 2 mm. long, those of uppermost leaves less than 1 mm. long. Larger blades (those not subtending branchlets) oblanceolate, obcuneate, oblong, or elliptic, usually coriaceous (more rarely membranaceous), 15–75 mm. long. Deciduous branchlets invariably unbranched, mostly 5–10 cm. long, sometimes (particularly those from lower nodes) up to 20 cm. long or at the apex reduced to c. 2.5 cm. long, 0.3–0.6 (–0.9) mm. thick, olivaceous, subterete, with 10–25 (–40) leaves; first internode mostly 5–12 mm. long (up to 20 mm. on lower branchlets), median internodes 2–8 mm. long. Leaves: stipules lanceolate, 0.7–1.2 (–1.5) mm. long, 0.25–0.4 (–0.5) mm. broad, acuminate, olivaceous with yellowish entire margins, the tip more or less scarious. Petioles of smaller leaves c. 0.4–1 mm. long, of larger leaves 1–1.5 (–2) mm. long. Leaf-blades coriaceous to membranous, mostly elliptic or oblong, sometimes slightly falcate, 3–15 (–20) mm. long, 2–8 (–11) mm. broad (those of the upper branchlets often strikingly smaller than those of the lower), obtuse to acute with a conspicuous scarious-indurate apiculum, obtuse at the base; above olivaceous, sublucid, the midrib plane or very slightly raised, the laterals usually obscure; beneath yellowish green or rarely whitened, the midrib conspicuously raised, the laterals (c. 4 or 5 on a side) and the fine reticulum of tertiaries subprominent to obscure; margins plane or reflexed, not revolute.

Monoecious; female flowers 1–3 (–4) at the distal nodes of the branchlet, male flowers at the proximal nodes (first node sometimes barren);

both sexes borne on the same or sometimes perhaps on different branchlets.

Male flower: pedicel 4–7 mm. long. Calyx-lobes 6, biseriate, subequal, ovate or triangular, (0.9–) 1–1.4 mm. long, (0.8–) 1–1.7 mm. broad, obtuse or acute, entire, yellowish or greenish white and often purplish-tinged at base, midrib pinnately branched. Disk-segments 6, obovate to squarish in outline, distal portion fleshy, purplish, petaloid, 0.4–0.65 mm. long, 0.5–0.9 mm. broad. Stamens 3; synandrium subsessile, (0.5–) 0.7–0.9 (–1) mm. across, round or trigonous in outline; connective more or less plane, purplish, (0.4–) 0.5–0.8 mm. in diameter; pollen grains c. 26–27 μ in diameter.

Female flower: pedicel (5–) 6–10 (–12) mm. long, olivaceous or stramineous, terete below, becoming angled and gradually thickened above. Calyx-lobes 6, biseriate, subequal, ovate to suborbicular, (1.5–) 1.7–2.3 mm. long and about as broad, blunt to subacute at the tip, entire, olivaceous, midrib pinnately branched; lobes spreading or reflexed in fruit. Disk-segments 6, obcuneate or obovate, purplish and petaloid as in the male, persistent with the fruiting calyx. Ovary smooth, depressed at anthesis, the horizontal styles nearly touching the disk; styles free, 0.4–0.5 mm. long, bifid, the branches divergent, the slender tips recurved.

Capsule oblate, rounded-trigonous, c. 3.7–4.2 mm. in diameter, smooth, stramineous, the veins completely obscure. Columella c. 1.3–1.5 mm. long. Seeds trigonous, (1.8–) 1.9–2.3 mm. long, (1.4–) 1.5–1.8 (–2) mm. radially, (1.4–) 1.5–2 mm. tangentially, dark brown to almost black, colliculose with slightly raised transversely elongated dots; hilum roundish, c. 0.3–0.4 mm. in diameter.

TYPE: "St. Domingue," *Bertero* (G, HOLOTYPE; P, ISOTYPE). The exact locality of Bertero's collection is not known.

DISTRIBUTION: calcareous areas, northern Hispaniola (MAP VII).

HAITI. NORD-OUEST: vicinity of Jean Rabel, rocky slope of mountain south of town, 4 Mar. 1929, *E. C. & G. M. Leonard 13709* (US); Massif du Nord, Port-de-Paix, Morne Fourris, deep limestone cliffs, alt. c. 400 m., 30 Apr. 1925, *Ekman H3960* (S, US). ARTIBONITE: vicinity of St. Michel de l'Atalaye, alt. c. 350 m., cultivated slope, Habitation Baille, 26 Nov. 1925, *Leonard 7477* (US); vicinity of Marmelade, alt. c. 800 m., dry bank, road to St. Michel, 21 Dec. 1925, *Leonard 8421* (US); Camp No. 4, Marmelade, pineland, alt. c. 2950–3050 ft., 1 & 2 Aug. 1905, *Nash & Taylor 1265*, *1276* (NY); Ennery, in thickets on soft limestone, c. 400 m., 14 Nov. 1924, *Ekman H2449* (S, US); Massif du Nord, Hinche, Morne Pedregal, Oligocene limestone, 600 m., 13 May 1926, *Ekman H6093* (S); vicinity of Ennery, alt. 325–900 m., dry bank, Puilboreau road, 13 Jan. 1926, *Leonard 8826* (NY, US); vicinity of Ennery, alt. 325–900 m., on rocks, 19–21 Jan. 1926, *Leonard 8989*, *9063* (US).

DOMINICAN REPUBLIC. MONTE CRISTI: Cordillera Central, Monción, at La Harquetta, limestone, c. 400 m., 29 May 1929, *Ekman H12661* (S). SANTIAGO: Cordillera Central, Santiago, road to Jánico, c. 350 m., Miocene limestone, hillsides, 16 Nov. 1930, *Ekman H16159* (S); Cordillera Septentrional, Santiago, Cuesta de Piedras, rocky slope, c. 200 m., 23 Nov. 1930, *Ekman H16231*

(S, US); El Buzo, 900 m. alt., 14 Jan. 1945, *Jiménez 301* (A, US). ESPAILLAT: near Salcedo, 31 Oct. 1954, *Jiménez 2763* (US). SAMANA: Samaná Peninsula, vicinity of Sanchez, sea level to 300 m. alt., base of limestone cliff, 29 Nov. to 12 Dec. 1920, *Abbott 165, 166* (US); Samaná, Boca de Río San Juan, steep cliffs, 17 May 1930, *Ekman H14998* (S).

Phyllanthus berteroanus is probably the most abundant species in sect. *Cyclanthera*, although in overall area of distribution it must yield first place to *P. lindenianus*. It appears to be common everywhere along the chain of mountains which roughly parallels the northern coast of Hispaniola. Morphologically *P. berteroanus* is the most sharply defined representative of sect. *Cyclanthera*; although it is somewhat similar in aspect to *P. lindenianus* var. *inaequifolius*, it can be only distantly related to that plant. The striking petaloid disk-segments, branching calycine midrib, and large fruit and seeds show that *P. berteroanus* occupies a very isolated position within sect. *Cyclanthera*. The unreduced and often coriaceous leaves on the main stem and the lack of iterative axes on the branchlets make it possible to identify this species from vegetative material alone.

As might be expected for such a wide-ranging species, there is considerable intraspecific variation in *P. berteroanus*, particularly in the size and texture of the leaves; but the variation patterns are so indefinite that it does not seem desirable to create any subspecific entities. Urban's *P. anisophyllus*, said to differ in its leaf form and disk-segments, was based on *Buch 1062* from Plaisance, Haiti, and *Abbott 165* from the Samaná Peninsula. The Buch collection has unfortunately not been examined, and Urban's specimen was presumably lost in the destruction of the Berlin Herbarium. However, the Abbott collection, although deviating from the norm by virtue of its larger and thinner leaves, certainly does not appear to represent a distinct species. The shape of the disk-segments varies from nearly square to obovate or obcuneate, the variation depending at least partially on the amount of lateral compression. At the present time it does not appear necessary to distinguish the Samaná Peninsula population even on the varietal level.

Sect. 10. **Urinaria** Webster, Contr. Gray Herb. **176**: 51. 1955.

Annual or perennial herbs with phyllanthoid branching; deciduous branchlets angled or winged, leaves hispidulous near margin, stipules conspicuously auriculate. Monoecious; female flowers solitary in the proximal

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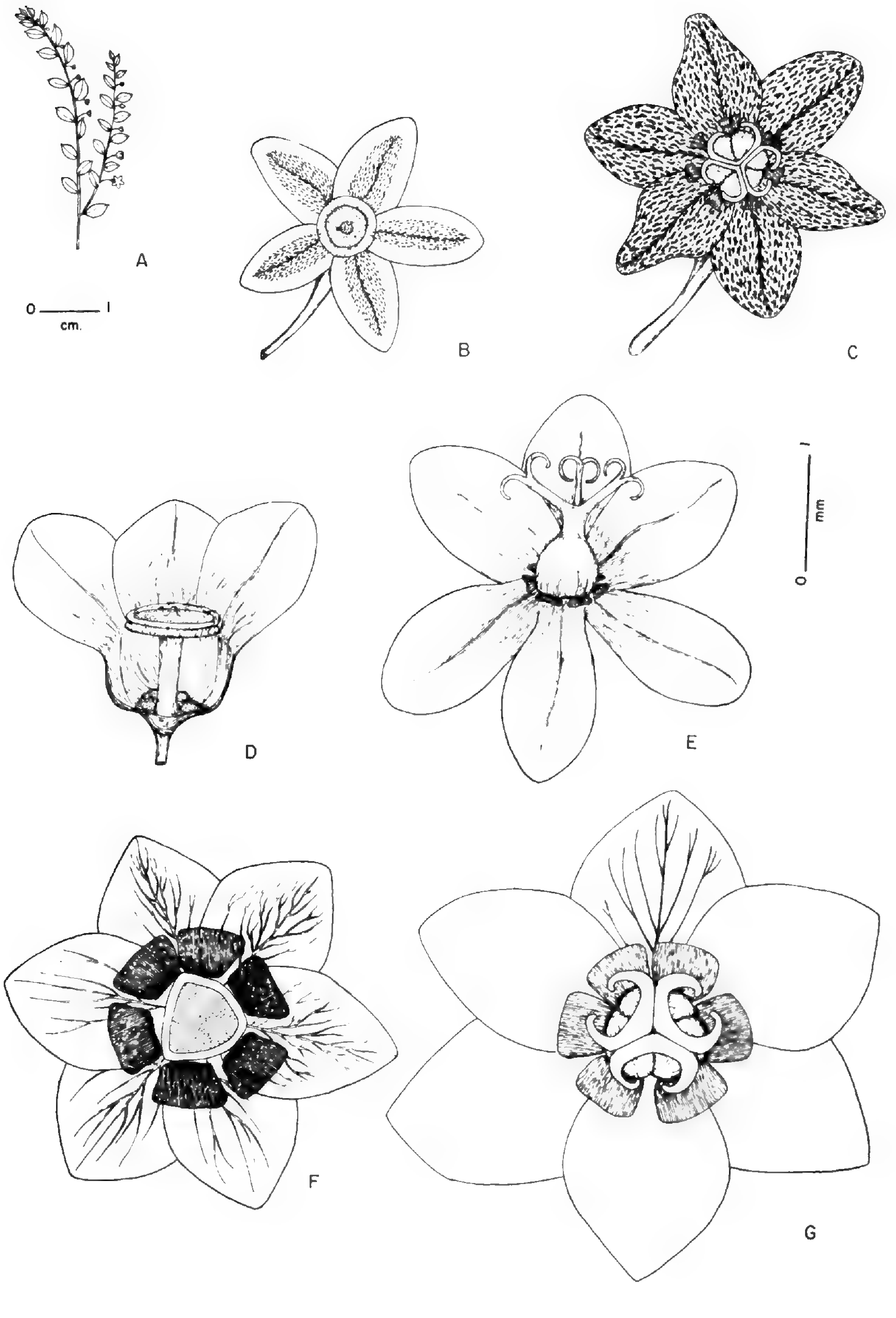
PLATE XVII. Section *Cyclanthera*.

FIGS. A–C. *Phyllanthus lindenianus* var. *inaequifolius* (Webster) Webster. A, branchlet showing iterative axis to right (*Proctor 10865* [A]); B, male flower (*Ekman H1344* [S]); C, female flower (*Ekman H1344* [S]). FIGS. D–E. *Phyllanthus abditus* Webster (*Ekman H5197* [S]). A male flower with half of calyx cut away to show calyx tube and synandrial column; B, female flower. FIGS. F–G. *Phyllanthus berteroanus* Muell. Arg. (*Ekman H1659* [S]). F, male flower; G, female flower (venation shown in only one calyx-lobe). (Figs. B–G all drawn to same scale.)



WEBSTER, WEST INDIAN PHYLLANTHUS

axils, male in cymules in the distal axils. Male flower: calyx-lobes 6; disk-segments 6, very small; stamens 3, filaments free or united; anthers erect, dehiscing vertically; pollen grains subglobose, 4-colporate, finely reticulate. Female flower: subsessile; calyx-lobes 6; disk a shallow cup; ovary conspicuously bullate, styles laterally fused at base. Capsule oblate, tuberculate; seeds trigonous, with sharp transverse ridges on back and sides, the lateral faces more or less deeply pitted.[17]

TYPE SPECIES: *Phyllanthus urinaria* L.

This section, included in sect. *Paraphyllanthus* by Mueller, is actually very distinctive on the basis of its characteristic stipules, spatial arrangement of the sexes, and unique seeds. It includes, in addition to the type species, four additional species described from India, Indo-China, the Philippines, and Tahiti, respectively: *P. hookeri* Muell. Arg., *P. arenarius* Beille, *P. benguetensis* C. B. Rob., and *P. societatis* Muell. Arg. Except for the problematical *P. croizatii* Steyerm. from Venezuela (which is probably only a form of *P. urinaria*), no indigenous representatives occur in the New World.

The phylogenetic relationships of sect. *Urinaria* are of considerable interest, because in many respects (particularly with regard to stipules and female flower) the species of this group resemble those of sect. *Loxopodium*. On the other hand, in branching habit the members of sect. *Urinaria* accord much more closely with sect. *Phyllanthus*. It appears at least possible that sect. *Urinaria* has evolved from sect. *Loxopodium* quite independently of sect. *Phyllanthus*, which is probably descended from some group in subg. *Kirganelia*. If this could be confirmed it would be a clear demonstration of the independent origin of phyllanthoid branching at least twice within the genus.

15. **Phyllanthus urinaria L.** Sp. Pl. 982. 1753; Muell. Arg. in DC. Prodr. 15(2): 364. 1866. (TEXT-FIG. 9).

Urinaria Indica, supina, cauliculus rubentibus Burm. Thes. Zeyl. 231. 1737.
Phyllanthus. . . floribus sessilibus, caule herbaceo procumbente L. Fl. Zeyl. 157–158. 1747.
Phyllanthus cantoniensis Hornem. Enum. Pl. Hort. Hafn. 29. 1807.
Phyllanthus alatus Blume, Bijdr. 594. 1826.
Phyllanthus lepidocarpus Sieb. & Zucc., Abh. Acad. Muench. 4(2): 143. 1843.
Phyllanthus leprocarpus Wight, Icon. Pl. Ind. Or. 5(2): *pl. 1895.* 1852.

PLATE XVIII. Section *Cyclanthera.*

FIG. A. Holotype specimen of *P. lindenianus* Baill. var. *lindenianus (Linden 1827 ex p.* [P]). FIG. B. Holotype specimen of *P. lindenianus* Baill. var. *inaequifolius* (Webster) Webster (*Ekman H1344* [S]). FIG. C. Holotype specimen of *Phyllanthus abditus* Webster (*Ekman H5197* [S]). FIG. D. Representative specimen of *Phyllanthus berteroanus* Muell. Arg., showing fully developed leaves on main axis (*Leonard 9063* [GH]).

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[17] See Plate XI, figs. 53 and 54.

WEBSTER, WEST INDIAN PHYLLANTHUS

Diasperus urinaria (L.) O. Ktze. Rev. Gen. 2: 601. 1891.
Phyllanthus chamaepeuce Ridl. Trans. Linn. Soc. Ser. II, 3: 345. 1893.

Erect or procumbent herb, normally annual; primary stem simple or becoming ramified, mostly 1.5–5 dm. high and 1–2.5 mm. thick, smooth and olivaceous to reddish above, nearly terete but with narrow acute ridges decurrent from the nodes. Cataphylls scarious, stramineous; stipules ovate-lanceolate, attenuate-acuminate, conspicuously auriculate at the base, the auricles denticulate or lacerate, often overlapping and stipule then appearing peltate, c. 2–3 mm. long, 0.8–1.2 mm. broad; blade ovate-lanceolate, acuminate, less conspicuously auriculate, displaced onto the base of the deciduous branchlet c. 1 mm. above the attachment of the stipules, 1.5–2.5 mm. long. Deciduous branchlets ascending, (3–) 5–10 cm. long, 0.5–0.7 (–0.9) mm. thick, olivaceous or sometimes reddish, flattened and acutely winged, the raised median area hirsutulous, with c. 20–35 leaves; first internode (3–) 5–12 (–15) mm. long, internodes between female flowers (2.5–) 3–5 (–7) mm. long, between male flowers mostly 1.5–2 mm. long. Leaves: stipules unequal, the longer of each pair c. 0.8–1.5 mm. long, triangular-lanceolate, attenuate-acuminate, not auriculate, entire, membranous-scarious, stramineous or brownish. Leaf-blades (6–) 8–20 (–25) mm. long, (2–) 2.5–6 (–9) mm. broad, membranous or somewhat firm, mostly oblong or oblong-obovate or nearly linear, sometimes slightly falcate, obtuse or acute and mucronulate at the tip, mostly obtuse and sometimes conspicuously asymmetric at the base; above bright or dark green, smooth, the raised midrib and laterals quite apparent; beneath pallid or sometimes reddish-tinged, minutely scabridulous on the face, hispidulous marginally and immediately intramarginally, midrib and the laterals (c. 5 on a side) raised and conspicuous, tertiaries forming a delicate, rather obscure reticulum.

Monoecious; well-developed branchlets nearly always floriferous; (5–) 8–15 (–20) proximal nodes with solitary female flowers; 5–10 (–15) succeeding distal nodes bearing abbreviated monochasia of 5–7 successively maturing male flowers; distalmost nodes and occasionally (here and there) some proximal nodes barren.

Male flower: Pedicel less than 0.5 mm. long, disarticulating above the middle. Calyx-lobes 6, elliptic to oblong-obovate, c. 0.3–0.45 mm. long, 0.2–0.4 mm. broad, obtuse, more or less entire, membranous, yellowish white, the midrib unbranched. Disk-segments 6, cuneate or roundish, c. 0.1 mm. across, obscurely glandular-papillate and crenulate. Stamens 3, filaments completely united into a slender column c. 0.1–0.15 mm. high; anthers sessile on the column but free from another, erect, c. 0.1–0.15 mm. long, 0.1 mm. broad; anther-sacs parallel, dehiscing vertically, the slits not confluent; pollen grains subprolate, c. 20 μ long and 16 μ broad, 4-colporate, colpi with median pores, exine finely reticulate.

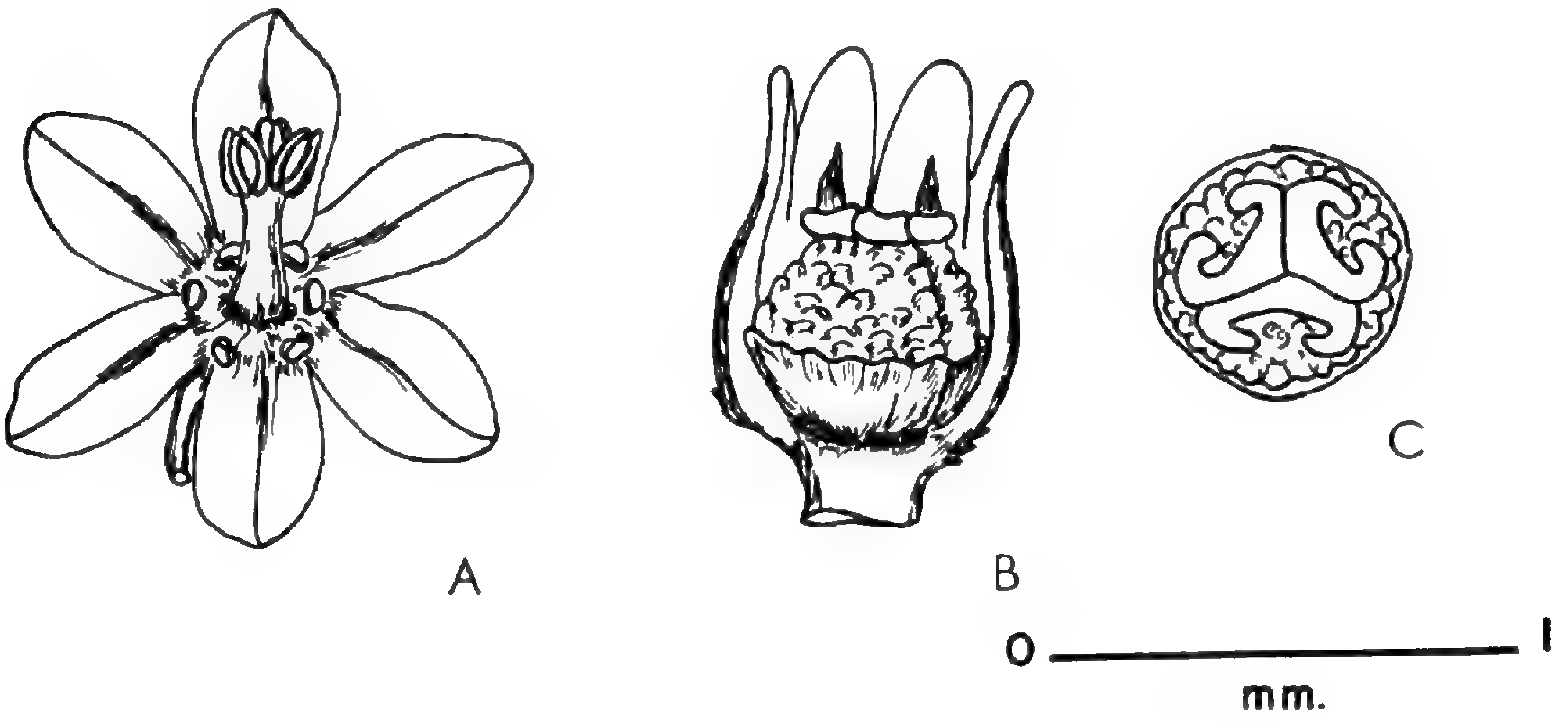
Female flower: Pedicel 0.5 mm. long or shorter, green or reddish, smooth, terete, becoming greatly thickened in fruit. Calyx-lobes 6, erect at anthesis, reflexing in fruit, linear-oblong or lanceolate, 0.6–0.9 mm. long, 0.2–0.3 mm. broad, obtuse or rounded at the tip, hispidulous dorsally at the base and on the olivaceous or reddish slightly raised midrib area, yellowish, scarious, margins minutely serrulate or entire. Disk patelliform, thin, 6-angled or obscurely crenulate. Ovary spheroidal, olivaceous or reddish, conspicuously bullate-papillate; styles flattened and laterally fused at the base into a horizontal triangular plate 0.35–0.4 mm. across, c. ⅓ parted, the branches divaricate and recurving at the tips.

Capsule c. 2–2.2 mm. in diameter, scurfy-tuberculate or nearly smooth, olivaceous or stramineous often with reddish blotches, nervation completely obscure. Seeds 1.1–1.2 mm. long, (0.8–) 0.9–1 mm. radially, 0.9–1 mm. tangentially, light greyish brown, with 12–15 sharp transverse ridges on the back and sides (these discrete or sometimes coalescing in pairs), often with 1–3 deep circular pits on the sides; hilum subterminal, depressed, more or less triangular.

Flowering all year.

Type: Ceylon, *Herb. Hermann* (BM). There are three specimens in Hermann's herbarium, of which vol. 4, fol. 55 probably represents the holotype, as it bears an annotated reference to Burman's description in the "Thesaurus Zeylanicus."

Distribution: Native to Asia, introduced at scattered localities throughout the tropics.



Text-fig. 9. *Phyllanthus urinaria* L. (*Webster & Wilson 4923*). A, male flower; B, female flower with two calyx-lobes removed; C, gynoecium and disk seen from above.

JAMAICA. St. Mary: Castleton grounds, 490 ft., *Harris 12142* (C, F, P, S, US). St. Andrew: vicinity of Kingston, *Britton 1708* (NY); Hope Grounds, 650 ft. alt., *Harris 12155* (F, NY, P, S, US); Hope River Valley, *Harris 9980* (F, US). St. Thomas: Bath, in shady places, *Harris 12195* (C, F, P, US); Corn Puss Gap, *Webster & Wilson 4923* (A, JAM, MICH). Portland: clay bank by roadside, Seamen's Valley, *Maxon & Killip 54* (F, NY, US); vicinity of Windsor, *Maxon & Killip 264* (F, NY, US).

LESSER ANTILLES. GUADELOUPE: Gourbeyre, *Duss 213* (P); Pointe-à-Pitre, *Duss 2922* (NY); champs cultivés, *L. Quentin 88* (P); champs, alt. 100 m., *R. Quentin 925* (P); Montebello, 60 m., *Questel 438, 441* (US); Baillif aux Vieux-Habitants, *Stehle 71* (US); friches de cannes-à-sucres, Pointe-à-Pitre, *Stehlé 238, 500* (NY); Abymes, alt. 19 m., *Stehlé 1193* (NY); Ste. Rose, champs et friches lateriques, *Stehlé 1829* (US); Basse Terre, 1877, *Thiebaut* (P). DOMINICA: Rouseau Valley, *Lloyd 558* (NY); roadside in cleared forest land, Sylvania Estate, alt. 549 m., *Hodge 575* (NY). MARTINIQUE: St. Pierre, *Belanger 292 ex p.* (G); Troisième pont, *Hahn 554* (G, L, P), *929* (P); Balata, *Mouret* (P); champ de bananes, Ravine-Vilaine, *Privault 44 ex p.* (P). ST. LUCIA: 1889, *Walsh* (NY); moist forest, *Velez 3312* (US). ST. VINCENT: Montrose Hills, 800 ft., *Eggers 6561* (US). GRENADA: Animas, mountains, banks in open places, *Broadway ex p.* (NY, mixed with *P. caribaeus*); Belvedere, 1600–1800 ft., *Eggers 6111* (GOET, L, P, US); Mt. Pleasant, 1500 ft., *G. S. Miller 159* (US). TOBAGO: damp ground, Caledonia, *Hunnewell 19935* (GH). TRINIDAD: Port of Spain, *Wall* (S); St. Ann's, Cascade, on banks, *Broadway 5057* (F, G, S); St. Joseph, D'Ade's Estate, in open ground, *Broadway 2638* (F, G, L).

None of the West Indian collections seen of this species was made prior to 1850, so that it is evidently a comparatively recent introduction to our area. Even now, after more than a hundred years, it has not established itself on Cuba, Hispaniola, or Puerto Rico. Definitely mesophytic and one of the most shade-tolerant of the herbaceous species, it does not appear likely to become a serious weed.

Phyllanthus urinaria is obviously a foreigner in the West Indies, for it differs in many details from the superficially similar native species of sect. *Phyllanthus*. The transversely barred seeds and hispidulous leaves are unique in the West Indies, and the tuberculate ovary and subsessile fruiting calyces offer additional characters which should make it one of the easiest species to identify. Furthermore, *P. urinaria* is distinguished physiologically from all of its congeners in our area by the sensitive reaction of the branchlets to touch; when a plant is disturbed sufficiently, the leaves fold together in the manner of *Mimosa pudica* leaflets, although much more slowly.

(To be continued)

STUDIES IN THE THEACEAE, XXIX
FURTHER STUDIES IN THE GENUS MELCHIORA

CLARENCE E. KOBUSKI

With four plates

SINCE DESCRIBING THE GENUS *Melchiora* last year (Jour. Arnold Arb. 37: 153–159. 1956), added information and material has come to my attention. Isotypes of new taxa, at that time either unknown or unavailable to me, have been added to our herbaria. Although these added specimens help confirm some of my suggestions they are still far too few in number for positive conclusions. It will probably be some time before enough material has been assembled to show conclusively whether two, three or even more taxa should be recognized. At present, two species and three varieties are recorded for the genus.

Photographs of the isotypes deposited in our herbaria are reproduced at the end of this paper.

MELCHIORA MANNII (OLIVER) KOBUSKI

Melchiora mannii (Oliver) Kobuski in Jour. Arnold Arb. 37: 155. 1956.

Adinandra mannii Oliver, Fl. Trop. Africa 1: 170. 1868. (See Kobuski, loc. cit. for more complete citation of literature).

This taxon is an endemic found only at the summit of the Pico on the island of São Tomé off the west coast of Africa in the Gulf of Guinea. Last year in discussing this taxon I quoted Exell as stating that he had made a search for *M. mannii* in November 1932 on the Pico in a "tremendous" rainstorm without success. He suggested that since a part of the summit had been cleared and planted with *Cinchona* it was possible that this taxon may have become extinct. In my apprehension over the taxon I mentioned forebodingly several instances where other taxa of this family had become extinct within our own generation. It is pleasant to be able to relate now that such is not the case.

Last October I received a pleased and excited letter from Prof. Th. Monod, Director of the Institut Français d'Afrique Noire at Dakar, stating that he had collected this species on a collecting trip to São Tomé. His is only the third collection of this species as far as I know (*Mann* in 1861 and *Campos* in 1907 are the other two) and the three collections were made at approximately fifty-year intervals!

Later Prof. Monod sent an excellent photograph showing eight flowers enlarged to near natural size. With his kind permission this photograph is being included in this paper. It shows remarkably well the "non spreading" character of the corolla, a most unusual character of this genus, very different from the spreading corolla of other members of the family.

FIGURE 1. Flowers of *Melchiora mannii* (Oliver) Kobuski collected and photographed by Prof. Th. Monod (no. *12228*) from Pico, São Tomé, the type-locality.

THE MELCHIORA SCHLIEBENII COMPLEX

Whereas *M. manii* appears to be confined to a small area at the summit of Pico on São Tomé, *M. schliebenii* and its varieties enjoy a much wider distribution having been collected (from known reports in literature) eight times in Tanganyika, twice in Belgian Congo, and once in Uganda. Even so, this actually is a sparse representation considering the comments on the field notes of the various collectors. Melchior, in the original presentation of the species referred to a letter from the collector (Schlieben), who stated that in the type-locality (Uluguru, Tanganyika) the species comprised seventy percent of the trees. Greenway noted on his no. *6556* that var. *greenwayi* was common on the stream banks in the Pare District, Tanga Province. Boutique and Troupin term var. *intermedia* the dominant feature of the forests in the Lake Kivu area of the Belgian Congo.

A distribution as extensive as this is enjoyed by only a few taxa in the family Theaceae and these taxa, in turn, are notorious in the variability of the usually "reliable" characters. One of these characters is pubescence and it is this character which in *M. schliebenii* shows the most variation. Only a much larger collection of material will show how stable this character is in the present group.

All the types of pubescence found on the taxa described in this complex are of the evanescent type, so common in the family. The leaves of var. *greenwayi*, densely pilose in the buds and younger growth become glabrous or glabrescent at maturity. The fine appressed pubescence found on the inner side of the sepals will wear off as will the thick pilose pubescence on the ovary and style. No fruiting material of the genus has been available to me for study. Melchior in his original presentation described the fruit of *M. schliebenii* and Boutique & Troupin, in turn included a description of the fruit of var. *intermedia* (*Adinandra intermedia*) in their work. In neither instance was any mention made of pubescence, hence one is justified in assuming that the fruit is glabrescent.

Verdcourt (Kew Bull. **1955**: 609. 1956) in a discussion of this complex separates the varieties of *M. schliebenii* (as *Adinandra schliebenii*) on the pubescence of ovary, leaves and sepals. An adaptation of his key using the same characteristics is as follows:

A. Ovary glabrous. . . . . *M. schliebenii* var. *glabra*.
AA. Ovary pilose.
    B. Leaves pubescent to velutinous below. . . . . *M. schliebenii* var. *greenwayi*.
    BB. Leaves glabrous entirely.
        C. Inner sepals ± pubescent outside. . . *M. schliebenii* var. *schliebenii*.
        CC. Inner sepals glabrous outside. . . . *M. schliebenii* var. *intermedia*.

In making a key to members of this family where pubescence is involved I have found in genus after genus that one of the most reliable basic characters is found in the terminal leaf-bud, which is usually present in most specimens. Only in the truly glabrous specimen will the leaf-bud be glabrous. In a pubescent or glabrescent specimen the leaf-bud will be pubescent. This character is quite consistent throughout the whole family. A key based primarily on the leaf-bud character (differing but little from Verdcourt's key) would appear as follows:

- A. Leaf-buds glabrous.
  - B. Ovary and lower part of the style pubescent.
    - C. Sepals and bracts glabrous on the interior side and pubescent on the unexposed (portion concealed by the imbrication in the bud) part of the exterior side. . . . . 1. *M. schliebenii* var. *schliebenii.*
    - CC. Sepals and bracts appressed pubescent on the interior side and glabrous or quickly glabrescent on the exterior side. . . . . 2. *M. schliebenii* var. *intermedia.*
  - BB. Ovary and style glabrous. . . . 3. *M. schliebenii* var. *glabra.*
- AA. Leaf-buds pubescent. . . . . 4. *M. schliebenii* var. *greenwayi.*

Melchiora schliebenii (Melchior) Kobuski in Jour. Arnold Arb. **37**: 156. 1956.

Adinandra schliebenii Melchior in Notizbl. Bot. Gard. Mus. Berlin **11**: 1076, 1097. 1934. — Kobuski in Jour. Arnold Arb. **28**: 95. 1947. — Boutique & Troupin in Bull. Jard. Bot. Bruxelles **20**: 65. 1950. — Verdcourt in Kew Bull. **1955**: 608. 1956.

1. Melchior schliebenii var. schliebenii

TANGANYIKA TERRITORY: Uluguru, in fog forest northwest side of Lupanga Mountains; tree 20–30 m., flowering and fruiting, with orange and red flowers, *H. J. Schlieben 3175* (ISOTYPES, AA and Yale), December 28, 1932.

During a recent conversation with Dr. William L. Stern, Curator of the Wood Collection and Herbarium of the Yale School of Forestry, I learned to my surprise that a set of the Schlieben collection from Tanganyika had been deposited at that institution. He has checked and sent me for annotation a sheet of the type-collection of this species. This is excellent news, indeed, since the Yale specimen proves to be the more complete of the two specimens examined. Up until recently, the type-collection cited above was the only representative of the species. However, another collection, *Drummond & Hemsley 1766*, from the same area is deposited in the herbarium of the Royal Botanic Garden at Kew and cited by Verdcourt in his most recent work.

Like var. *intermedia* this taxon has glabrous leaf-buds, with the ovary and lower part of the style pubescent.

The sepals and bracteoles, however, are glabrous on the interior side and pubescent on the unexposed parts of the exterior side. The disposition of the pubescence on the inner three sepals is very interesting and very characteristic of many taxa in the family Theaceae. The portions of the exterior side of the sepals exposed in the bud are glabrous. This means that the two outer sepals are entirely glabrous. The next two sepals are pubescent on the half side which is covered while the uncovered half is glabrous. The inner sepal, because of its position in the imbrication is generally pubescent over the entire exterior surface or generally so.

Melchiora schliebenii (Melchior) Kobuski var. **intermedia** (Boutique & Troupin) Kobuski, comb. nov.

Adinandra intermedia Boutique & Troupin in Bull. Jard. Bot. Bruxelles **20:** 62. 1950.

Adinandra schliebenii Melch. var. *intermedia* (Boutique & Troupin) Verdcourt in Kew Bull. **1955:** 608. 1956.

Melchiora intermedia (Boutique & Troupin) Kobuski in Jour. Arnold Arb. **37:** 157. 1956.

Adinandropsis, sp. nov. Pitt-Schenkel in Jour. Ecol. **26:** 80. 1938, nom. nud.

BELGIAN CONGO: PROV. KIVU: Mayamoto, forêt ombrophile de montagne, fond de ravin, alt. 2350 m., *A. Michelson 742* (TYPE, BRLU; ISOTYPE, A), Déc. 1947.

We appreciate very much and are most grateful to the Jardin Botanique de l'Etat of Brussels for sending us an isotype of this taxon for our herbaria. Besides the type which was collected in Belgian Congo, Boutique and Troupin cited three other specimens, a second from the type region, and one each from Kigezi in Uganda and Mt. Usambara in the Territory of Tanganyika. This area of distribution comprises a region extending well over seven hundred miles and the authors report the taxon to be the dominant plant of the Kivu region.

The sepals and bracts are glabrous on the exterior surface and appressed pubescent on the interior surface. In this character it is similar to var. *greenwayi*. However, the latter variety has leaf-buds and, of course, mature leaves which are strictly glabrous.

Melchiora schliebenii (Melchior) Kobuski var. **glabra** (Verdcourt) Kobuski, comb. nov.

Adinandra schliebenii Melchior var. *glabra* Verdcourt in Kew Bull. **1955:** 608. 1956.

NO SPECIMENS EXAMINED.

This appears to be a completely glabrous variation of the typical variety. In the original description Verdcourt mentions only the glabrous ovary. However, in his short discussion he states that he had considered including the new variety under var. *intermedia* but because of the "peculiar" plants as yet undescribed from the area of the W. Usambaras he suggested that the glabrous ovary may be correlated with a limited distribution.

Two specimens were cited by Verdcourt [*Procter 183* (EA) and *Drummond & Hemsley 2536* (K)] both collected in the Lushoto District at altitudes of 2220 m. and 2230 m. respectively. Furthermore, it was suggested by the collectors that both representatives grew on the exposed ridgetops or, when in the forests, in the drier parts.

It is not unusual for taxa in the family Theaceae to take on a glabrous character when found growing in high dry exposed places.

Unfortunately, no duplicates of the type of this variety have been available to me. It would be interesting to know whether the interior side of the bracts and sepals are appressed pubescent as in var. *intermedia* or are strictly glabrous.

Melchiora schliebenii (Melchior) Kobuski var. **greenwayi** (Verdcourt) Kobuski, comb. nov.

Adinandra greenwayi Verdcourt in Kew Bull. **1953**: 84. 1953.
Adinandra schliebenii Melchior var. greenwayi (Verdcourt) Verdcourt in Kew Bull. **1955**: 608. 1956.

TANGANYIKA TERRITORY: TANGA PROV.: Pare Distr., S. Pare Mts. Mtonto, alt. 6500 ft., locally common on stream banks in *Ocotea-Podocarpus-Rapanea-Myrica* evergreen forest on steep mountain slopes, *P. J. Greenway 6556* (TYPE, K; ISOTYPES A and EA), July 5, 1942 (much branched evergreen tree with ascending branches up to 80 ft. tall; the bark reddish brown, much fissured in reticulate patches; the flowers large tubular creamy brown with green tipped petals; the mature leaves with a brownish cream band each side of the main vein).

A very ample specimen of the type number of this taxon was given us by the East African Herbarium at Nairobi, Kenya, East Africa.

The sepals and bracts as in var. *intermedia* are glabrous on the exterior surface and appressed pubescent on the interior surface. However, the terminal leaf-buds differ from all other taxa in this complex in being tomentose. This character is retained into the younger stages of the mature leaves but later in the older leaves tends toward glabrescence. This taxon may represent the original entity in the complex.

At present these varieties seem clearly distinguishable. One must remember, however, that the species is one of wide distribution and is found in considerable abundance in several areas. The herbarium specimens available for study are as yet far too few in number to assume that the varieties recorded above will be maintained when further collections are examined, as they are based primarily on the pubescence, a character very variable in this family. As I mentioned before, I feel that the original element in the complex is var. *greenwayi* and that the other three are variations from it, with var, *glabra* the most recent and perhaps the least dependable of the group.

ARNOLD ARBORETUM AND GRAY HERBARIUM,
HARVARD UNIVERSITY.

EXPLANATION OF PLATES

PLATE I. Isotype of *Melchiora mannii* (Oliver) Kobuski. *G. Mann 1066* in the Gray Herbarium.

PLATE II. Isotype of *Melchiora schliebenii* (Melchior) Kobuski. *H. J. Schlieben 3175* in Yale University.

PLATE III. Isotype of *Melchiora schliebenii* (Melchior) Kobuski var. *intermedia* (Boutique & Troupin) Kobuski. *A. Michelson 742* in the Arnold Arboretum.

PLATE IV. Holotype of *Melchiora schliebenii* (Melchior) Kobuski var. *greenwayi* (Verdcourt) Kobuski. *P. J. Greenway 6556* in the Royal Botanic Garden, Kew.

Melchiora mannii (Oliver) Kobuski

MELCHIORA SCHLIEBENII (MELCHIOR) KOBUSKI

MELCHIORA SCHLIEBENII (MELCHIOR) KOBUSKI
VAR. INTERMEDIA (BOUTIQUE & TROUPIN) KOBUSKI

MELCHIORA SCHLIEBENII (MELCHIOR) KOBUSKI
VAR. GREENWAYI (VERDCOURT) KOBUSKI

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STUDIES IN THE GENUS COCCOLOBA, IV. THE SPECIES FROM PUERTO RICO AND THE VIRGIN ISLANDS AND FROM THE BAHAMA ISLANDS

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NATHANIEL BRITTON and his colleagues have published treatments for the species of *Coccoloba* known from Puerto Rico and the Virgin Islands and from the Bahama Islands as parts of larger floristic works. Since both of these floras are in use today, it is desirable to present two treatments to parallel Britton's work and to bring up to date the nomenclature as well as the species definition. Since Britton's work on these island areas appeared, there have been relatively few additional collections from these areas and the need for more material of many species remains critical. A field knowledge of the species over the larger area of the West Indies has brought about a better understanding of the morphological variation represented in the areas considered in this paper. As a result, several of Britton's species have been reduced to synonymy and others have been assigned to older taxa not fully understood at the time of Britton's publication.

The species of *Coccoloba* in Puerto Rico, the Virgin Islands and the Bahamas as recognized by Britton and his colleagues are listed below with their equivalents in the present study:

Coccolobis bahamensis	*Coccoloba tenuifolia*
Coccolobis borinquensis	*Coccoloba swartzii* f. *urbaniana*
Coccolobis diversifolia	*Coccoloba swartzii*
Coccolobis grandifolia	*Coccoloba pubescens*
Coccolobis klotzschiana	*Coccoloba microstachya*
Coccolobis krugii	*Coccoloba krugii*
Coccolobis laurifolia	*Coccoloba diversifolia*
Coccolobis northropiae	*Coccoloba northropiae*
Coccolobis obtusifolia	*Coccoloba microstachya*
Coccolobis pirifolia	*Coccoloba pyrifolia*
Coccolobis rugosa	*Coccoloba rugosa*
Coccolobis rupicola	*Coccoloba costata*
Coccolobis sintenisii	*Coccoloba sintenisii*
Coccolobis swartzii var. *portoricensis*	*Coccoloba swartzii*

Coccolobis uvifera	*Coccoloba uvifera*
Coccolobis venosa	*Coccoloba venosa*

In two earlier works Baron H. F. A. Eggers published studies of the flora of St. Croix (St. Croix's Flora, 110. 1876, The Flora of St. Croix and the Virgin Islands, Bull. U.S. Nat. Museum 13: 88. 1879). I do not always agree with the species to which Britton and Wilson have assigned Eggers' species and varieties. I have seen a large number of Eggers' specimens through the courtesy of the Director of the Botanical Museum and Herbarium at Copenhagen. While Eggers cited few collection numbers in the two publications mentioned above, his annotations of specimens and the localities given can be taken to indicate the specimens he had for study. The species and varieties which Eggers cites should be referred as follows:

Coccoloba diversifolia	*Coccoloba krugii* × *C. uvifera*
Coccoloba laurifolia	*Coccoloba diversifolia*
Coccoloba leoganensis	*Coccoloba diversifolia*
Coccoloba nivea	*Coccoloba venosa*
Coccoloba obtusifolia	
var. *jacquinii*	*Coccoloba microstachya*
var. *barbadensis*	*Coccoloba swartzii*
var. *parvifolia*	*Coccoloba microstachya*
Coccoloba punctata	
var. *jacquinii*	*Coccoloba swartzii*
var. *barbadensis*	*Coccoloba krugii* × *C. uvifera*
var. *microstachya*	*Coccoloba microstachya*
var. *parvifolia*	*Coccoloba microstachya*
Coccoloba rugosa	*Coccoloba rugosa*
Coccoloba tenuifolia	*Coccoloba diversifolia*
Coccoloba uvifera	*Coccoloba uvifera*

Coccoloba P. Br. ex L. Syst. Nat. ed. 10, 1007, 1367. 1759; Taxon 3: 114, 156, 233. 1954, nom. conserv.

Guaiabara Miller, Gard. Dict. ed. 4, 2: 1754.
Coccolobis P. Br. Civ. Hist. Jam. 209, *pl. 14*, *f. 3.* 1756.

KEY TO THE SPECIES FOUND IN PUERTO RICO AND THE VIRGIN ISLANDS

Perianth lobes investing the achene; leaves usually membranaceous; ochreolar sheaths commonly elongating with the flowers; bracts usually black in color. . . . . *C. venosa.*

Hypanthium investing the achene, the perianth lobes appressed against the apex of the achene or coronate on the achene; leaves coriaceous to fleshy, rarely membranaceous; ochreolae not elongating with the flowers but broken early; bracts usually straw colored or brown.

Pedicels shorter than the ochreolae in flower and in fruit.

Leaves of normal shoots characteristically 2–5 cm. long.

Leaves ovate, cordate at the base, greenish tan in color even when fresh; venation inconspicuous above, primary veins evident by color below; nodes swollen and bead-like when fresh but only slightly larger than internodal diameter when dry; fruit 4–5 mm. long, strongly triangular in cross section . . . . *C. krugii.*

Leaves ovate-oblong, normally rounded at the base and not cordate, dark brown to black on drying; primary and secondary veins conspicuous on both surfaces, densely reticulate; nodes bead-like, swollen and conspicuously larger than the internodal diameter when dry; fruit round in cross section, not angled. . . . . *C. microstachys.*

Leaves of normal shoots characteristically 7–12 cm. long.

Leaves normally ovate-lanceolate; venation mostly inconspicuous on both leaf surfaces; blades characteristically and conspicuously lighter in color below when dry; fruit globose, ca. 4 mm. in diameter. . . . . *C. pyrifolia.*

Leaves mostly broadly ovate to elliptic; primary veins conspicuous on both surfaces, secondary venation finely reticulate, evident but not conspicuous; blades only slightly lighter in color below; fruit ovoid, 8–10 mm. long, 6 mm. diameter.

Leaves thick and fleshy when fresh, heavy and coriaceous when dry; inflorescence axis stout, the flower clusters often appearing to be sunken in the axis. *C. swartzii f. urbaniana.*

Leaves not evidently thick and fleshy, when dry only thinly coriaceous; inflorescence axis not fleshy, the flower clusters not imbedded in the axis. . . . . *C. swartzii.*

Pedicels longer than the ochreolae in flower and in fruit.

Leaves large, usually 25 cm. wide or more.

Leaves bullate between the primary veins, glabrous, the basal lobes of the blade often surrounding the stem; stem angled or keeled, when dry conspicuously so; inflorescence red. . . . . *C. rugosa.*

Leaves reticulate but not bullate, pubescent at least when young; stems not evidently angled; inflorescence not noticeably red in color. . . . . *C. pubescens.*

Leaves smaller, usually less than 10 cm. wide, rarely 15–20 cm. wide, never strongly bullate or with lower leaf surface deeply chambered by the protruding veins.

Leaves suborbicular, thick and fleshy, one basal lobe of the blade usually overlapping the petiole; fruit obpyriform 1.2–2 cm. long. . . . . *C. uvifera.*

Leaves ovate to elliptic or obovate.

Fruit obpyriform, broadest above the middle; leaves with one basal lobe slightly overlapping the petiole. . . . . . *C. uvifera × C. krugii.*

Fruit broadest below the middle; leaf bases variable but without a basal lobe overlapping the petiole.

Inflorescences with 10 to 20 pistillate flowers or clusters of staminate flowers. . . . . *C. diversifolia.*

Inflorescence with 50 or more pistillate flowers or clusters of staminate flowers.

Inflorescence and flowers red, pedicels 4–5.5 mm. long. . . . . *C. sintenisii.*

Inflorescence and flowers usually green, not bright red; pedicels 1.5 mm. long.

Primary venation conspicuous, secondary venation inconspicuous. . . . . *C. costata.*

Primary venation and secondary venation conspicuous, finely reticulate. . . . . *C. uvifera* × *C. krugii.*

Coccoloba venosa L. Syst. Nat. ed. 10, 1007. 1759; Fawcett & Rendle, Jour. Bot. **51**: 123. 1913; Britton & Wilson, Sci. Surv. P.R. **5**: 269. 1924; Howard, Jour. Arnold Arb. **30**: 398. 1949.

Coccoloba punctata L. Sp. Pl. ed. 2, 523. 1762.

Coccoloba nivea Jacq. Hist. Stirp. Amer. 115, *pl. 78.* 1763; Enum. Pl. 19. 1762.

Trees to 10 m. tall; branches terete, glabrous, the nodes not tumid; ochreae membranaceous, deeply cleft, acuminate on one side, or truncate, to 2 cm. long, glabrous or with flattened glands; leaf blades oblong-lanceolate to elliptic, the apex short acuminate, the base narrowed and slightly cordate or cuneate or obtuse, 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; midrib and primary veins slightly prominent on both surfaces, the primary veins 8–13 pairs, straight or arcuate, bifurcate and anastomosing at the margins, the petioles 5–10 mm. long, glabrous; leaves of the adventitious shoots about the same size, the internodes much elongate and the ochreae to 4 cm. long; inflorescence terminal oı 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; ochreolae membranaceous, enlarging with the expanding bud, each flower with an ochreola, to 2 mm. long, 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 fruit broadly ovoid, the perianth lobes fleshy, white or pink, enclosing the black achene, the hypanthium scarcely evident in the fruit, the fruit 3–4 mm. long and broad.

DISTRIBUTION: Cuba (introduced), Jamaica (in literature but no specimens have been located), Hispaniola, Puerto Rico and the Virgin Islands, and the Lesser Antilles to Trinidad and Tobago.

Puerto Rico: Aybonito to Buenvista de la Plata, *Sintenis 2083* (GH, US); Cayey, *Sintenis 2215* (NY); Coamo Springs, *Britton & Cowell 1329* (NY, US), *Goll 653* (US), *737* (US); Comerio, *Johnston 920* (NY); Guanica, *Britton & Shafer 1891* (NY, US); Gurabo, *Stevenson 2899* (US); Humacao, *Sargent 3014* (US); Las Pijeras, *Britton, Britton & Marble 2219* (NY, US); Ponce to Coamo, *Heller 509* (NY, US); Ponce to Juana Mata, *Goll 805* (US); Ponce to Santa Isabel, *Britton & Britton 7342* (NY); Pumula, *Sargent 9133* (NY); Sardinera, *Britton, Cowell & Hess 1787* (NY); Yabucoa, *Eggers 425* (B, GH); Yuncos, *Sintenis 1942* (B, F, GH, MO, NY, S, US); without specific location, *Wydler 347* (NY), *Schwanecke* s.n. (B). **Vieques Island:** Isabel Segunda, *Shafer 2450* (NY, US). **St. Croix:** Crequis, *Eggers s.n.* (US); Caledonia Gut, *Eggers s.n.* (NY); Christiansted, *Quinn 1130* (NY); Northside Belvidere, *Ricksecker 456* (F, GH, MO, NY, US); Prosperity Hills, *Eggers s.n.* (A); without specific location, *Oersted s.n.* (US). **St. Thomas:** Collections by Crudy, Eggers, Forstrom and Oersted without specific location or collection numbers. **Tortola:** Sage Mt., *J. S. Beard 330* (A, MO); Sea Cow Bay, *Shafer 1125* (F, NY, US).

Beard reports this species to be called "Trible Grape" on Tortola while it is commonly known as Chiggery Grape and Calambreña in Puerto Rico.

Britton and Wilson list *Coccoloba excoriata* L. as a synonym of this species in their treatment of the genus. The Linnean species, however, is properly referred to *C. tenuifolia* L. See Howard Jour. Arnold Arb. **28**: 92–95. 1957.

Coccoloba krugii Lindau, Engler Bot. Jahrb. 13: 145. 1890, Symb. Antill. **1**: 222. 1899; Britton & Wilson, Sci. Surv. P.R. **5**: 267. 1924; Howard, Jour. Arnold Arb. **37**: 337. 1956.

Coccoloba børgesenii Schmidt, Fedde Repert. Sp. Nov. **24**: 75. 1927.
Coccoloba børgesenii forma *ovato-lanceolata* Schmidt, Fedde Repert. Sp. Nov. **24**: 76. 1927.

Shrub or small tree to 6 m. tall; branches terete, glabrous, slightly geniculate and nodose; ochrea membranaceous, persistent, 3–5 mm. long; petioles borne at the base of the ochrea, corky at the base, 5–6 mm. long; blade 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 margin flat or recurved, the 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, the apex obtuse or rounded, the base cordate or rounded; adventitious leaves from the base of the 1 cm. long ochrea with petioles 1 cm. long and blades cordate or elliptic to 7 × 6 cm. long and broad; inflorescence terminal, 5–8 cm. long, rachis glabrous, the staminate flowers 1–3 per node, the pistillate flowers borne singly, the bracts broadly ovate, membranaceous, 1 mm. long; ochreolae membranaceous, flaring to 1 mm. long; pedicels wanting or shorter than the ochreolae, 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 outline, 4–5 mm. long, 3–3.5 mm. in diameter, the perianth lobes appressed, above half the length of the fruit.

DISTRIBUTION: Bahamas, Haiti, Dominican Republic, Jamaica, Puerto Rico, Anagada, Antigua, Barbuda, St. Martin.

Puerto Rico: Guanica near Salinas, *Britton, Britton & Boynton 8314* (NY); Guanica in woods on Monte Cobana, *Sintenis 3776* (MO, NY); Ponce, *Underwood & Griggs 673* (NY, US); *Heller 6211* (A, F, GH, MO, NY, US); *Britton & Cowell 1289* (NY, US); Icacos Cay, *Britton 7153* (NY); Vieques Island, *Shafer 2785* (NY, S, US); Guayanilla, *Britton & Shafer 1841* (F, MO, NY, US). **Anagada:** *Fishlock 26* (NY), *27* (NY); *Britton & Fishlock 1001* (NY), *1063* (F, NY, MO, US), *J. Beard 323* (A).

Coccoloba krugii Lind. × **C. uvifera** L., hybr. nov.

Shrub of 6 feet or small tree; young branches terete, striate, puberulent to pubescent; ochrea 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, blades ovate to ovate-elliptic, apex obtuse to broadly rounded, rarely acuminate with an obtuse point, the base oblique, cordate to rounded, one basal lobe often overlapping the petiole, 6 × 3, 8 × 6, 11 × 8 cm. long and broad, the midrib and veins prominent below, sub-prominent above when dry, ultimate venation reticulate, primary veins 6–7, arcuate and anastomosing near the margin, 2–3 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 ochreolae membranaceous, to 1 mm. long, puberulent, the pedicels shorter than the ochreolae; staminate flowers 2–4 per node, the pistillate flowers solitary at the nodes, hypanthium to 1 mm. long, perianth lobes orbicular, 1.5–2 mm. long and broad, filaments of fertile stamens 2 mm. long; pedicels in fruit equal to twice the length of the ochreolae, fruit fusiform to fusiform-ovoid, 11 mm. long, 8 mm. in diameter, the perianth lobes not coronate.

Puerto Rico: Morrillos de Cabo Rojo, *Britton, Cowell & Brown 4709* (F, NY, US); Ponce, *F. H. Sargent 564* (US). **St. Croix:** La Vallee, *Ricksecker s.n.* (F); Oxholmia, *Borgesen* (C); Rustup Twist, *Ricksecker 465* (F, GH, MO, NY, US); Saltpond, *Raunkiaer s.n.* (C); *Eggers* without location or number (C). **St. Thomas:** without specific location or number: *Eggers* (US), *Ehrenberg* (B), *Raunkiaer* (C); *Holdridge 122* (NY). **Little St. James:** *Britton & Rose 1407* (NY, US). **St. Jan:** *Raunkiaer s.n.* (C). **Virgin Gorda:** *Fishlock 286* (GH), *353* (NY, US); *A. C. Smith 10563* (A).

Judging from the variety of determinations which exist on the specimens cited above, the plants representing this hybrid swarm have caused difficulty to other taxonomists. In addition to the citations given, I have seen thirty-five other sheets with data as to locality, collector, or collector's number, which are insufficient to allow citation. Twenty-five such sheets from the Copenhagen herbarium are old collections obviously from the onetime Danish possessions in the West Indies. These specimens present a range of variation which includes the often diverse forms represented in the collections cited.

The majority of the specimens assigned to this hybrid population were sterile and represented portions of adventitious shoots. Some attached or associated fertile branches gave the impression of unusually large specimens of *Coccoloba krugii* through the long and tenuous inflorescence and through the fruit. In all but two collections the pedicels in both flower and fruit were short. A few specimens had associated fruits resembling those of *C. uvifera.*

Two collections from Virgin Gorda are referred to this hybrid population. One was made by W. C. Fishlock from the "mountain" and a more recent collection by A. C. Smith was more adequately described as a tree, 4–5 m. tall in low thick woods at the summit and on the eastern slope of Virgin Peak at an altitude of 150–420 m. These two collections represent a heavy and fleshy phase of the hybrid. They seem to bear the same relationship to the hybrid population as *C. swartzii* forma *urbaniana* does to *C. swartzii* on the mainland of Puerto Rico. The Fishlock material is in flower and the Smith specimen in fruit. Both specimens are gnarled in appearance and on both the leaves are variable in shape but predominantly broadly ovate. The apparent thickness or leathery appearance of the blades is striking. The apex is rounded and emarginate and the base strongly obliquely cordate. Representative leaves are 6.5 × 5 to 10.5 × 8 cm. long and broad. The venation is conspicuous on both surfaces and the ultimate venation coarsely reticulate. The inflorescence slightly exceeds the length of the leaves and the plants are dioecious. The pedicels of both the flowers and fruits in the collections by Fishlock and Smith are 1.5–2 mm. long. In the other collections cited the pedicels in flower and fruit are 1 mm. in length but appear smaller in contrast. Fishlock reported the common name of "white grape" for this plant on Virgin Gorda, while *C. uvifera* is known as "sea grape" and *C. krugii* as "white wood."

Coccoloba microstachya Willd. Sp. Pl. **2**: 459. 1800; Lindau, Engler Bot. Jahrb. **13**: 146. 1890.

Coccoloba parvifolia Poir. in Lam. Encycl. **6**: 64. 1804.
Coccoloba klotzschiana Meisn. DC. Prodr. **14**: 155. 1856; Lindau, Engler Bot. Jahrb. **13**: 148. 1890.
Coccoloba microstachya var. *ovalifolia* Meisn. DC. Prodr. **14**: 162. 1856.
Coccoloba microstachya var. *lanceolata* Meisn. DC. Prodr. **14**: 162. 1856.
Coccoloba punctata Griseb. in part, Flora Brit. W.I. 163, 1859, not Linnaeus.
Coccoloba microstachya var. *rotundifolia* Urban ex Lindau, Engler Bot. Jahrb. **13**: 147. 1890.
Coccoloba obtusifolia Lindau, Symb. Antill. **1**: 222, 1899; Britton & Wilson, Sci. Surv. P.R. **5**: 268. 1924, 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; ochrea membranaceous, cylindrical, pubescent, 4 mm. long; petioles 3–6 mm. long, flattened above, normally pubescent; 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 margin entire, often undulate, sometimes tightly recurved; midrib and veins prominulous on both surfaces, forming a dense reticulum, although blades relatively thick and often somewhat fleshy in fresh condition, the veins 7–9 pairs, prominent or numerous and all equal and less conspicuous, straight or arcuate, curved and anastomosing at the margin; glabrous above, pilose or glabrate below, occasional hairs remaining on the veins or rarely the entire leaf surface persistently pubescent; apex acute, acuminate rounded or emarginate, the base narrowed, rounded or slightly cordate; leaves of adventitious shoots ovate-lanceolate, 10.5 × 5.5 to 16.5 × 5 cm. long and broad on petioles 7 mm. long with ochreae 8 mm. long, the adventitious leaves cordate at the base, generally tapering or acuminate at the apex and often conspicuously puberulent below; inflorescence terminal, 5–10 cm. long, the rachis usually pubescent, tenuous, rarely stout, often geniculate, commonly recurved; staminate flowers two, rarely one or more than two at the nodes; pistillate flowers solitary, the bracts broadly ovate, 0.5 mm. long, puberulent; ochreolae membranaceous, puberulent, to 0.5 mm. long, erect and surrounding the flower in the staminate plants, generally appressed or flattened against the rachis in the pistillate plants in flower and fruit, pedicels none or shorter than the ochreolae, 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.

Puerto Rico: Guayanilla: *Britton & Shafer 1817* (F, GH, NY, MO, US); *Sintenis 4868* (MO, US); Guanica, *Britton & Britton 9594* (S), *Sintenis 3707* (B), *3431* (MO, US), *Gregory 181* (NY), *Holdridge 181* (A); Mayaguez, *Heller 4546* (A, B, E, F, GH, NY, Mich. MO, NY, US), *Britton, Cowell & Brown 4359* (NY, US), *Britton & Hess 2715* (F, NY, US); Ponce, *Heller 6128* (A, E, F, GH, MO, NY, US), *Underwood & Griggs 686* (NY, US); Cabo Rojo, *Sintenis 545* (GH, S, US), *Velez 1096* (NY); Cayo Muertos, *Britton, Cowell & Brown 4999* (NY); Punta Guaniquilla, *Britton, Cowell & Brown 4566* (F, GH, NY, US), *4573* (NY, US); Rincon, *Sintenis 5498* (F, NY), *5543* (E, F, NY); Coamo, *Sintenis 3328* (E, GH, S, US); Peñon, *Shafer 1985* (NY, US); Cerro Ventana, *Shafer 2976* (NY, US); Santa Maria to Caballo Colorado, *Shafer 2689* (NY, US); Enseñada Hondo, *Britton & Britton 9645* (NY). **Culebra Island:** *Britton & Wheeler 8A* (NY, US), *32* (F, NY, US). **Mona Island:** *Stevens 6170* (NY), 6213 (NY), *Britton, Cowell & Hess 1710* (NY). **Vieques Island:** *Shafer 2805* (NY, US). **St. Thomas:** Bolongo Hill, *Eggers 160* (C, S); Flaghill, *Eggers s.n.* (US); Bordeaux, *Britton & Marble 1378* (C, F, NY, US), *Ostenfeld 328* (C), *330* (C). Without specific location: *Eggers 135* (B), *124* (GH), *714* (A), *Britton, Britton & Shafer 159* (C, F, NY, US), *Paulsen 146b* (NY). Collector not specified: Herb. Kunth, type of *C. klotzschiana*. **St. Jan:** Bethania, *Britton & Shafer 192* (NY, US); Solomon's Bay, *Eggers 3314a* (C). **Tortola:** *Fishlock 124* (F, NY). **Virgin Gorda:** *Fishlock 20* (GH, NY), *279* (GH, US). **Anguilla:** *Boldingh 3483b* (NY). **St. Croix:** Oxholmia, *Borgesen 64* (C); Fair Plains, *Eggers s.n.* (C); Kingshill *Eggers s.n.* (C); Salt River, *Paulsen 264* (C); Folly Hill, *Raunkiaer s.n.* (C); Rustup Twist, *Mrs. J. J. Ricksecker 365* (F, MO, US); Salt River Cliff, *A. E. Ricksecker 459* (F, GH, MO, NY, US); Christiansted, *Rose, Fitch and Russell 3582* (NY, US); Anna's Hope, *Thompson 398* (GH, NY); Mt. Eagle, *Thompson 434* (GH, NY).

The holotype of this species is *Willdenow 7703* in the Willdenow Herbarium in Berlin. In his original monograph of this genus, Lindau accepted *Coccoloba microstachya* Willd. and recognized three varieties. *Coccoloba microstachya* var. *ovalifolia* was described earlier by Meisner and included the holotype. *Coccoloba microstachya* var. *lanceolata* was described also by Meisner. Lindau describes a variety *rotundifolia* attributed as a manuscript name by Urban. In the synonymy of *C. microstachya* var. *ovalifolia*, Lindau cites *C. obtusifolia* Jacquin. The two specimens in the Willdenow Herbarium in Berlin are *7703*, the type of the species, and *7702*, the type of *C. microstachya* var. *lanceolata* Meisner. Both are probably from St. Croix and were probably collected by Vahl. Although Lindau listed four Sintenis collections from Puerto Rico, he failed to cite a type when he described *C. microstachya* var. *rotundifolia.*

In a later treatment of the genus for the West Indies (Symb. Antill. 1: 222. 1899), Lindau recognized the earlier publication of the Jacquin name *Coccoloba obtusifolia* and, accepting this as the correct name for the species, listed in synonymy *C. microstachya* and the three varieties recognized in his earlier publication. The rejection of the morphological varieties is based on a better understanding of the variation within this species and particularly within the development of an individual plant. I agree with Lindau's concept of the morphology of the species, but cannot agree with his acceptance of the name *C. obtusifolia* Jacquin. The description and illustration of the plant Jacquin considered *C. obtusifolia* is clearly not the same plant called *C. microstachya* and typified by the Willdenow specimens. Further, *C. obtusifolia* Jacquin is based on a plant from Carthagena in Colombia. This is the plant which Lindau describes as *C. billbergii* (Engl. Bot. Jahrb. **13**: 219. 1890) and this species is not known from the West Indies.

Although Willdenow described *Coccoloba microstachya* as having glabrous leaves and stems, the type specimen in the Willdenow herbarium shows a minute but distinct pubescence. In the large number of specimens examined in the herbarium and in the field, the amount and the evidence of the indument varies. The pubescence is often represented only by bases of hairs recognized as clear, lighter colored dots or cells in the epidermis of the dried leaves. Generally a slight pubescence remains on the rachis of the inflorescence and is evident when all other portions of the specimen are glabrous. The extreme in foliar pubescence was seen on a specimen collected by Boldingh (*3483B*) from Anguilla where the lower leaf surface of the mature foliage was almost tomentose.

The variation in leaf shape is great, not only in populations but in individual plants. The three taxa which Lindau recognized in 1890, as he reported later, can be found on a single plant or in a single collection. Within the fourteen sheets of the four Sintenis collections that I have examined, all three varieties can be recognized. Some of the herbarium specimens cited seem to have been selected deliberately in the field to show gross and exaggerated variations. The largest adventitious leaves are on the specimens from St. Croix and many of the collections consist only of such shoots and leaves. However, a Britton & Wheeler collection (*32*) shows both the large leaves of the adventitious shoots as well as the smaller leaves, presumably of the same plant although no mention is made of this in the field notes.

Several specimens from St. Croix show an almost teratological thickening of the inflorescence axis. While this is common in other species, and particularly in *Coccoloba swartzii*, it appears unusual in *C. microstachya.*

Coccoloba parvifolia Poir. is based on a Vahl collection and the type is in the Jussieu Herbarium. I have examined a photograph of the type sheet and agree that this species can be referred to the synonymy of *Coccoloba microstachya* Willd. Meisner, however, recognized this species and considered it an "obscure" species from South America. However, the Vahl collection is probably from St. Croix.

The type specimen of *Coccoloba klotzschiana* in the De Candolle Herbarium at Geneva and the fragment of this in the herbarium of the New York Botanical Garden indicate this species may also be referred to *C. microstachya.*

In the extreme forms of *Coccoloba microstachya*, it is difficult to distinguish between this and *C. swartzii.* Usually, however, *C. swartzii* may be recognized by the larger leaves, longer and thicker inflorescence axes, tapered fruit with imbricated perianth lobes, the lack of pubescence (except in forma *pubescens*) and the darker, almost black color of the leaves when dry. By comparison, *C. microstachya* has smaller leaves, tan to brown in color rather than black, exaggerated tumid nodes, shorter and more tenuous inflorescences and fruit with coronate perianth lobes.

Coccoloba pyrifolia Desf. Cat. Hort. Paris ed. 3, 69, 389. 1829; Howard, Jour. Arnold Arb. **37**: 335. 1956.

Coccoloba pirifolia Lindau, Engl. Bot. Jahrb. **13**: 144. 1890, Symb. Antill. **1**: 222. 1899.
Coccolobis pirifolia Lindau, Brit. & Wils. Sci. Surv. P. R. **5**: 267. 1924.
Coccoloba kunthiana Meisner, DC. Prodr. **14**: 166. 1857.
Coccoloba punctata var. *jacquini* Griseb. Fl. Brit. W. I. 163. 1859.

Shrub of 9 ft. to a tree of 30 ft.; trunk to 14 inches diameter at breast height; branches striate, glabrous, the nodes not conspicuously swollen; ochrea subcoriaceous, glabrous, shriveling rather than deciduous, 1 cm. long; petiole inserted below the ochrea, glabrous, 0.6–1.5 cm. long; blade ovate-lanceolate, broadly ovate or occasionally completely orbicular, 4.5 × 2.5, 9 × 5, 12 × 6 cm. long and broad, coriaceous, glabrous, opaque to almost shining, the margin entire, sometimes recurved, the midrib slightly evident below, prominent above, the primary veins flat, slightly impressed above, very slightly evident below, the secondary venation obscure, the apex obtuse, acute or rarely acuminate, the base rounded, narrowed or sub-cuneate; inflorescence terminal, spike-like, 1–2 times the length of the leaf or terminal on lateral shoots, 8 to 31 cm. long, glabrous, the staminate and pistillate flowers borne singly, the bracts triangular to 1.5 mm. long, the ochreolae membranaceous, equalling the bracts; pedicels wanting; hypanthium 1 mm. long, the perianth lobes ovate, to 2 mm. long, the filaments of fertile stamens 3 mm. long; fertile pistil to 2.5 mm. long; fruit globose, ca. 4 mm. in diameter, rounded at the base, obscurely 3-angled, the perianth lobes coronate, laxly acuminate; achene tan in color.

DISTRIBUTION: Endemic to Puerto Rico.

Puerto Rico: Mayaguez, *Cowell 730* (F, US), *731* (F, NY, US), *Otero & Alvarez 540* (A, F), *Sintenis 1018* (BM, US), *Heller 4560* (A, E, F, GH, Mich., MO, NY, US); Sierra de Luquillo, *Sintenis 1405* (F, MO, S), *1501* (BM, GH, NY, US), *Britton & Bruner 7551* (NY); Santurce, *Heller 614* (F, NY, US), *1259* (F, NY), *1268* (NY, US); La Estancita, *Eggers 1173* (US); Mt. Alegrillo, *Britton, Stevens & Hess 2572* (F, MO, NY, US), *Sintenis 238* (GH, MO, S, US), *Hess 645* (NY); Vega Alta, *Britton, Britton & Brown 6796* (F, NY, NEOTYPE; US); Camuy, *F. H. Sargent B-200* (US); Guayamo, *Britton, Britton & Brown 6544* (F, NY, US); Martin Peña, *J. R. Johnston 1867* (NY, US); Mt. Morales, *Britton & Marble 1058* (NY, US); Maricao, *F. H. Sargent 397* (US); Bayamon, *Sintenis 990* (BM, GH, US), *Britton, Britton & Boynton 8455* (GH, NY, US); Lago San Jose, *Hioram 372* (NY); Vega Baja, *Stevens 1932* (NY); Yauco, Indiera Baja, *Britton & Britton 7227* (NY); Cayey, *Otero 730* (A, NY); Espinosa above Toa Baja, *Britton & Britton 9709* (NY); San Juan, *Gerhart & Holdridge 536* (NY); Cataño, *Britton, Britton & Brown 6980* (NY); Sierra de Naguabo, *Shafer 3480* (NY); Toro Negro, Doña Juana, Gregory 54 (NY).

Coccoloba pyrifolia Desfontaines was described in the third edition of the catalogue of plants in the botanic garden at Paris and was based on material under cultivation there. The origin of the plant is given as the warmer Antilles. No holotype exists for this species and no lectotype has been selected, to the best of my knowledge. There is in the herbarium at Geneva a specimen without collector's name or date, bearing a label indicating its origin as "hort. paris." It is possible that this specimen represents the original material cultivated and described in 1829 and could possibly be considered as the type. It seems more desirable to select a neotype from more recent collections and so *Britton, Britton & Brown 6796* is designated the type collection, and is deposited at the New York Botanic Garden herbarium. The species has been reported from Puerto Rico, St. Thomas, Cuba and Jamaica. I have seen the collections which Lindau cited from the herbaria at Berlin and Göttingen and there are currently no collections from St. Thomas. Lindau's reference to the occurrence of this species on St. Thomas cannot be checked. Likewise the Wilson specimen from Jamaica which Lindau states is in the Grisebach Herbarium cannot be located. Fawcett & Rendle repeat this reference which cannot be verified. The two collections by Charles Wright from Cuba which Sauvalle refers to this species in his Flora Cubana (139. 1873) are *Wright 2253* which is *Coccoloba praecox* Wright ex Lindau and *Wright 2256* which is the type of *C. reflexa* Lindau. It appears that *C. pyrifolia* is currently limited to Puerto Rico. The original spelling of the specific name is retained in this treatment, although all recent authors have preferred to use *Coccoloba pirifolia.*

Meisner's original description of *Coccoloba kunthiana* contains few diagnostic characters and is clearly referable to the synonymy of this species. I have seen specimens in the De Candolle Herbarium on which Meisner's species is based and conclude that the differences recognized by various authors in the past have been primarily of growth characters. The plants with older and shorter compacted branches are named *C. kunthiana* and are similar to Meisner's type. These specimens also have smaller ovate leaves which are generally obtuse at the apex. Specimens from obviously faster growing shoots have larger leaves which are acute or acuminate at the apex and possess longer inflorescences. These specimens, almost without exception, have been referred to *C. pyrifolia.* It is quite clear from a study of the material cited and from a field knowledge of the species that only a single taxon is represented and that the larger acute leaves are produced on adventitious or vigorously growing shoots.

Coccoloba pyrifolia is easily recognized by the long thin inflorescences with sessile flowers. It is most easily distinguished from *C. swartzii* by having leaves which dry dark brown and almost shiny above and light brown or tan beneath and which have very inconspicuous venation.

Coccoloba swartzii Meisner, DC. Prodr. **14**: 159. 1856; Lindau, Engler Bot. Jahrb. **13**: 157. 1890; Howard, Jour. Arnold Arb. **30**: 420. 1949, **37**: 324. 1956.

Coccoloba swartzii var. (?) *portoricensis* Meisn., DC. Prodr. **14**: 160. 1856; Lindau, Engler Bot. Jahrb. **13**: 157. 1890; Britton & Wilson, Sci. Surv. P.R. **5**: 270. 1924.
Coccoloba barbadensis Lindau, Engler Bot. Jahrb. **13**: 148. 1890, not Jacq.
Coccoloba diversifolia Lindau, Symb. Antill. **1**: 223. 1899; Britton & Wilson, Sci. Surv. P.R. **5**: 267. 1924.
Uvifera swartzii Ktze., Rev. Gen. **2**: 562. 1891.
Coccoloba neglecta Fawcett & Rendle, Jour. Bot. **51**: 124. 1913; Flora Jam. **3**: 116. 1914.
Coccoloba punctata Grisebach, Krebs, Eggers, and Northrop, not Linnaeus.
Coccoloba coronata of Millspaugh, not Linnaeus.

Trees 8–20 m. tall; branches terete, the youngest puberulent, becoming glabrate, the nodes slightly tumid; ochrea 10–12 mm. long, the basal portion 3–5 mm. long, coriaceous, persistent, the upper portion 5–7 mm. long, membranaceous, deciduous, puberulent to glabrate; petiole attached at the base of the ochrea, 10–18 mm. long, puberulent or glabrate; leaf blades ovate to elliptic, 2.2 × 1.3, 7 × 5, 11 × 9, 15 × 7.5 cm. long and broad, entire, coriaceous, usually turning black on drying, glabrous, pit-like depressions on the upper surface, small glands on the lower surface, the midrib and veins inconspicuous or flat above, prominent below, the primary veins 6 or 7 pairs, arcuate anastomosing, secondary venation conspicuous, reticulate, the apex acute, often rounded, the base narrowed, rounded or slightly cordate, usually oblique; leaves of adventitious shoots on 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; inflorescence terminal, 10–15 cm. long, the rachis glabrous or with glandular exudate, rarely papillose; staminate flowers in clusters of 3–5 flowers with tightly concentric membranaceous ochreolae forming a truncate cylinder after the flowers have fallen; pistillate flowers solitary, the ochreolae erect in flowers, flattened against the rachis in fruit, the bracts ovate, 1–1.5 mm. long, the ochreolae membranaceous 1–1.5 mm. long, the flowering pedicels shorter than the ochreolae, the hypanthium 0.5 mm. long, the perianth lobes 1–1.5 mm. long, the fertile stamens with filaments 1 mm. long; fruit ovoid 8–10 mm. long, 6 mm. in diameter, the perianth lobes 1–1.5 mm. long coronate in fruit.

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

Puerto Rico: Lago San Jose, *Hioram s.n.* (NY); Maricao, *Sintenis 258* (B, GH, MO, NY, S, US); Dorado, *Britton, Britton & Brown 6741* (F, NY); Cayey to Aibonito, *Britton & Britton 9630* (NY); Monte Montoso, *Britton & Cowell 4125* (F, NY, US); La Estancita, *Eggers 1193* (US); Santurce, *Heller 4666* (A, F, GH, Mich., NY, US). **St. Croix:** Salt River, *Thompson 580* (US); Sandy Point, *Raunkiaer 2508* (C); Jolly Hill, *Raunkiaer s.n.* (C); Mt. Eagle, *Thompson 427* (G, NY); Signal Hill, *Ricksecker 448* (F); Water Gut, *Isert s.n.* **Vieques Island:** *Shafer 2733* (NY, US). **St. Jan:** Mt. Eagle, *Ravn s.n.* (C). **Virgin Gorda:** *Fishlock 126* (NY). **St. Thomas:** *Oersted s.n.* (US).

A full discussion of the identification of *Coccoloba swartzii* Meisner and the application of the name *Coccoloba barbadensis* Jacquin was published in the Journal of the Arnold Arboretum as the second paper in this series (37: 317–339. 1956). Specimens from Puerto Rico now assigned to this species would previously have been referred to *C. swartzii* var. *portoricensis*, being intermediate in all characters between the typical expression of *C. swartzii* from Jamaica, the type locality, and *C. swartzii* var. *urbaniana* (*C. borinquensis* Britton). The specimens from St. Croix and other of the Virgin Islands are unlike the few plants from Puerto Rico and more similar to specimens from the Lesser Antilles. Considering the species as it occurs in many populations from Jamaica and Hispaniola south to Barbados and St. Lucia, there is no question that the Puerto Rican specimens are only slight variations in a greater range and should be included in the typical variety of *C. swartzii.*

In their studies for the Flora of Puerto Rico, Britton and Wilson assigned these specimens to *C. diversifolia* Lindau. I have already pointed out the general misapplication of this name (Jour. Arnold Arb. 30: 421. 1949).

Coccoloba swartzii forma **urbaniana** (Lindau) Howard, Jour. Arnold Arb. 37: 328. 1956.

Coccoloba urbaniana Lindau, Engler Bot. Jahrb. **13**: 155. 1890 in part, Symb. Antill. **1**: 225. 1899.
Coccolobis borinquensis Britton, Sci. Surv. P.R. **5**: 267. 1924.

DISTRIBUTION: Endemic to Puerto Rico.

Puerto Rico: Sierra de Naguabo, Loma Icaco, *Shafer 3448* (NY, TYPE of *C. borinquensis*), *Britton, Britton & Cowell 207* (NY); Sierra de Luquillo, *Sintenis 1527* (F, GH, HOLOTYPE; MO, NY, S, US), *Wilson 213* (F, NY, US), *Gregory 56* (NY), *Britton & Bruner 7665* (NY), 7676 (NY), *Barbour & Gerhart 9729* (NY); Indiera Baja, *Britton & Britton 7228* (GH, NY, US); Camp Dona Juaña, Villalba, *Gregory 64* (NY); Maricao Forest, *Sargent A-13* (US), *R. A. Howard 12602* (GH), *Winters 2213* (A).

Lindau described *Coccoloba urbaniana,* citing four collections, two by Crueger (*2694 & 2692*) from Trinidad and two by Sintenis (*1527 & 1585*) from Puerto Rico. His description, however, is obviously based on the material from Puerto Rico. No holotype was selected at the time. In his second publication of monographic studies on the genus *Coccoloba* in the Symbolae Antillanae, Lindau lists and keys *Coccoloba urbaniana*, but cites only the Sintenis collections. In fact, the two Crueger collections are not cited anywhere in this publication. It appears that Lindau was, in practice, accepting the species *Coccoloba urbaniana* for Puerto Rico by excluding the Trinidad material.

Britton in 1924 described *Coccoloba borinquensis*, selecting *Shafer 3448* as the type specimen. He reports that this collection had been "erroneously included by Lindau in Coccoloba Urbaniana Lindau of Trinidad." The Shafer material was collected in 1914 and I can find no indication that Lindau saw the type specimen at the New York Botanical Garden or any duplicates or fragments of this collection. I can only conclude that Britton was referring to a misidentification and that he had overlooked the later Lindau reference which essentially limits the species to Puerto Rico.

Coccoloba borinquensis Britton has been considered endemic to Puerto Rico and has been collected many times, principally in the Luquillo Mountains and the Maricao National Forest. I have studied several populations of this plant in areas similar to mossy forests where it was most abundant. The species as recognized by Britton is a shrub, or rarely a small tree, and is characterized by anomalous and apparently teratological development of the inflorescence axis and the leaves. Both are enormously thickened in living condition and when dried as specimens. In many specimens the rachis thickens as the fruit develops, so that when the fruit falls, the pedicel is immersed in the fleshy axis tissue and the dried inflorescence axis appears to be deeply pitted. The anomalies in the collections cited are numerous. In collections by Sargent, Wilson and Gregory the axis varies in thickness along its length, being thin, almost tenuous at the base and swollen in the middle and at the apex. Many of the specimens in the collection by Sintenis are thickened and branched at the upper end. One of the specimens collected by Gregory is flattened and obviously fasciated at the apex.

The leaves likewise show variation of an anomalous nature in both living condition and when dried. Many of the leaves seemed almost succulent when fresh, but thick and heavy rather than coriaceous when dry. The veins vary in the degree of prominence in the specimens cited, but such a character is not taxonomically reliable.

Populations of this plant seen in Puerto Rico and the collections on hand show a definite gradation of the characters Britton used to identify this species into the typical form of *Coccoloba swartzii.* However, the conspicuous nature of the abnormality in the field as well as in the herbarium makes it desirable to acknowledge these Puerto Rican populations as forms.

Meisner described with a query a variety of *Coccoloba swartzii* called var. ***portoricensis.*** Subsequent monographers and workers on the West Indian flora have been unable to place this taxon. Lindau in 1890 studied a drawing of the specimen Meisner cites and thought it might be related to *Coccoloba diversifolia* Jacq. (*C. laurifolia* Lindau) or *Coccoloba swartzii* Meisner (*C. diversifolia* or *C. barbadensis* Lindau). Meisner did not give the name of the collector and as Britton did not recognize *Coccoloba swartzii* Meisner from Puerto Rico, he also was unable to associate the variety Meisner described with any other species. I have seen the Meisner material at the De Candolle Herbarium in Geneva. It was collected by C. G. Bertero in 1820. A portion of this collection appears in the material I have on loan from the Missouri Botanical Garden herbarium. The Bertero material typifying *C. swartzii* var. ***portoricensis*** is intermediate between the anomalous *C. swartzii* forma ***urbaniana*** and the typical *C. swartzii.* It is easily matched by material from the Dominican Republic collected near Puerto Plata and specimens from Seibo, by other collections from Puerto Rico and by some from Jamaica. *Coccoloba swartzii* forma ***urbaniana*** intergrades through material such as *Coccoloba swartzii* var. ***portoricensis*** into typical material of *C. swartzii.* The transition is so gradual and yet so complete throughout a number of collections that it is impossible to recognize the Meisner variety as a valid taxon.

Coccoloba rugosa Desf. Cat. Hort. Paris, ed. 3, 389. 1829; Weddel, Ann. Sci. Nat. ser. 3, **13**: 262. 1849; Meisner, DC. Prodr. **14**: 152, 1856; Lindau, Engl. Bot. Jahrb. **13**: 203. 1890.

Coccolobis rugosa Brit. & Wils., Sci. Surv. P.R. **5**: 269. 1924.

Coccoloba macrophylla Desf. Tabl. 38. 1804, nomen; Desf. ex Hooker, Bot. Mag. **76**: *t. 4536.* 1850.

Coccoloba macrantha Steud. Nom. **1**: 390. 1821, nomen.

Shrub or tree to 15 m. tall, trunk to 10 cm. diameter breast height, frequently unbranched or with few very long erect strict branches, these stout, sulcate-angled to almost winged or sharply ridged, glabrous, ochreae 4–7 cm. long, rigid, coriaceous, oblique at the apex, persistent; petioles very short or wanting; leaf blades obovate or rhomboidal when young becoming orbicular to obovate, 25 × 26, 37 × 42 to 60 × 45 cm. long and broad, rigid coriaceous, conspicuously bullate or wrinkled, the margin recurved, glabrous, venation immersed above, prominent below, ultimate nerves conspicuous, blade punctate dotted above, appearing punctate below due to heavy lignification in mesophyll around veins, apex obtuse, base cordate to cordate clasping, the basal lobes often extending 15 cm. below the petiole; inflorescence terminal, 30–45 rarely to 75 cm. long, densely flowered, minutely puberulent, ochreae of inflorescence axis to 4 cm. long, membranaceous above, coriaceous below, slightly puberulent, staminate flowers in clusters of 4 to 18, the pistillate flowers in clusters of 2–6, bracts lanceolate, acute, 1–2 mm. long, puberulent, ochreolae, membranaceous, to 1.5 mm. long, puberulent, pedicels 5–13 mm. long, puberulent, hypanthium 2 mm. long, perianth lobes 1.5 mm. long, ovate, reflexed at maturity of flower, stamens 6–12, usually 8, functional stamens with filaments 2 mm. long, pistil rudiment shorter, sterile stamens 1 mm. long, functional pistil 1.5–2 mm. long, styles 1 mm. long; fruit ovoid, orange red in color, obscurely 3-angled, slightly constricted to a short stipitate base, the apex acute with the achene generally protruding beyond the perianth lobes when mature, mature fruit 5–7 mm. long, 3–5 mm. in diameter, perianth lobes appressed and imbricated, not coronate.

DISTRIBUTION: Endemic to Puerto Rico.

Puerto Rico: Catano, *Britton & Britton 9334* (NY, US), *Britton, Britton and Brown 6994* (F, GH, NY, US); Cayey, *Sintenis 2171* (GH, US); Humacao, *Sintenis 5178* (B, G, GH, MO, S, US); Lago San Jose, *Hioram s.n.* (NY), *Dale s.n.* (NY); Martin Peña, *Stevenson 1424* (US); Santurce, *Heller 1358* (F, NY, US); Sierra de Luquillo, La Estancita, *Eggers 827* (B, G, GH), *Eggers 655* (C); Sierra de Naguabo, *Shafer 3671* (NY, NEOTYPE; US). CULTIVATED SPECIMENS: Hort. Paris (C, G, GH).

Desfontaines in a series of publications listed the species of *Coccoloba* growing under cultivation in the Botanical Gardens in Paris. In one of these lists published in his Tableau de l'ecole de botanique du Muséum d'Histoire Naturelle (Paris), p. 18. 1804, Desfontaines lists the name *Coccoloba macrophylla* but as a nomen nudum without a description. In the second edition of the same work, page 46, 1815, *Coccoloba macrophylla* is not listed and a new name, *Coccoloba rugosa*, is given but without a description. *Coccoloba rugosa* is also listed in the third edition (1829) of the Catalogue and this time validly published with a description on page 389.

Specimens of *Coccoloba rugosa* were widely distributed to other botanical gardens in that period and numerous specimens are found in European herbaria, generally without data other than the name and the notation, "hort. paris." In Geneva, for example, there are four sheets of this species, two labelled *Coccoloba rheifolia,* one labelled *Coccoloba macrophylla* and one sheet labelled *Coccoloba rugosa* and indented under this name *Coccoloba macrophylla.* W. J. Hooker was unable to find a description of this apparently widely cultivated plant and so in 1850, with John Smith, published a plate illustrating *Coccoloba macrophylla* and a description in the Botanical Magazine (**76**: *pl. 4536.* 1850). The plant was then under cultivation at Kew and its source was given as Desfontaines. The description and illustration of Hooker and Smith was copied, translated and republished by Lindley and Paxton (Flor. Gard. 1: 191, *f. 94.* 1850–1) and Lemaire (Jard. Fl. **1**: *tab. 47.* 1851 and Fl. de Serres **6**: 267, *tab. 617.* 1850). Planchon apparently saw the later publication and in Fl. de Serres **7**: 160. 1851 referred to an earlier publication of Weddel (Ann. Sc. Nat. 3rd. ser. **13**: 262. 1849) which stabilized the nomenclature by placing *Coccoloba macrophylla* in synonymy with *Coccoloba rugosa.*

Hooker makes the suggestion that Desfontaines himself realized the unsuitability of the epithet *macrophylla* for this species and adopted the more appropriate name of *Coccoloba rugosa.* Previous students of this group have failed to indicate a type specimen. Although horticultural material from Paris is available, the specimens seen are either sterile or with immature flowers. *Shafer 3671* has been selected as the type number. It is a pistillate plant with mature fruit and this neotype is the specimen in the herbarium of the New York Botanic Garden.

Both Meisner in his treatment of the species for the Prodromus and Lindau in his monograph refer to specimens of this species from St. Thomas. Britton and Wilson report the plant is "not known on St. Thomas at the present time; it may have grown there before the forests were cut away." The specimen from St. Thomas in the Delessert Herbarium was attributed to *Ventenat 142.* A similar specimen in the Copenhagen Herbarium collected by Ventenat originated in the Vahl Herbarium. The reference of these two specimens to St. Thomas can be seriously questioned. I was unable to locate the species growing in St. Thomas in 1950.

The specimens mentioned above which originated as "hort. paris" bearing the name *Coccoloba rheifolia* raise the question of the correct assignment of this species described by Desfontaines to *Coccoloba latifolia* Lam. as Lindau has done (Engler, Bot. Jahrb. **13**: 133. 1890). Certainly the flowering specimens cited bearing the name *C. rheifolia* should be assigned to *C. rugosa.*

Coccoloba rugosa is similar to *C. sintenisii* in having the long pedicels and brightly colored inflorescences. *Coccoloba rugosa* is easily distinguished by the larger sessile and rugose leaves. It is known in Puerto Rico as "ortigon."

Coccoloba pubescens L. Syst. Nat. ed. 10, 1007. 1759; Hooker, Bot. Mag. **59**: *t. 3166.* 1832; Fawcett & Rendle, Jour. Bot. **51**: 123. 1913.

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, lapsus calami.
Coccoloba grandifolia Jacq., Enum. 19. 1760.
Coccolobis grandifolia Brit. & Wils., Sci. Surv. P.R. **5**: 269. 1924.
Coccolobis pubescens Sandwith, Jour. Bot. 78: 98. 1940.
Coccolobis antiguensis Sandwith, Jour. Bot. 78: 98. 1940.

Mature tree to 40 feet tall, diameter 12 inches, much branched above; adventitious shoots generally strict and sparsely branched, to 30 feet tall; branches stout, terete, slightly swollen at nodes, strongly grooved or striate; ochreae 2 cm. long, membranaceous and evanescent above, coriaceous and persistent below; petioles stout, 1–2 cm. long, densely tawny pubescent; blades large, generally orbicular, except for 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, apex rounded, base rounded to cordate, the basal lobes commonly encircling the stem, terminal leaflet commonly rhombic, longer than broad when mature, densely tomentose; veins slightly impressed above, all venation conspicuous and reticulate below, midrib and secondary veins persistent pubescent above, the others sparsely pubescent when young becoming glabrate above, margin irregular commonly undulate; mature branches terete, swollen at the nodes, lenticels not conspicuous, tomentose to pilose; ochreae to 1 cm. long, generally completely deciduous, pubescent; mature shoot leaves vary considerably in size and shape, leaves of completely mature plant (as represented by *Howard 12143, 12352*) with petioles 3–6 mm. long, inserted below the ochreae, densely short pubescent, blades broadly orbicular to orbicular-ovate, 7.5 × 10, 4 × 6 cm. grading into size of leaves of adventitious shoot, rugose or bullate; apex rounded, base cordate, the lobes rounded and only rarely approximate, sparsely pubescent above to glabrate, densely or sparsely pubescent below or glabrate, margin undulate, venation of 5 pairs of primary veins, arcuate to the margin, strongly anastomosing, slightly impressed above, conspicuous and reticulate below; inflorescence terminal, often stout, basal ochreae to 7 mm. long, membranaceous, peduncle to 1.5 cm. long, rachis minutely and often densely puberulent, 10–18 cm. long on mature shoots, to 45 cm. long on adventitious shoots, bracts broadly ovate, about 1 mm. long, puberulent, ochreolae membranaceous, spreading, 1 mm. long, minutely puberulent or glabrate; staminate flowers 2–4 per locus, pedicels 2–3 mm. long, puberulent, perianth lobes broadly orbicular 1.5 mm. long, 2 mm. wide, puberulent outside, hypanthium 0.5–1 mm. long, filaments 2 mm. long, anthers 0.5 mm. long, pistillate rudiments glabrous, 0.5–1.5 mm. long; pistillate flowers 2–3 at a locus, 2–3 mm. long, hypanthium to 1 mm. long, puberulent, perianth lobes orbicular 1–1.5 mm. long and wide, puberulent outside; stamens rudimentary, 0.5–1 mm. long, sterile; pistil glabrous or rarely slightly puberulent 1–2 mm. long, slightly 3-angled, style glabrous, 1–1.5 mm. long, stigmas flattened or slightly bilobed; fruit globose to ovoid, 5–6 mm. long and 4–5 mm. in diameter, fruiting perianth imbricate at apex, not turbinate, hypanthium with conspicuous vascular bundles, achene sub-globose, dark brown, shining, slightly tri-radiate at the apex, fruiting pedicels puberulent, 3–4 mm. long.

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

Puerto Rico: Guajataca, *Sargent B-1* (US); La Chiquita near Maricao, *Britton & Cowell 4272* (F, NY, US); Maricao Insular forest, *Howard 12600* (G); Maricao, *Stevens & Hess 3715* (NY); Utuado, *Britton & Cowell 981* (NY, US). *Sintenis 5925* (GH, US). COMMON NAME: "Moralon."

Coccoloba pubescens was described by Linnaeus in his Systema in 1759 at which time he cited a Plukenet illustration and description. Unfortunately the Plukenet illustration is poor and does not match any of the material I have cited as to leaf shape or the relative length of the petiole. In fact, the illustration shows a leafy branch arising from an ochrea in the position of a petiole or leaf. Fawcett and Rendle (Jour. Bot. **51**: 123. 1913) reported there was no specimen of this species in the Linnaean Herbarium but that the Plukenet specimen was preserved in the Sloane Herbarium at the British Museum. An examination of this specimen showed it consisted of a terminal and juvenile leaf and bore little relationship either to the drawing of the plant as seen in the field or to the herbarium specimens cited above.

The specific location from which the type specimen originated was presumably Barbados. I have seen and collected the species on islands from St. Lucia to Hispaniola. *Coccoloba pubescens* is also reported from Mexico, Guiana and Brazil, but I have not seen specimens from these areas. Patrick Browne described a plant from Jamaica which was referred to this species by Fawcett & Rendle. Recent collectors have failed to locate the species in the area mentioned by Browne and it must be concluded that Browne's reference applies to adventitious leaves of *Cordia sebestena* (see Howard, Jour. Arnold Arb. **38**: 105. 1957).

A study of a great number of colonies in the West Indies has indicated that there is a tremendous range of variation in single plants and in colonies of this species. *Coccoloba pubescens* is generally found in drier areas commonly on the windward slopes and generally near the seacoast. The large leaves of the plants appear to be unaffected by salt spray. It has also been found in the mountains and occasionally in more moist wooded areas. Specimens planted in the Maricao National Forest in Puerto Rico, an area of very moist environment, apparently are doing well.

In general appearance in the field, *Coccoloba pubescens* is a conspicuous plant. The habit is wand-like, unbranched except near the top and bearing extremely large leaves. A plant 20 feet tall may be only 1–2 inches in diameter at breast height. These invariably are young saplings of adventitious shoots which are produced when the original trunk is felled. John Beard's illustration of *Coccoloba pubescens* in St. Lucia (as *C. grandifolia* in The Natural Vegetation of the Windward and Leeward Islands, *f. 32.* 1949) is a good example of such a stand of young trees and adventitious shoots. The wood of even young plants is hard and is valued for charcoal. These plants are cut frequently, which prevents many stands from reaching maturity. Most descriptions of this species have been compiled from a study of herbarium specimens of these young plants or of adventitious shoots.

The only undisturbed mature trees I have seen in the islands from St. Lucia to Jamaica were found in remote and undisturbed areas of Hispaniola. Thus the description given here, while at variance with most published descriptions, is based on a field knowledge of this species and exemplified by personal collections (*Howard 12143* and *12352*) from above Puerto Escondido and from Beata Island in the Dominican Republic. Several of Ekman's collections from within Barahona peninsula agree with this description; e.g., *Ekman H-6947.*

A real problem is encountered in compiling a description of this species. Herbarium material cited in general represents adventitious shoots or young plants. These abnormal specimens with large leaves represent the plant as commonly seen in the field. I now know that the plants may remain in the juvenile leaf condition for as long as twenty-five years. One such specimen is in a fence row of known age in the Dominican Republic. Only one terminal branch of the tree developed the smaller leaves characteristic of the fully mature plant.

Coccoloba pubescens will produce flowers and fruit while bearing juvenile leaves. The inflorescences of such plants may reach 45 cm. (*Howard 11863*) in length and Eggers reports one specimen with a raceme 65 cm. long. This is in contrast to a raceme of 15–18 cm. in a fully mature branch. The flowering or fruiting herbarium specimens will show all the range of size from the largest leaves (50 × 80 cm.) to that reported for fully mature leaves 4 × 6 cm. or 7.5 × 10 cm. (*Howard 12143*). It is difficult to visualize this range of variation unless one has seen it in the field.

The development and amount of pubescence is likewise a variable character. Observations made in the field indicate that the amount of pubescence may be a matter of individual plant variation in a colony. Generally the immature leaves are pubescent and become glabrous except on the veins. However, some large thin young leaves of adventitious shoots were found to be glabrous, while older leaves on the same shoot were pubescent. Generally the leaves of the adventitious shoots bore more pubescence than those of older shoots. Britton and Wilson in describing this species for Puerto Rico and the Virgin Islands offer a complete description that in some aspects appears to be original. It is certainly not taken directly from Lindau's monograph, nor can I find any similarity in the descriptions of more recent students of the West Indies. However, Britton and Wilson's description is not supported by herbarium material of fertile plants. There are in the herbarium of the New York Botanical Gardens two photographs mounted on herbarium sheets, one of a woman holding the large leaf from an adventitious shoot of this plant and one of a thicket composed of this plant, all of which bear large leaves. It appears to me that Britton must have seen mature plants in the field, although herbarium records and many portions of his published description indicate a knowledge of the large-leaved adventitious shoots only.

I saw many areas on the south coast of Puerto Rico where single or few plants of *Coccoloba pubescens* were present. I did not see a single mature tree with the smaller leaves and the inflorescences and fruit of the older plant. Plants with adventitious shoots and leaves comparable to those photographed and described by Britton (e.g. 1 m. in diameter) were seen only in plantings of this tree in the Maricao National Forest in regions of higher rainfall.

Britton and Wilson report this to be a tree "to 25 m. high," the racemes "densely many-flowered, 4–7 dm. long," characteristics which do not agree with specimens I have seen in the field. The remainder of Britton's description of the vegetative portions applies to the exaggerated, abnormal individual in adventitious shoot condition.

In the second edition of Species Plantarum the species name of this binomial was misprinted as *Coccoloba rubescens.*

The epithet *Coccoloba grandifolia* Jacq. published in 1760 is a synonym of *C. pubescens* L. Britton and Wilson and a few other recent authors have accepted Jacquin's name, apparently overlooking the earlier valid publication of *C. pubescens* by Linnaeus.

In 1940 Sandwith described a new species under the name *Coccolobis antiguensis* based on collections by *Box 1496* and *301.* This species was suggested as allied to *C. pubescens* but differed in the aspect of the leaf. It was further suggested that *C. antiguensis* might represent a hybrid between *C. uvifera* and *C. pubescens.* In 1950 I searched the area around Carr's Gut for the single tree from which Box made the two collections cited by Sandwith. Unfortunately, the tree could not be located and may no longer exist, as the area was heavily cultivated and drastically cut over. In the specimens cited above, all the characters given for *C. antiguensis* can be found. The collection *Box 301* is definitely taken from an adventitious shoot. The U. S. National Herbarium specimen of this number (*US 1535774*) is the typical rhombic terminal leaf of adventitious shoots of *C. pubescens. Box 1496* is a fertile collection; however the tortuous stems, the pubescence and the flat blades can be found in many other specimens. *Coccoloba antiguensis* is known only from pistillate material. A collection by John Beard and one of my own from the Wallings area of Antigua show the same plane leaves with the veins slight on the lower leaf surface. *Beard 283* can be considered a match for *Box 1496* in the foliage. Beard's collection is in fruit and the fruits are typical of *C. pubescens.*

Coccoloba uvifera L. Syst. Nat. ed. 10, 1007. 1759; Lindau, Engl. Bot. Jahrb. **13**: 204. 1890, Symb. Antill. **1**: 231. 1899; Fawcett & Rendle, Fl. Jam. **3**: 119. 1914.

Polygonum uvifera L. Sp. Pl. 365. 1753.

Guaiabara uvifera (L) House, Am. Midl. Nat. **8**: 64. 1922.
Coccolobis uvifera Brit. & Wils., Sci. Surv. P.R. **5**: 268. 1924.

Tree of strand areas, 2–15 m. tall; branches terete, stout, papillose to pilose, the nodes not tumid; ochreae rigid, coriaceous at the base, membranaceous at the apex, 3–8 mm. long, puberulent to pilose; petioles stout, 7–10 mm. long, papillose to pilose; leaf 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 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, secondary venation minutely reticulate or obscure; apex rounded, truncate or emarginate, the base rounded to broadly cordate, one lobe often extended around the petiole; leaves of adventitious or fast-growing shoots usually variable in size and shape, but commonly obovate; inflorescence stout, 15–13 cm. long, rachis puberulent; staminate flowers in clusters of 1–7, the pistillate flowers solitary, the bracts ovate, 1–1.5 mm. long, 2 mm. broad, puberulent, the ochreolae 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, the 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, perianth rose-purple when mature, the achene black.

DISTRIBUTION: General along beaches of Florida, Bermuda, the Bahamas through the Caribbean area to South America.

Puerto Rico: Cataño, *Millspaugh 178* (F, NY); Condado, *Britton, Britton & Brown 7065* (NY); Fajando, *Evermann 1243* (US), *1245* (US), *Heller 1013* (US); Mayaguez to Guanajubo, *Sintenis 765* (GH, US); Ponce, *Sargent 568* (US); San Juan, *Rose 21607* (US), *Sintenis 765b* (US); Santurce, *Stevenson 343* (US), *Heller 1392* (F, NY); Yauco, *Underwood & Griggs 719* (F, NY, US). **Culebra Island:** *Millspaugh 1786* (F). **Mona Island:** *Stevens 6339* (NY). **Vieques Island:** *Morrow 143* (US), *Shafer 2586* (NY, US). **Anagada:** *Britton & Fredloch 970* (NY, US). **St. Croix:** *James 8* (GH), *Ricksecker 17* (F, MO, NY), *Mrs. J. J. Ricksecker 108* (F, MO). **St. Thomas:** *Eggers 216* (GH), *328* (B), *Hjalmarsson 17* (S); *Kuntze 5586* (NY). **Virgin Gorda:** *Fishlock 333* (NY).

Coccoloba diversifolia Jacq. Enum. Pl. 19. 1760, Hist. Stirp. Amer. 114, *pl. 76.* 1763; Howard, Jour. Arnold Arb. **30**: 421. 1949.

Coccoloba laurifolia Lindau, Engl. Bot. Jahrb. **13**: 158. 1890; Urban, Symb. Antill. **1**: 227. 1899; Fawcett & Rendle, Flora Jam. **3**: 116. 1914 and all recent authors, not Jacquin.
Coccolobis laurifolia Brit. & Wils., Sci. Surv. P.R. **5**: 268. 1928, not Jacq.
Coccoloba longifolia Schmidt, Fedde Rep. Sp. Nov. **24**: 73. 1927, not Fischer.
Guaiabara laurifolia House, Am. Midl. Nat. **8**: 64. 1922 (as *Guaibara*).

Shrub or small tree to 7 m. tall; branches terete, often geniculate by limited growth, glabrous, the nodes rarely slightly tumid; ochreae coriaceous in the persistent lower portion, membranaceous and deciduous above, 3–5 mm. long; petioles 7–10 mm. long, glabrous, leaf blades ovate, oblong, elliptic, lanceolate or obovate, variable on a single shoot, the apex rounded, obtuse, acute or acuminate, the base cuneate to rounded or subcordate, 4 × 3.5, 7 × 5.5, 8 × 4.5, 12 × 8 cm. long and wide, coriaceous, often shining above, dull beneath, glabrous, the 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, the margin entire, commonly slightly recurved; leaves of adventitious shoots similar in shape to those of normal growth but larger in size, 17 × 8, 24 × 13, 32 × 12.5 cm. long and wide on petioles 1–2.5 cm. long; leaves of windswept specimens often much smaller than those of normal shoots, 2 × 1.3, 3 × 2 cm. long and wide; inflorescence terminal 4.9, 9, 11 to 18 cm. long; rachis glabrous; staminate flowers in clusters of 2–5, the pistillate flowers solitary; bracts ovate, less than 0.5 mm. long, 1 mm. broad, glabrous; ochreolae membranaceous, less than 0.5 mm. long, glabrous, the flowering pedicels 2–4 mm. long, glabrous; hypanthium 1 mm. long, the perianth lobes 2 × 2, to 3 × 1 mm. long and broad, filaments of functional stamens 1 mm. long, fruiting pedicels 3–4.5 mm. long; fruit globose to obpyriform 10 × 7, 12 × 8, 13 × 8 cm. long and thick, perianth lobes appressed at the apex of the achene.

DISTRIBUTION: Florida and the Bahamas, through the West Indies to South America.

Puerto Rico: Bayamon, *Britton & Britton 7944* (NY), *Heller 400* (F, NY, US), *4687* (F, GH, MO, NY, US), *Johnston 904* (US); Cabo Rojo, *Sintenis 714* (GH, S, US), *771* (MO, US), *Howard 12604* (GH), *12605* (GH); Coamo Springs, *Britton, Britton & Marble 2232* (NY, US), *Britton, Britton & Brown 5904* (FM, NY); Guanica, *Sintenis 3507* (FM, NY); Luquillo Mts., *Holdridge 522* (NY); Guayanilla, *Britton & Shafer 1812* (NY, US); Martin Peña, *Stevenson 1234* (US), *1859* (NY); Ponce, *Heller 6189* (A, F, GH, MO, NY, US); Ponce to Penuelas, *Britton & Cowell 1309* (NY, US); Quebradellas, *Stevens 1720* (NY); Sardinera to Ubero, *Britton, Cowell & Hess 1774* (NY, US); San German, *Sargent 446* (US); San Juan, *Gerhart & Holdridge 525* (NY); Santurce, *Heller 1301* (F, NY, US); Yauco, *Gardner s.n.* (NY). **Mona Island:** *Stevens 6312* (NY), *6379* (NY), *6380* (NY), *6436* (NY). **Vieques Island:** *Shafer 2795* (NY, US). **St. Croix:** Kingshill, *Eggers s.n.* (US).

The proper application of the names *Coccoloba laurifolia* Jacq. and *C. diversifolia* Jacq. was discussed in the first paper of this series in the Journal of the Arnold Arboretum **30**: 421. 1949.

Coccoloba sintenisii Urb. ex Lindau, Engl. Bot. Jahrb. 13: 157. 1890.

Coccolobis sintenisii Britton & Wilson, Sci. Surv. P.R. **5**: 268. 1924.

Tree 20–30 ft. tall, diameter at breast height 4–12 inches, bark rough, scaly, gray; branches glabrous, lenticels linear; ochreae glabrous, membranaceous and deciduous above, the basal portion coriaceous, persistent, extending 3–4 mm. above the attachment on the adaxial side of the petiole but to 1 mm. on the opposite side, petiole inserted on a conspicuous base, 6 mm. long above the base of the ochreae, petiole 2–4 cm. long, stout, i.e. 5 mm. diameter, its thickness diminishing rapidly in the blade, glabrous; mature leaf blade oval to oblong, 9 × 12, 10 × 16, 13 × 16, to 14 × 19.5 cm. long and broad, thick coriaceous, entire, glabrous on both surfaces, the apex obtusely acuminate to obtuse, often almost apiculate, the base unequally cordate, the midrib and primary veins conspicuous below, primary veins immersed or both primary veins and midrib evident above, the ultimate venation inconspicuous on both surfaces; leaves of adventitious shoots to 18 × 24 cm. long and broad on petioles to 5 cm. long; inflorescences generally terminal on lateral shoots, rarely lateral or terminal on main shoots, 5–15 cm. long, the rachises, pedicels and flowers brightly colored, crimson when fresh and purplish red when dry, basal ochreae membranaceous and deciduous or slightly coriaceous at the base, this portion persistent to 6 mm. long and slightly puberulent, the rachis thick, occasionally flattened, usually striate, glabrous, bracts broadly ovate, less than 0.5 mm. long, ochreolae less than 0.5 mm. long, flowering pedicels 4–5.5 mm. long, glabrous; staminate flowers with hypanthium 1–2 mm. long, the perianth lobes 2–2.5 × 1.5–2 mm. long and broad, the stamens with filaments united at the base to 1 mm., the free portion 1.5–2 mm. long, the pistil rudimentary 1–1.5 mm. long; pistillate flowers borne singly, the perianth lobes 1.5 mm. long, 1–1.3 mm. wide, the rudimentary stamens 8–10, the filaments dilated and united at the base, less than 1 mm. long, the pistil obconical, the ovary 1.5–2 mm. long, the styles 3, equal, 1–1.5 mm. long, the fruiting inflorescences 10–20 cm. long, stout at the base, tapering rapidly, the pedicels in fruit 5–6 mm. long; fruit ovoid, very slightly pedunculate, 4–5 mm. in diameter, the perianth lobes persistent, generally appressed but free, to 3 mm. long, the achene circular in transverse section, the hypanthium not evidently vascularized.

DISTRIBUTION: Endemic to Puerto Rico.

Puerto Rico: Coamo Springs, *Britton & Britton 10052* (NY), *Britton, Britton & Brown 6038* (NY); CCC Camp Susua, *Velez 1120* (NY); Maricao, *Sintenis 223* (B — TYPE), *Sargent 393* (US); Maricao National Forest, *Howard 12603* (GH); Rio de Maricao, *Britton, Stevens & Hess 2430* (NY, US), *Britton & Cowell 4218* (F, NY, US); Sabana Grande, *Sargent 620* (US).

Coccoloba sintenisii is clearly a distinct species characterized by the long pedicels in both flowering and fruiting condition and by the bright red color of the inflorescence.

Britton applied an herbarium name to the specimens from Coamo Springs. A description had been compiled and was found among Dr. Britton's unpublished manuscripts. Other than the reduced brilliance of color in the inflorescence, I can see no significant difference in these specimens from the type or from the specimens cited above. The material from

Coamo Springs can be included within the definition of *C. sintenisii.* Staminate and pistillate flowers are borne singly in all specimens I have seen, although only one staminate specimen is known.

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

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

Small tree of shrubby growth or tree to 10 m. tall; branches stout with a ferrugineous to golden pubescence this often persisting only in protected spots or at the apex; ochreae membranaceous 4–6 mm. long, ferrugineous puberulent to sub-glabrous; leaf blades generally ovate to elliptic, less commonly suborbicular to obovate-orbicular, the apex obtuse or rounded, the base generally slightly and unequally cordated to narrowly unequally decurrent on the petiole, 2.5 × 2.5, 5 × 5, 7 × 5, 11 × 8 to 18 × 12 cm. long and broad, coriaceous, golden shining above, dull brown below, midrib and veins impressed above, prominent below, the primary veins 5–7 pairs, arcuate, anastomosing, the blades sparsely pitted above and below, often showing anomalous peltate or variously shaped resinous stomatal secretions below, these abundant when leaf is young and scattered and few in mature leaves, otherwise glabrous; petioles stout, 8–10 mm. long, slightly puberulent; 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, the bracts ovate, 0.5 mm. long, the ochreolae membranaceous, 0.5 mm. long, the flowering pedicels 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, 3 mm. thick, the perianth lobes coronate.

DISTRIBUTION: Cuba, Hispaniola, Puerto Rico.

Puerto Rico: Aybonito, *Sintenis 5934* (GH); Utado at Los Angeles, *Sintenis 5994* (B — TYPE of *C. rupicola*, GH, NY, US); Larez, *Winters s.n.* (A).

The previous treatment considering *Coccoloba costata* which I published was without the benefit of field study of its related species, *C. samuelssonii*, *C. helwigii* and *C. verruculosa* in Hispaniola and *C. rupicola* of Puerto Rico. Following an examination and study of numerous stands of all but the last of these species in the field, I can only conclude that they represent races, at most, of a single species. As *Coccoloba costata* is the oldest name available, I am referring five species or previously recognized taxa found in Hispaniola and Puerto Rico to *C. costata* and am extending the range of this group to the Greater Antilles, excluding Jamaica.

Coccoloba costata has been considered for many years an endemic species of Cuba. In 1929 Schmidt referred a single Ekman collection from Haiti to this species at the same time he described *C. samuelssonii* and *C. helwigii.* Only two subsequent collections by Ekman have been so annotated. Schmidt compared *C. costata* with his new *C. samuelssonii* and differentiated between them on the shape of the leaf base and the texture and shine of the leaf surface. These are extremely weak characters in the genus *Coccoloba*, holding true only if the actual type specimens of each species were considered. The variation in *Coccoloba samuelssonii* as represented by Schmidt's determinations of Ekman collections and my own observations in the field are tremendous.

Coccoloba helwigii described by Schmidt was based on *Ekman 8523*, cited as the type, and *Ekman 4944*. Schmidt characterized this new species as having generally suborbicular leaves which are minutely punctate below. On the basis of these two characteristics Schmidt compared it with *C. leoganensis* (his *C. rotundifolia*) and *C. buchii.* The leaf shape is matched in other Ekman specimens such as *Ekman 4684*, referred by Schmidt to *C. costata* forma, *Ekman 2855*, referred to *C. costata*, and *Ekman 8721*, referred to *C. samuelssonii.* As all of these collections show variations on single sheets from leaves suborbicular in shape to leaves ovate-orbicular or even broadly ovate, it is felt that the smaller leaves of the type specimens of *C. helwigii* represent the smaller end of the range of variation in leaf size.

The minute punctations seen and mentioned by Schmidt are excretions from the stomata of the leaf. The chemical nature of the substance has not been determined. However, the material dries into peltate, appressed or stalked artifacts which can be lifted free from the stomata and the leaf with a needle. Similar excretions are found in other specimens of *C. costata* which I have seen, but are more distinctly developed in the Hispaniolan specimens than in the Cuban and Puerto Rican material. The original collections cited for *C. helwigii* are unique in having the excretions in every stomatal opening which gives the entire lower leaf surface the aspect of being dotted in dark brown color. This condition, however, seems characteristic of younger leaves, for some of the older and larger leaves on the type sheet of *C. helwigii* are glabrous or lack these artifacts. The same type of excretion is found on the type specimens of the four species cited here in synonymy.

Lindau described *Coccoloba verruculosa*, basing the species on *Eggers 1762* from Hispaniola and *Sintenis 5994* from Puerto Rico. The original description is next to that of *C. costata* in his species order. Using Lindau's key, these two species fall into groups separated by the length of the flowering pedicel. However, the key distinction is not borne out in the species descriptions. From the published descriptions (Engl. Bot. Jahrb. 13: 154–155. 1890), the major differences cited are those of pubescence and number and length of pedicels. Lindau overlooked the pubescence which is present on *Eggers 1762* and *Sintenis 5994* and which is comparable to that of *C. costata.* The difference in number and length of the flowering pedicels is a sexual character not recognized by Lindau or Schmidt. *Coccoloba verruculosa* is based on a staminate plant and *C. costata* on a pistillate specimen (*Wright 1393*). *Coccoloba verruculosa* is clearly the same as *C. costata.*

The Sintenis collection *5994* from Puerto Rico has had a turbulent history. Lindau cited it in the original description of *C. verruculosa* although the specimen is poor, being only an old and staminate inflorescence axis. In spite of the condition of the specimen, Urban selected several minor and variable characteristics in the length of the petiole, the shape of the leaf base and the nature of the leaf surface and described *C. rupicola,* citing *Sintenis 5994* as the type and only collection. Britton and Wilson had a fragment of the same sterile material and were only able to append the species to their key to the genus as "species not grouped, known from foliage only." However, in their discussion they state that "Lindau erroneously regarded it as the same as *C. verruculosa* Lindau of Hispaniola." *Coccoloba verruculosa* does not differ from *C. costata* in any significant manner and must be included in the latter species.

A second Sintenis collection from Puerto Rico from Aybonito between Algarrobo and Caribbeanos, *Sintenis 5934,* was included in *Coccoloba costata* by Lindau. This material consists of faster growing shoots and is sterile. Urban (Symb. Ant. 4: 656. 1911) felt it represented some other species and Britton and Wilson repeated the suggestion but cited the collection under *C. costata,* appending it to the list of known species.

The two Sintenis collections *5934* and *5994* were until recently the only material of this species known from Puerto Rico. Britton and his colleagues collected intensively in Puerto Rico but failed to find material which could be referred here. Recently Mr. Harold Winters sent me material which he had collected in July 1956 from the limestone hills north of Larez in Puerto Rico. This collection was of ample material with mature fruit and displayed a considerable range of leaf variation. In all characteristics this recent material substantiates the earlier conclusion of the proper association of the Puerto Rican and Hispaniolan species with *C. costata* of Cuba.

COCCOLOBA IN THE BAHAMA ISLANDS

In their publication The Bahama Flora (New Era Printing Company, 1920), Britton and Millspaugh present a key to the genus *Coccoloba,* recognizing six species in the flora, one of which they described as new. Recent collections have failed to add to this number. Several changes of names are required for the species and the generic description used in The Bahama Flora should be altered to recognize the dioecious, rarely monoecious plants having flowers that are functionally unisexual. The staminate flowers are usually in clusters of 2–5 at each node of the inflorescence axis, while the pistillate flowers are borne singly. The key to the species, however, needs little change.

With the resurgence of interest in the Bahama Islands, both by tourists and botanists, it is hoped that additional collections of the vegetation can be made. Some of the gaps in the distribution of the species cited in this paper are probably nothing more than a lack of collections.

In general, the specimens of all species of *Coccoloba* seen in and from the Bahamas are smaller in size than representatives of the same species from other and adjacent islands of the West Indies. The reduction in size seems complete, from the stature of the plants to the size of the leaves on both normal and adventitious shoots, and is evidenced, as well, in the flowers and fruits. This reduction in size is particularly evident in collections referred to *Coccoloba swartzii*. The xerophytic conditions of the islands in the Bahamas, coupled with the inhospitable substrata of limestone, coral and sand, may naturally stunt the species. It is hoped that some fruits of *C. uvifera*, *C. diversifolia*, *C. swartzii*, *C. tenuifolia* and *C. krugii* which have been sent to several of the Bahama Islands from Jamaica, Cuba and the Dominican Republic may grow and, in a few years, allow comparison with voucher specimens of the parent trees on file in the herbaria of the Arnold Arboretum and the Gray Herbarium.

KEY TO THE SPECIES IN THE BAHAMAS

Flowering and fruiting pedicels 1 mm. or more long, exceeding the ochreolae.
  Leaves very large, suborbicular, generally broader than long, 7–20 cm. wide. .... *C. uvifera*.
  Leaves ovate to elliptic, obovate or orbicular, longer than broad.
    Primary veins arcuate, anastomosing near the margin.
      Leaves coriaceous; racemes stiff erect or spreading; fruit 7–14 mm. long. .... *C. diversifolia*.
      Leaves chartaceous; racemes thin, long and drooping; fruit about 4–6 mm. long. .... *C. tenuifolia*.
    Primary veins free to the margin of the leaves. .... *C. northropiae*.
Flowering and fruiting pedicels less than 1 mm. long and not exceeding the ochreolae.
  Inflorescence longer than the leaves; leaves reticulate veined on both surfaces when dry, turning dark brown or black; fruit dark brown, round in cross section. .... *C. swartzii*.
  Inflorescence shorter than the leaves; ultimate leaf venation inconspicuous above, evident below, leaves drying pale tan or green, petioles often buff-colored; fruit reddish brown, distinctly triangular in section. ...... *C. krugii*.

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

Coccolobis uvifera Britton & Millspaugh, Bahama Flora 116. 1920.

Abaco: *Brace 1476* (NY). **Acklin's Island:** *Brace 4514* (F). **Andros:** *A. E.*

Wright 269 (F, GH). **Anguilla:** *Wilson 7960* (F). **Crooked Island:** *Brace 4681* (F). **Inagua:** *Harshberger 16* (US), *Nash & Taylor 1028* (NY), *1055* (F, US), *1226* (NY). **New Providence:** *Dewey 561* (US), *C. F. Millspaugh 2101* (F), *Northrop 80* (A, F, GH). **North Bimini:** *Howard 10188* (A), *10201* (A), *10216* (A). **Silver Cay:** *Millspaugh 2455* (F). **Turks Island:** *Nash & Taylor 3772* (F, US). **Watling's Island:** *Hitchcock s.n.* (F).

A description of the species and complete synonymy is given earlier in this paper. Britton and Millspaugh refer *Coccolobis leoganensis* Jacq. to synonymy here. This is now regarded as a distinct and endemic species of Hispaniola.

Coccoloba diversifolia Jacq. Enum. Pl. 19. 1760.

Coccolobis laurifolia Britton & Millspaugh, The Bahama Flora 117. 1920.
Coccolobis tenuifolia Northrop, Mem. Torrey Bot. Club **12**: 34. 1902, not L.
Coccolobis wrightii Northrop, Mem. Torrey Bot. Club **12**: 34. 1902, not Lindau.

Abaco: Great Cistern, *Brace 1679* (NY); Old Kerr's Point, *Brace 2012* (FM). **Acklins Island:** *Brace 4453* (FM, NY). **Andros:** Deep Creek, *J. I. & A. R. Northrop 721* (FM, G, NY); Long Bay Cay, *Small & Carter 8584* (FM, G, NY, US); Crow Hill, Bay Cay, *Small & Carter 8717* (FM, G, NY, US); Mangrove Cay, *Small & Carter 8491* (FM, G, NY, US); Nicols Town, *J. I. & A. R. Northrop 443* (A, G, FM, NY); Calabash Bay, *A. E. Wright 266* (FM, G, NY); Mangrove Cay, *Brace 4937* (FM, NY). **Berry Island:** Great Stirrup Cay, *Britton & Millspaugh 2271* (FM, NY, US). **Cat Island:** *Wilson 7174* (FM, NY). **Crooked Island:** Landrail Point, *Brace 4571* (NY, FM), *Hitchcock s.n.* (MO). **Exuma:** Harvest Cay, *Wilson 7889* (FM, G, NY); Georgetown, *Britton & Millspaugh 3121* (FM, NY, US), *Britton & Millspaugh 2776* (FM, NY). **Eleuthera:** Harbour Island, *E. G. Britton 6382* (FM, NY, US), *J. T. Rothrock 570* (FM). **Great Ragged Island:** Hog Cay, *Wilson 7873* (FM, G, MO, NY). **Great Bahama:** *Britton & Millspaugh 2602* (FM, NY, US). **Green Cay:** *Coker 238* (NY). **Fortune Island:** *Eggers 3850* (A, G, US), *3996* (G), *Hitchcock s.n.* (MO). **Inagua:** *Hitchcock s.n.* (FM, MO), *Nash & Taylor 1056* (FM, NY); Mathewtown, *Nash & Taylor 880* (FM, NY), *1452* (NY); Balsam Hill, *Nash & Taylor 1270* (FM, NY). **Little San Salvador:** *Britton & Millspaugh 5687* (FM, NY). **Long Cay:** *Brace 4045* (FM, NY). **New Providence:** Hog Island, *Wilson 8307* (FM, NY), *8315* (FM, NY), *Britton & Brace 353* (FM, G, NY); Nassau, *Ames s.n.* (A), *Britton 76* (NY), *86* (NY); Grantstown, *Wilson 8182* (FM, NY), *8176* (FM, NY); West End Bight, *Millspaugh 2292* (FM, NY); West Bay St. Road, *Millspaugh 2164* (FM), *2195* (FM), *2159* (FM), *Hitchcock s.n.* (FM, MO), *Britton & Britton 115* (NY), *Degener 18971* (A), *18972* (A, MO), *18973* (A), *Britton & Brace 476* (F, NY). **North Caicos:** *Wilson 7709* (F, GH, NY), *Proctor 9043* (A), *9076* (A). **Rose Island:** *Wilson 7902* (F, GH, NY), *Britton & Millspaugh 2128* (F, NY), *2124* (F, NY, US). **South Cat Cay:** *Millspaugh 2431* (F, NY), *2434* (F, NY). **South Bimini:** *Millspaugh 2379* (F, NY), *2382* (F, NY), *R. A. & E. S. Howard 10039* (A), *10040* (A), *10041* (A), *10238* (A), *10247* (A), *10252* (A), *10253* (A). **Watling's Island:** *Wilson 7249* (F, GH, NY).

A full description of the species and the synonymy were given earlier in this paper.

Coccoloba tenuifolia L. Syst. Nat. ed. 10. 1007. 1759, Amoen. **5**: 397. 1760, Sp. Pl. ed. 2, 524. 1762; Fawcett & Rendle, Flora Jam. **3**: 119, 1914, Jour. Bot. **51**: 124. 1913; Howard, Jour. Arnold Arb. **30**: 407. 1949, **38**: 93. 1957.

Coccoloba leptostachyoides Lindau, Engl. Bot. Jahrb. **13**: 207. 1890.

Coccolobis ? frutescens, foliis subrotundis, fructu minore trigone Brown, Hist. Jam. 210, *t. 14, f. 3.* 1756.

Coccoloba excoriata L. Syst. Nat. ed. 10, 1007. 1759; Fawcett & Rendle, Flora Jam. **3**: 121. 1914.

Coccolobis bahamensis Britton, Bull. N.Y. Bot. Gard. **4**: 116. 1905; Britton & Millspaugh, The Bahama Flora 117. 1920.

Coccolobis obtusifolia Northrop, Mem. Torrey Bot. Club **12**: 34. 1902, not Jacq.

Shrub, rarely a small tree 6 to 15 feet tall; branches terete, light brown in color, glabrous or puberulent; ochreae membranaceous above and deciduous, coriaceous and persistent below, puberulent; the leaves characteristically borne on lateral shoots and crowded, the petioles short persistently puberulent, 6–9 mm. long, arising from a conspicuous base above the base of the ochreae, the blades generally elliptic, occasionally obovate, ovate, oblong or sublanceolate, 3.5 × 2, 7 × 4.5, 8 × 6, 9.5 × 6 to 12 × 10 cm. long and broad, membranaceous to subcoriaceous, the apex acute, short acuminate or rarely obtuse, the base narrowed and unequally rounded to subcordate, the margin entire to undulate, the blade often conspicuously umbonate in the field; midrib and veins flat or impressed above, prominent beneath, primary veins 4–6 pairs, arcuate, the ultimate venations finely reticulate, glabrous above, finely puberulent below, generally tomentose in the axils of the veins and extending on to the lamina persisting or evident as clear hair bases; adventitious shoots with leaves evenly distributed, petioles 2–5 cm. long, the blades 7 × 9 to 18 × 16 cm. long and broad; inflorescence terminal from the lateral leafy shoots, to 8 cm. long, weak and hanging generally strongly curved, the rachis puberulent becoming glabrate; staminate flowers 1–4 at the node, the pistillate flowers usually solitary, the bracts broadly ovate, to 0.5 mm. long, the ochreolae membranaceous, 0.5 mm. long, the pedicels 1 mm. long, the hypanthium 1–1.5 mm. long with apparent basal stalk more conspicuous in the pistillate flower, the perianth lobes 1–1.5 mm. long and broad, the functional stamens 1–1.5 mm. long, the functional pistil 1.5 mm. long; fruiting pedicels 1–1.5 mm. long, the fruit ovoid 5–6 mm. long and 4 mm. in diameter with a short stalk 0.5 mm. long, the perianth lobes appressed, the achene tan in color.

DISTRIBUTION: Bahamas, Cuba and Jamaica.

Andros: Mangrove Cay, *Small & Carter 8513* (FM, NY), *8525* (FM, K, NY, US), *8537* (FM, NY), *8509* (FM, NY, K, US), *8511* (FM, K, NY, US); Deep Creek, *J. I. & A. R. Northrop 706* (FM, G, K, NY); Long Bay Cay, *Small & Carter 8572* (BM, FM, G, NY, K, US); Nicholl's Town, *Small & Carter 8938* (NY); *Brace 5075* (FM, NY), *5276* (FM, NY), *5235* (FM, NY).

Acklin's Island: *Brace 4373* (FM, NY). **Caicos:** North Caicos, *C. F. & C. M. Millspaugh 9137* (FM, NY, US), *Proctor 9086* (A). **Eleuthera:** Harbour Island, *E. G. Britton 6376* (FM, NY, US); *Brace 5429* (FM, NY), *5614* (FM, NY). **Great Exuma:** *Britton & Millspaugh 2955* (FM, NY). **Inagua:** *Nash & Taylor 1280* (BM, FM, NY), *1352* (FM, NY — type of *C. bahamensis*). **New Providence:** *Britton & Brace 647* (FM, G, K, NY, US); *Eggers 4486* (K, NY). **Watling's Island:** *Wilson 7244* (FM, K, NY), *7355* (FM, G, K, NY).

Coccoloba northropiae Britton, Bahama Flora 117. 1920 (as *Coccolobis*), Howard, Jour. Arnold Arb. **30:** 411. 1949.

Coccoloba leoganensis var. *parvifolia* Griseb. Cat. Pl. Cub. 61. 1866.
Coccoloba retusa Lindau, Engl. Bot. Jahrb. **13:** 150. 1890, in part; Northrop, Mem. Torrey Bot. Club **12:** 34. 1902. Not Griseb.

Shrub or small tree to 4 m. tall; branches terete, pilose becoming glabrate, nodes slightly tumid; ochreae membranaceous, 2–3 mm. long, glabrous; leaf blades orbicular to obovate or elliptic, the apex rounded, obtuse or emarginate, the base narrowed, 3 × 2.5, 4 × 3 cm. long and wide, thinly coriaceous, glabrous, turning black on drying, commonly shiny above, dull beneath, the midrib and primary veins equally prominent on both surfaces, the secondary venation reticulate, primary veins 4–6 pairs, straight, diffuse branching and becoming reticulate near the margin, not arcuate and anastomosing, margin entire, flat; petioles 3–5 mm. long, short pilose pubescent; leaves of adventitious shoots variable in shape, 5 × 3, 6 × 4 cm. long and wide, on petioles to 7 mm. long; inflorescence terminal 5–7 cm. long, the rachis puberulent, the female more so than the male, the bracts ovate, less than 0.5 mm. long, the ochreolae membranaceous, less than 0.5 mm. long; male flowers in clusters of 2, the female flowers solitary, the flowering pedicels 0.5–1 mm. long, the hypanthium 1 mm. long, the perianth lobes 1 mm. long and wide, the fertile stamens less than 1 mm. long, the stamens of pistillate flowers rudimentary, less than 0.5 mm. long; fruiting pedicels 1.5 mm. long, the fruit ovoid, to 5 mm. long, 3 mm. thick, the perianth lobes appressed against the apex of the achene.

DISTRIBUTION: Cuba, Bahamas.

Andros: *J. I. & A. R. Northrop 662* (NY), *705* (A, GH, NY), Mangrove cay near Lisbon Creek, *Small & Carter 8483* (F, GH, NY, US). **Eleuthera:** Gregory Town, *Coker 358* (NY). **Great Exuma:** *Britton & Millspaugh 2982* (F, NY, US). **New Providence:** Nassau, *Curtis s.n.* (NY — holotype).

Coccoloba swartzii Meisner, D.C. Prodr. **14:** 159. 1856.

Coccolobis diversifolia Britton & Millspaugh, The Bahama Flora, 117. 1920; Northrop, Mem. Torrey Bot. Club **12:** 34. 1902.

Abaco: *Brace 1481* (FM, NY), *1697* (NY). **Bimini:** South Bimini, *R. A. & E. S. Howard 10164* (G). **Caicos:** North Caicos, *Wilson 7708* (FM, G, NY), *7744* (G, FM, NY); *Proctor 9060* (A). **Crooked Island:** *Brace 4658* (FM, MO, NY, US). **Fortune Island:** *Rothrock 264* (FM, G, NY). **Great Bahama:** *Britton & Millspaugh 2544* (FM, NY), *2396* (FM, NY). **Inagua:** *Nash & Taylor 909*

(FM, NY), *1009* (NY), *1014* (FM, NY), *1428* (NY). **Little Inagua:** *Wilson 7769* (FM, G, NY). **Long Island:** *Britton & Millspaugh 6316* (FM, NY); *Coker 520* (NY). **New Providence:** *Britton & Brace 231* (FM, NY), *324* (FM, G, MO, NY, US); *Britton & Millspaugh 2175* (FM, NY); *Degener 18970* (A); *Hitchcock s.n.* (MO); *J. I. & A. R. Northrop 143* (FM, G, NY). **Rose Island:** *Britton & Millspaugh 2122* (FM, NY, US); *Wilson 7900* (FM, G, NY).

A complete description of this species and the synonymy was given earlier in this paper. The variations of *C. swartzii* throughout its range was discussed in the second paper of this series (Jour. Arnold Arb. **30**: 420. 1949).

Coccoloba krugii Lindau, Engl. Bot. Jahrb. 13: 145. 1890.

Coccolobis krugii Britton & Millspaugh, The Bahama Flora 118. 1920.

Acklin's Island: *Brace 4387* (FM, NY, US), *4495* (FM, NY); *Eggers 3960* (B, US). **Cat Island:** The Bight, *Britton & Millspaugh 5917* (FM, NY); Fort Hine, *Britton & Millspaugh 5948* (FM, NY); Orange Creek, *Britton & Millspaugh 5779* (FM, NY); Port Howe, *Hitchcock s.n.* (MO). **Caicos:** Dellis' Cay, *C. F. & C. M. Millspaugh 9225* (FM, G, NY); South Caicos, *Wilson 7594* (FM, G, NY); West Caicos, *Wilson 7754* (FM, G, NY); North Caicos, *Proctor 8845* (A), *9180* (A). **Crooked Island:** *Brace 4748* (FM, NY); *Hitchcock s.n.* (FM, MO). **Fortune Island:** *Eggers 3998* (US), *3801* (US); *Rothrock 261* (FM, G, NY). **Inagua:** *Nash & Taylor 968* (FM, NY), *1059* (FM, NY); *Hitchcock s.n.* (MO). **Long Cay:** *Brace 4040* (FM, NY, US). **New Providence:** *Curtis 71* (A, G, FM, NY, MO, US); *Britton & Brace 361* (FM, NY), *363* (FM, NY, US), *864* (FM, NY), *372* (FM, NY), *375* (FM, NY). **Watling's Island:** *Britton & Millspaugh 6194* (FM, NY); *Coker 473* (NY); *Wilson 7215* (FM, G, MO, NY), *7324* (FM, G, MO, NY).

A complete description of this species was given earlier in this paper.

THE POTENTIALITIES AND LIMITATIONS OF WOOD ANATOMY IN THE STUDY OF THE PHYLOGENY AND CLASSIFICATION OF ANGIOSPERMS

I. W. Bailey

VESSELS

In our reconnaissance of the tracheary cells of the vascular land plants (Bailey and Tupper, 1918), which led to so many subsequent investigations of evolutionary trends in the xylem of angiosperms, we presented two types of evidence. (1) *Intensive* investigations were made of variations in the size, form and pitting of tracheary cells in different parts of the same plant and in different plants of the same species grown under varying environmental influences. (2) *Extensive* comparative data, obtained from a wide range of randomly selected representatives of the gymnosperms and dicotyledons, were statistically analyzed and tabulated. The latter data, in spite of demonstrated variations within single plants and single species, revealed surprisingly consistent changes in the size, form and pitting of tracheary cells at successive levels in the evolution and specialization of vessels in the dicotyledons as-a-whole.

Similar evolutionary trends in the development and specialization of vessels in the primary xylem of monocotyledons have been demonstrated by Cheadle (1942, 1943a, 1943b, 1944).

At present, the development and specialization of vessels in dicotyledons and monocotyledons provide two of the most, if not the most, comprehensive and reliable evolutionary trends that are preserved in surviving representatives of the angiosperms. It should be recognized in this connection that no longer are there uncertainties regarding the directions in which the evolutionary trends are progressing. This is due to the obvious fact that the structure of geologically ancient land plants negates any possibility of deriving tracheids from vessels. As re-emphasized by Frost (1930a, 1930b, 1931), since vessels clearly evolve by modification of tracheids, the most primitive vessels are composed of members which closely resemble tracheids in size, form and pitting. The most highly specialized vessels are those whose constituent tracheary cells least resemble tracheids.

The most primitive vessels in the metaxylem and secondary xylem of dicotyledons and in the metaxylem of monocotyledons are composed of members which closely resemble thin-walled, scalariformly pitted tracheids. Thus, the vessel-members are long, comparatively slender in relation to their length, and (as viewed in tangential longitudinal sections of the xylem) have gradually tapered, extensively overlapping ends. They are thin-walled and angular in cross-sectional view. They differ from tracheids at functional maturity solely in the dissolution of pit membranes in a number of the bordered pit pairs in their overlapping ends. In the secondary xylem of dicotyledons, such vessels are more or less uniformly distributed and are infrequently in contact laterally with one another. However, where lateral contacts do occur the intervascular imperforate pitting is scalariform.

The members of the most highly specialized vessels — in contrast to those of the most primitive ones — are short, comparatively broad for their length and tend to be oval or circular in cross-sectional view. They have truncated ends regardless of variations in their diameter. There is a single perforation at each end of the cell. The vessels commonly tend to be more or less extensively aggregated in the secondary xylem, and the intervascular pitting is alternating-multiseriate.

In view of such structural differences as these, it is possible to arrange the vessels of both the dicotyledons and monocotyledons in evolutionary trends of increasing specialization. It is important to bear in mind that this can be accomplished *entirely independently* of the various systems of classifying the taxa of angiosperms, thus avoiding circular arguments based upon assumptions regarding the primitive or specialized character of various representatives of the angiosperms. In other words, primitive vessels are distinguished from specialized ones *solely* upon their own structural differences, and *entirely* without reference to the putative primitiveness of the plants in which they occur.

PARALLEL AND CONVERGENT EVOLUTION IN VESSELS

Comprehensive summations of evidence now indicate that there has been an independent, but parallel, evolution of vessels in dicotyledons and monocotyledons, Bailey (1944), Cheadle (1953). Therefore, if the angiosperms are monophyletic, the monocotyledons must have been derived either from vesselless dicotyledons or from common vesselless ancestors. Furthermore, in both of the principal divisions of the flowering plants, as in *Selaginella* and *Pteridium*, vessels evolved by modification of scalariformly pitted tracheids, in striking contrast to the Gnetales where vessels evolved from tracheids having circular bordered pits with conspicuous tori. Thus, available evidence negates any possibility of deriving the angiosperms from the Gnetales, Coniferales, Taxales or Ginkgoales. The similarity between the highly specialized vessels of *Gnetum* and of certain dicotyledons is owing to convergent, rather than parallel, evolution.

The wide range of variability in the reproductive organs of vesselless dicotyledons suggests that vessels may have originated more than once in primitive representatives of the dicotyledons. In addition, much evidence is now available which demonstrates that similar trends of specialization of vessels have occurred independently in many families of the dicotyledons. In other words, similarities due to parallel evolution are surprisingly common in the xylem of dicotyledons.

CORRELATIONS BETWEEN VESSELS, CAMBIAL INITIALS IMPERFORATE TRACHEARY CELLS, WOOD PARENCHYMA AND RAYS

In the case of the secondary xylem of dicotyledons, it is possible by statistical correlations to show that during the evolution and specialization of vessels there are concomitant changes in the fusiform initials of the cambium, Bailey (1920a, 1923), and also in the ground mass of imperforate tracheids which tend to assume an increasingly fiber-like form, Bailey and Tupper (1918), Bailey (1936). In addition, it is possible by statistical correlations to obtain significant clues regarding primitive forms of wood parenchyma (Kribs 1937) and wood rays (Kribs 1935, Barghoorn 1940, 1941a, 1941b), and to study a number of their salient trends of specialization.

CAMBIAL INITIALS

As in the case of vesselless dicotyledons and gymnosperms, the most primitive kinds of vessel-bearing secondary xylem are formed by a cambium having long fusiform initials with gradually tapered, extensively overlapping ends as seen in tangential sections. The anticlinal divisions of these initials are pseudo-transverse, and the resulting cells elongate extensively before they in turn divide anticlinally. Thus, there is a wide range of variability in the length of neighboring initials. Since the frequency of anticlinal divisions and the amount of apical elongation are not constant, the average or mean length of the fusiform initials varies markedly in different parts of a fully matured plant. The most significant of these variations is the increase in mean size during the lateral enlargement of stems, due largely to an increase in mean length of the fusiform initials, but also to a less conspicuous increase in their tangential diameter. Important also are reductions in length of initials at nodes as contrasted with internodes of young stems, at the junctions of large stems with branches or roots, and in burly tissues due to injuries or other abnormalities. Furthermore, dwarfing due to extremely retarded growth in unfavorable habitats reduces the mean size more or less markedly. One should bear in mind in this connection that the fusiform initials continue to divide periclinally, thus forming tracheary derivatives, during their intervals of elongation between successive anticlinal divisions. Therefore, since vessel members elongate slightly, if at all, during tissue differentiation, their variations in length closely parallel the variations in length of the cambial initials.

Secondary xylem containing the most highly specialized vessels is formed by a cambium having short initials with abruptly tapered ends and slight overlap. The anticlinal divisions are radial longitudinal and, owing to the elimination of apical elongation between such divisions, the neighboring initials are of relatively uniform length and exhibit a stratified or storied arrangement in surface view of the cambium. The mean length of the initials varies somewhat in different parts of a fully matured plant and in plants grown under different environmental influences, but the variations are slight in comparison with those that occur in primitive cambia of dicotyledons and gymnosperms. For example, in different parts of a vesselless tree (*Pseudotsuga menziesii*) selected for comparison, the mean lengths of the fusiform initials varied between 900 μ and 6000 μ, the shortest initial being 280 μ and the longest 8600 μ. In contrast to this, the mean lengths of the initials in different parts of a tree having a storied cambium (*Robinia pseudoacacia*) varied between 150 μ and 190 μ, the shortest initial having a length of 70 μ and the longest one a length of 320 μ.

As in the case of primitive vessels, the mean length of the members of highly specialized vessels closely approximates the mean length of the cambial initials. However, the girth of the vessel members presents an entirely different problem. In primitively vesselless forms of secondary xylem, the tangential diameter of the tracheids is determined by the tangential diameter of the fusiform initials, whereas the radial dimension is due largely to radial expansion during tissue differentiation. It is for this reason that the tracheids exhibit radial seriations in cross sections of the secondary xylem, except in certain cases where the seriations are disturbed by excessive intrusive elongation of the tracheids during tissue differentiation. Furthermore, as the tangential diameter of the fusiform initials tends to increase as a stem enlarges in circumference (Bailey, 1920b), the tracheids of the later-formed xylem tend to be correspondingly broader, as well as much longer, than they are in the first-formed secondary xylem. On the contrary, the girth of vessels is determined by both tangential and radial expansion during tissue differentiation. Where the vessel members are much broader than tracheids, as they so commonly are in highly specialized vessels, they afford no reliable clue regarding the tangential diameter of the cambial initials. It should be noted in passing that the girth of highly specialized vessels varies widely, not only in different taxa and in plants grown under different environmental conditions, but also in different parts of the same plant. The vessels of the later-formed secondary xylem commonly tend to be conspicuously broader than those of the first-formed secondary xylem (Bailey and Howard, 1941). However, such variations in girth are due largely to variations in the amount of lateral expansion during tissue differentiation rather than to differences in the diameters of cambial initials.

IMPERFORATE TRACHEARY CELLS

During the evolution of the taller vascular land plants, there has been a constant necessity of maintaining an equilibrium between rates of conductions and strength in stems (Bailey, 1953). Among vesselless gymnosperms, there is at times a more or less obvious tendency to form tracheids which vary in strength and in their permeability to ascending sap, certain of the vertically contiguous tracheids being broader, thinner-walled and more profusely pitted, whereas others are more slender, thicker-walled and have a reduced number of relatively small, circular bordered pits. This tendency toward "division of labor" in conduction and strength is most obvious and sharply defined in gymnosperms having pronounced growth rings in their secondary xylem, viz. layers of relatively weak, highly permeable tracheary tissue alternating with dense much stronger ones.

In certain of the vesselless dicotyledons, as in certain of the Bennettitales (*sensu lato*), which do not have a conspicuously zonate secondary xylem, the broader, thinner-walled tracheids tend to have abundant scalariform pitting and to be more or less randomly or irregularly distributed throughout the groundmass of secondary xylem. On the contrary, in the vesselless dicotyledons, *Tetracentron* and *Trochodendron*, as in certain remarkable representatives of the Bennettitales (*sensu lato*) recently described by Hsü and Bose (1952) and Bose (1953), which have conspicuous growth layers, the broad, thin-walled tracheids of the early-wood have profuse scalariform pitting, whereas the slender, thick-walled tracheids of the late-wood are provided with a few, small, circular, bordered pits only.

If the vessels of dicotyledons were derived from scalariformly pitted tracheids in zonal arrangement, it might be anticipated that the most primitive vessels in the secondary xylem would be aggregated in concentric zones. This obviously is not the case, and indicates that they developed by modification of scalariformly pitted tracheids that were loosely diffused throughout the groundmass of thick-walled, mechanically stronger tracheids.

The division of labor between strength and conduction in tracheary cells becomes increasingly intensified during the evolution and specialization of vessels in the secondary xylem of the dicotyledons. As revealed by significant statistical correlations in the dicotyledons as-a-whole, the imperforate tracheids become increasingly fiber-like at successive levels in the evolutionary specialization of vessels and cambial initials, due to proportionally greater elongation during tissue differentiation and to reduction and elimination of borders about the pits.

Even during the earlier stages of the evolution of vessels, there is a tendency for enhanced elongation of the thick-walled tracheids during tissue differentiation, but it is not sufficient to compensate for the marked reduction in length of the cambial initials, i.e. when comparisons are made with vesselless dicotyledons and gymnosperms. As the specialization of vessels progresses, the elongation of the imperforate tracheary cells tends to become proportionally greater until elongations of several hundred percent are not infrequently attained. However, the enhanced elongation does not neutralize the shortening effect of excessive reduction in length of the cambial initials. Thus, the imperforate tracheary cells tend, in general, to become shorter as vessels attain successive levels of increasing evolutionary specialization.

WOOD PARENCHYMA

Wood parenchyma strands ordinarily do not elongate or enlarge their tangential diameter appreciably during tissue differentiation. Since their length and tangential diameter is determined largely by the cambial initials, their size and the size and number of their constituent cells decreases concomitantly with the reduction in size of cambial initials. It should be noted in this connection that, particularly in the case of highly specialized tracheary tissue, the wood parenchyma strands provide reliable clues regarding the dimensions of cambial initials. Furthermore, when they occur in extensive aggregations, they provide a means of determining whether the cambium is of a storied or non-storied type.

The distribution of wood parenchyma in vesselless dicotyledons varies between absent, scanty diffuse, diffuse-in-aggregates and narrow tangentially banded. It is not possible at present to determine with certainty whether absence of wood parenchyma in vesselless dicotyledons is a primitive or a derived condition. However, collateral evidence indicates that the tangentially banded parenchyma of *Pseudowintera* is derived by a modification of the diffuse pattern.

Among woods having primitive vessels, nearly 90 percent have diffuse parenchyma, commonly of the diffuse-in-aggregates type. Absence of wood parenchyma may approximate 10 percent, whereas narrow, tangentially banded apotracheal and scanty paratracheal types are of rare occurrence. Broad-banded apotracheal and abundant paratracheal forms of distribution occur in woods whose vessels have attained relatively high levels of evolutionary specialization. Various mixtures of apotracheal and paratracheal patterns are produced in association with transitional and highly specialized forms of vessels.

Although available statistical data (Kribs, 1937), demonstrate that the various forms of aggregated, apotracheal and paratracheal parenchyma are derived from a primitive, diffuse, apotracheal distribution, they do not provide a thoroughly reliable basis for arranging the diversified patterns in a single linear series of increasing structural specialization. Summations of morphological evidence from various taxa of the dicotyledons now indicate that reductions in the amount of wood parenchyma to terminal, scanty paratracheal, or absent occur independently at various levels of the evolutionary specialization of vessels. Uncertainties exist, however, in dealing with various mixtures of apotracheal and paratracheal parenchyma which may have developed in more than one way. For example, broad-banded apotracheal may have given rise to banded with included vessels, to aliform paratracheal to abundant vasicentric, or vasicentric paratracheal may have led to aliform to tangentially confluent, or both kinds of specialization may have occurred independently in different taxa. Such uncertainties cannot be clarified until more detailed and comprehensive studies have been made of a number of the larger families of the dicotyledons.

WOOD RAYS

Since the rays in secondary xylem are formed by ray initials of the cambium, their dimensions ordinarily are not directly influenced by those of the fusiform initials which form tracheary cells and wood parenchyma strands. However, owing to the fact that new ray initials are periodically formed by division of fusiform initials, there are at times indirect effects that should not be overlooked, particularly in the case of storied cambia.

The ray initials of vesselless dicotyledons and of dicotyledons having primitive forms of vessels are of two distinctly different shapes and aggregations. As viewed in tangential longitudinal sections, there are (1) erect ray initials in vertically uniseriate arrangement and (2) more nearly isodiametric ones in multiseriate aggregation. The multiseriate aggregations terminate both upward and downward in uniseriate extensions of erect initials. Two types of wood rays are formed by these initials, (1) high-celled uniseriate rays, and (2) multiseriate rays whose constituent cells are vertically short in comparison with those of the uniseriate rays except in their high-celled uniseriate extensions. These extensions appear to be uniseriate rays that are attached to the upper and lower margins of the multiseriate rays.

During the evolutionary specialization of vessels, divergent modifications of this primitive form of ray structure occur. Some of the more significant changes involve (a) reduction and elimination of multiseriate rays, (b) reduction and elimination of uniseriate rays, (c) reduction and elimination of all rays, (d) reduction in the height of ray cells with concomitant increase in their radial expansion during tissue differentiation, leading to the formation of so-called homogeneous rays, viz. composed throughout of more or less conspicuously "procumbent" cells, (e) excessive reductions or amplifications in the width of multiseriate rays, and (f) arrangement of low rays in transverse stratification where the secondary xylem is formed by a storied cambium.

Although transitional stages in the attainment of the end-products of each of these trends of specialization can be arranged in evolutionary series, the different trends of specialization cannot be combined in a single linear series which closely parallels that of the evolutionary specialization of vessels. Each trend of specialization, with the exception of storied rays, may occur at different levels of the increasing specialization of vessels.

THE ROLE OF WOOD ANATOMY IN TAXONOMY

Recognizing that the salient trends of evolutionary specialization in the xylem have been revealed by statistical analyses of the dicotyledons *as-a-whole*, the question arises, how and to what extent may they be utilized in studying relationships within orders, families, genera and species.

It is no longer justifiable to assume, as has so frequently been done in the past, that one organ or part of a plant is inherently more conservative and reliable than are all others. From the point of view of the dicotyledons *as-a-whole*, it is evident that each organ or part may be relatively uniform morphologically in certain taxa whereas it is highly variable in others. Furthermore, the rates of evolutionary modification in different parts frequently are not closely synchronized. Thus, any particular evolutionary trend, however reliably established, applies to a single part of the plant *only* and does not *by itself*, provide a reliable basis for classifying the plants from which the evidence was obtained in a similar phylogenetic sequence, since evidence from other parts of the plant may negate such an arrangement. If a truly natural classification of dicotyledons is to be attained, it must be based upon harmonizing evidence from all organs and parts of the plants. It is in this synthesizing task that wood anatomy has a significant role in taxonomy.

There has been, and still exists, a tendency among those who concentrate their attention largely upon the study of wood anatomy to base conclusions regarding relationships and classification solely upon similarities and differences in the structure of the xylem. Such conclusions are unreliable unless supported by the totality of evidence from other parts of the plants. This is owing to the fact that similarities in the xylem, which may be due to parallel evolution, are not necessarily indicative of close genetic relationship of plants unless supported by strong corroborative evidence. Nor are conspicuous differences in the xylem necessarily indicative in all cases of remote relationship, since the evolutionary modification of the xylem may be accelerated in plants where a totality of evidence from all organs and parts is indicative of relatively close relationship.

Thus far, the evolutionary trends in the cambium and xylem of dicotyledons, when considered by themselves, have been most reliable and significant in *negations*. This is owing to the fact that plants which have retained primitive cambia and xylem cannot be derived from plants which have attained uniformly high levels of structural specialization. For example, the monocotyledons cannot be derived from the Ranunculaceae or Piperaceae. Within the dicotyledons, herbs, vines, lianas, succulents and many extreme xerophytes have attained high levels of tracheary specializations and cannot have given rise to trees and shrubs which retain relatively primitive forms of xylem. The relatively highly specialized xylem of the Amentiferae negates any possibility of considering them the primitive stock from which other dicotyledons have been derived.

There are certain details of the trends of specialization in the xylem which need to be more clearly and generally understood in shifting from a consideration of the dicotyledons *as-a-whole* to investigations of the taxonomy of individual taxa of restricted size. In revealing salient trends of evolutionary specialization by analyses of data obtained from the dicotyledons *as-a-whole*, variations due to obtaining specimens from different parts of the plant, from plants of different growth rates, from genetically different taxa, etc., tend to neutralize one another. In addition, various localized, divergent trends of specialization do not obscure or confuse the major trends of evolution in the dicotyledons *as-a-whole*. However, when one becomes concerned with taxa of decreasing size, viz. families, subfamilies, tribes, genera and species, such variations and deviations become increasingly significant.

DEVIATIONS IN THE SYNCHRONIZATION OF STRUCTURAL CHANGES IN TRACHEARY CELLS

When *averaged* data are obtained from the dicotyledons *as-a-whole*, the successive evolutionary modifications of the cambium and of the length, form and pitting of its tracheary derivatives tend *in general* to be relatively closely synchronized in passing from the most primitive to the most specialized conditions. It should be kept in mind in this connection, however, that changes in the form, perforations and imperforate intervascular pitting of vessel members tend to be retarded in the metaxylem and first-formed secondary xylem (Bailey, 1944), as also not infrequently in the vessels of smaller diameter in the later-formed secondary xylem. Furthermore, there are families and genera in which one or another of the generally coordinated changes is accelerated or retarded in relation to the others. For example, accelerations in the transformation of scalariform to simple perforations, coupled with retardation in the lateral enlargement of vessels, may at times lead to the formation of relatively long vessel members with steeply inclined, rather than transversely oriented, simple perforation plates. Conversely, excessive enlargement of vessels, coupled with retarded changes in the perforations, may result in broad vessel members with nearly transversely oriented scalariform perforation plates. Precocious enlargement of vessels in vines and lianas, with concomitant changes in perforations and intervascular pitting, results at times in vessel members that are excessively long for their general level of morphological specialization. Conversely, extreme dwarfing, coupled with retardation of changes in perforations and intervascular pitting, frequently leads to the formation of vessel members that are short for their general level of primitive morphological structures. The changes in perforations and in intervascular pitting may be retarded or accelerated in relation to one another, as may those that occur in vessels as contrasted with imperforate tracheary cells.

In view of the occurrence of such localized variations as these, it is evident that considerable caution must be exercised in attempting to arrange the tracheary tissues of the species of a given genus or the genera of a particular family in linear evolutionary series which provide reliable evidence in discussions of relationships, particularly in taxa whose representatives fall within a relatively narrow range of the evolutionary specialization of vessels, e.g. Compositae, Leguminosae, etc. In the case of such taxa, undue emphasis should not be placed upon differences in the dimensions of tracheary cells, in the inclination of perforations, or in the character of intervascular pitting in *randomly collected samples* of various species and genera. Detailed and laborious consideration must be given to the ranges of variability within each plant and within each species if comparable statistical averages are to be obtained.

LOCALIZED DIVERGENT TRENDS OF SPECIALIZATION

It is evident that in dealing with wood rays and with patterns of wood parenchyma distribution one is concerned with a number of divergent trends of specialization rather than with single unidirectional series of increasing evolutionary modification. Each of these trends of modification may occur independently at different levels of the structural specialization of vessels. In other words, parallel evolutionary changes in wood rays and wood parenchyma occur independently in many taxa of the dicotyledons.

Although the major trend of specialization in fusiform initials and in their tracheary derivatives is unidirectional, there are various localized divergent specializations which merit careful consideration in the discussion of taxonomic problems. For example, the tendency to form "tertiary" helical thickenings in tracheary cells is a divergent trend of specialization that has occurred independently in gymnosperms as well as in many taxa of the dicotyledons. Their presence in vessels is not indicative necessarily of close genetic relationship. Nor can it be assumed that such vessels are derived from tracheids with helical thickenings. Another common divergent trend of specialization is the tendency of imperforate tracheary cells to retain their living contents which divide forming septa internal to the lignified secondary wall. Such septate fiber-tracheids and libriform fibers, which function in storage of starch, crystals, etc. as well as mechanically, develop independently at various levels of the evolutionary specialization of vessels. Their occurrence in different taxa is not indicative necessarily of close taxonomic affinities.

Excessive thickening or attenuation of the walls of tracheary cells, unusual enlargement or reduction in the diameter of vessels, and unusually extensive aggregations of vessels in diversified patterns are of not infrequent occurrence in various taxa of the dicotyledons. It is advisable to deal with such structural modifications in terms of localized divergent specializations rather than to endeavor to incorporate them as parts of a single major unidirectional trend of evolutionary specialization. For example, there are taxa whose vessel members have attained relatively high levels of structural specialization as regards their length, form, perforations and pitting, but the vessels are thin-walled and angular in cross-sectional view. *A priori* the latter diagnostic feature might be interpreted as a retention of a primitive structural character. However, summations of evidence in various taxa indicate that there has been a reversionary trend of specialization to a thin-walled angular condition.

The formation of so-called vascular tracheids and vasicentric tracheids similarly represents divergent trends of specialization that occur independently in various taxa. By classical definition, these cells are included in a broad general category of tracheary elements. However, they do not provide a sound basis for concluding that the evolution of vessels from tracheids is a truly reversible process. This is due to the fact that the end products of these trends of specialization differ markedly from the typical tracheids of vascular land plants in form and in their behavior during tissue differentiation.

CONCLUSIONS

The chief trends of evolutionary specialization in the cambium and xylem of dicotyledons are now so reliably established (except in the case of certain patterns of wood parenchyma distribution) that they can be utilized to advantage in studying salient problems of phylogeny and classification. When considered by themselves, they are most significant in *negations*, since a taxon which retains primitive forms of cambium and xylem cannot be derived directly from a taxon which has attained a uniformly high level of structural specialization. Unfortunately, owing to the frequent occurrence of parallel evolutionary changes, they cannot be utilized in *positive* assertions of relationship or phylogenetic derivation without corroborative evidence from other parts of the plant. However, since evidence from all organs and parts of the plant must be harmonized if a natural classification of plants is to be attained, evidence from wood anatomy should be given due consideration in taxonomy.

It should be emphasized, in conclusion, that the salient trends of evolutionary specialization in the cambium and xylem have been established by statistical analyses of the dicotyledons *as-a-whole*. In obtaining significant statistical averages from large volumes of randomly selected data, the effects of minor variations and localized divergent specializations are minimized. On the contrary, in dealing with the taxonomy of taxa of diminishing size, such variations and localized deviations become increasingly important. More attention should be devoted in the future to much neglected detailed investigations of the ranges of structural variability in individual plants and in individual species and genera. Furthermore, it is essential that anatomical data be obtained from plants of which herbarium vouchers are available.

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STUDIES IN THE BORAGINACEAE, XXIX.
ECHIOCHILON AND RELATED GENERA

IVAN M. JOHNSTON

THE THREE GENERA here discussed, *Megastoma*, *Sericostoma* and *Echiochilon*, include a total of nineteen species endemic in the deserts of northern Africa (Senegal to Somaliland), Arabia, Iran, and Pakistan. Most of these species are rare or very local and subsequent to their original description have been mentioned only briefly and rarely, if at all, in the literature. The many unique or very uncommon features to be observed in the floral structure of these plants have been overlooked or unappreciated.

The relationship of the three genera to the other members of the Boraginoideae is not clear. Although they have features prevailingly suggestive of a relationship among the Lithospermeae, in fruiting structures they are most like the Eritrichieae. Our genera seem to have no obvious direct relations with any of the Old World Boraginoideae. Surprisingly, they seem to be in greatest agreement with *Amblynotopsis* of Mexico and *Antiphytum* of southern Brazil and Uruguay.

Preliminary work on the present report was carried on at the British Museum of Natural History, in the Herbarium at Kew, and in the Herbarium of the Natural History Museum in Paris during a visit to Europe in 1952. Through the kindness of those in charge, I was able to borrow selected specimens from these herbaria for detailed study at the Arnold Arboretum. Subsequently, recently accessioned new collections of *Echiochilon* at Kew and the British Museum have been sent me on loan for identification by Mr. E. Milne-Redhead and Miss Hillcoat. Also of great interest and usefulness has been the loan of the Somali *Echiochilon* from the Botanical Institute, Florence, loaned me by Professor R. E. G. Pichi-Sermolli.

KEY TO THE GENERA

Corolla glabrous inside, minute, shorter than the calyx, throat bearing five obscure weak circular convex invaginations; anthers affixed at or below the middle, becoming dorsiventrally compressed; pollen 3-porate; small annual herbs ranging from the Canary Islands, across North Africa to eastern Arabia. . . . . I. *Megastoma.*

Corolla abundantly and conspicuously villose in the throat, throat not at all invaginate; anthers affixed above the middle, becoming strongly compressed laterally; pollen usually 2-colpate but in a few species sometimes also 3-colpate; plants usually fruticose and perennial, only one species annual.

  Gynobase plane or even depressed at the center; nutlets with a stout downward directed stipe bearing the attachment at its lower end; stigmas terminal, projecting above the sterile tip of the style; filaments affixed at the summit of the corolla-throat directly beneath the base of the corolla-sinus;

corolla-lobes equalling or even longer than the tubular portion (i.e., tube + throat) of the corolla; calyx deciduous at maturity, the lobes strongly imbricate; cymes usually glomerate, few-flowered; plant of Pakistan and adjacent India. .... II. *Sericostoma.*

Gynobase elevated, attenuate, usually narrowly pyramidal and more than half the height of the nutlets; stigmas subterminal, always surpassed by the protracted sterile tip of the style; nutlets with a prolonged sessile lateral attachment; filaments affixed deep in the corolla-throat; corolla-lobes shorter than the tubular portion of the corolla; calyx persistent, the lobes valvate or at least not evidently imbricate; corolla small to large, radially symmetric to strongly zygomorphic; inflorescence usually with numerous flowers, usually elongating and becoming unilaterally racemose. .... III. *Echiochilon.*

I. **Megastoma** Coss. & Dur. ex Benth. & Hook. Gen. Pl. 2: 851 (1876), in synonomy; Bonnet & Barratte, Ill. Phan. Tunis. *t. 11, f. 4–11* (1895), illustration with analysis; Bonnet & Barratte, Cat. Pl. Vasc. Tunis 301 (1896), description; Johnston, Contr. Gray Herb. **73**: 64 (1924) and **74**: 19 (1925); Brand, Pflanzenr. Heft **97**: 77, *f. 6* (1931). — Type species: *M. pusillum* Coss. & Dur.

Small annual herb, much branched, erect or becoming decumbent, cinereous with abundant appressed hairs, lowest leaves and branches opposite; leaves all cauline, narrow, abundant; plant fertile nearly throughout and hence developing no sharply delimited inflorescences; flowers produced abundantly along nearly all the leafy stems and branches to form very numerous ill-defined unilateral racemose clusters, the inflorescence never scorpioid; calyx 5-parted, accrescent, base rounded and usually developing a stout pedicel, lobes linear, decidedly unequal (especially in age), connivent in fruit, smallest lobe adaxial, largest lobe one of the two abaxial lobes; corolla white or slightly yellowish or pinkish, minute, shorter than the calyx-lobes, regular, subtubular, completely glabrous or with only a few minute hairs on the outer surface of some corolla-lobes; lobes small, ovate, erect or ascending, rounded at summit; tube (including the throat) cylindric, 3–4 times as long as the lobes; throat not differentiated as to form, inside bearing an ill-defined, circular, low-convex, weak invagination a short distance below each corolla-lobe; annulus not developed; stamens 5, equal, included in the lower half of the corolla-tube; filaments about as long as the anther, arising all at the same elevation very low in the corolla-tube; anther ovate or somewhat cordate, attached at or slightly below the middle, dorsiventrally compressed even after dehiscence, broader than thick and broadest above the base, apex obtuse and sometimes more or less apiculate, base broad and somewhat cordate; thecae distinct but remaining closely juxtaposed below the middle of the anther, their bases rounded or sometimes somewhat apiculate; connective linear, inconspicuous; pollen with 3 coarse circular pores, in polar profile three-sided with the pores forming the truncate corners, ca. 20 μ broad, in lateral profile elliptic ca. 14 μ high and 20 μ broad, the pores equatorial; gynobase elongate, erect, narrowly pyramidal, 4-angled, from just above the broadened base gradually narrowed to the pointed apex which bears the short style, after the fall of the nutlet the concave sides of the gynobase above the middle commonly bearing a short bristle-like section of the funicle projecting vertically from the broken end of the funicular canal; stigmas terminal, deeply bilobed, lobes subglobose, usually barely surpassing the tips of the nutlets in height; nutlets lance-ovate, usually all four maturing, back convex, base rounded, apex acute, venter with the suture open to form a conspicuous, elongate, narrowly triangular attachment-scar; attachment-scar distinctly lateral, extending from just above the nutlet-base upward almost to the nutlet-apex, 2–2½ times as long as broad, all in a single nearly vertical plane except the broadened lower end which may be slightly oblique and slope somewhat towards the nutlet-base.

Megastoma pusillum Coss. & Dur. in Bonnet & Barratte, Ill. Phan. Tunis. *t. 11, f. 4–11* (1895) — Type from "Tunisie méridionale: alluvions de *l'Qued Zitoun* (*Letourn.*)."

Small herb, 2–15 cm. tall, usually repeatedly branched, clothed with closely to loosely appressed stiffish straight pale hairs 0.5–1 mm. long; cotyledons frequently persisting even on fruiting plants, blades orbicular, ca. 2 mm. diameter, supported on a very broad short petiolar base which is connate and sheathing below the middle, lower surface of cotyledon glabrous, upper surface hispidulous, the hairs pale and bulbose at the base; leaves numerous, linear or oblanceolate-linear, 5–25 mm. long, 1–2.5 mm. broad, largest ones towards the base of the plant, flat or more or less conduplicate, thickish, veinless, midrib prominent if at all only on the lower surface, both leaf-surfaces bearing appressed stiff hairs arising from thickened bases, apex of blade obtusish or sometimes acute; flowers abundant, borne along most of the leafy stems and forking branches and, in the fruiting state, forming many leafy-bracted unilateral racemes 2–6 cm. long; calyx at anthesis 2–3 mm. long, becoming 4–7(–10) mm. long in fruit, frequently with a pedicel 0.5–1 mm. long; corolla 2–2.5 mm. long, lobes 0.6–0.7 mm. long and nearly as wide, tube about 1 mm. thick, faucal invaginations weak and obscure, 0.2–0.3 mm. diameter, borne about 0.2 mm. below the base of the corolla-lobes; filaments 0.2–0.3 mm. long, arising 0.5–0.7 mm. above the base of the corolla-tube; anthers 0.25–0.3 mm. long, 0.2 mm. broad; gynobase narrow, elongate, 0.1–1.4 mm. tall, ca. 0.5–0.8 mm. broad at the very base; style 0.2–0.3 mm. long; nutlets 1.3–1.8 mm. long, ca. 1 mm. broad above the base, usually sparsely verrucose, with a narrowly triangular lateral scar almost as long as the nutlet-body.

Canary Islands, western Mauritania and southern Morocco eastward, in Algeria, Tunis, Egypt and eastern Arabia, usually in deserts and chiefly in sandy places.

Canary Islands: Fuerteventura near port of Tarajalejo, sand, April 1912, *O. Burchard 335* (K). Mauritania: Tasiast, Oued Tenebrouret, ca. lat. 21°, long. 15–16°, abundant, Feb. 2, 1937, *Murat 1946* (G). Algeria: El Golia, in petrosis aridissimis, March 29, 1904, *L. Chevallier* (K); Ghardaia, in aridis glareosis, Feb. 1902, *L. Chevallier 455* (G); Biskra, sur les collines incultes, May 10, 1853, *B. Balansa* (G). EGYPT: Arabian Desert near Ain Shams to the north of Heliopolis, May 8, 1908, *Emile Burdet 341* (G); in deserto Belbeys, *Schubert* (K). ARABIA: Kuwait, Airdrome, sandy soil, corolla minute white or pinkish, May and June, 1935, *Dickson 209* and *253* (K); Bahrain Island, desert at pipeline, Awali wadi, March 13, 1950, *R. Good 215* (K); Bahrain Island, Jebel Dukhan, March 16, 1950, *R. Good 216* (K, BM); Jabal Hafit, Oman, April 25, 1948, *W. Thesiger* (BM).

The genus *Megastoma* is notable for its very small subtubular corollas which are shorter than the very unequally lobed calyx. The corolla has very obscure faucal swellings but no differentiated annulus, and is completely glabrous except for a few minute hairs on the outer surface of some of the corolla-lobes. The anthers are short and broad and cordate at the base. The thecae are distinct from the base upward nearly to their middle and almost to the attachment of the anther.

The nutlets and gynobase are beautifully illustrated by Bonnet & Barratte, the swellings in the corolla-throat, which they failed to notice, are shown somewhat diagramatically in the figure given by Brand. Both Bonnet & Barratte and Brand incorrectly illustrated and described the stigmas of *Megastoma* as simple and capitate. Actually the stigma is bilobed and frequently almost completely divided. Under high magnification it usually appears to consist of two closely juxtaposed subglobose stigmas terminal on the style.

II. **Sericostoma** Stocks ex Wight, Icones Pl. Ind. Orient. 4^2: 15, *t. 1377* (1848). — Type species: *S. pauciflorum* Stocks ex Wight.

A low spreading shrub with numerous slender much-branched stems, strigose, cinereous; leaves oblanceolate, oblong, or lanceolate, usually acute, thickish, loosely conduplicate, veinless, midrib evident if at all only on lower surface, lowest leaves on the shoot opposite; inflorescence terminal on the branches and branchlets, 3–6-flowered, at first glomerate but eventually short-racemose, bracts 1–2; calyx 5-fid, base thickened and elongate in age and eventually disarticulating; lobes imbricate, lanceolate, acute, subequal; corolla radially symmetric, white, minutely villulose on the surface of some of the corolla-lobes but otherwise glabrous outside, inside abundantly white villose in the throat; lobes as long as the corolla-tube or slightly longer, oblong, minutely lacerate near apex, spreading or recurving; tube (including the undifferentiated throat) stout, weakly ampliate; stamens almost completely exserted; filaments subulate, equal, about as long as the anther, affixed at the top of the throat directly beneath the sinus, anther narrowly oblong, erect, affixed above the middle, with rounded ends, in age with thecae explanate and back to back with the pallid inner surfaces parallel and facing laterally in opposite directions, the dehisced anthers accordingly appearing to be very strongly compressed laterally; connective very narrow and inconspicuous; pollen bicolpate, usually more or less bilaterally symmetric, 19–23 μ high, 21–24 μ broad, polar profile elliptic, lateral profile quadrate to transversely rectangular; gynobase not elevated, a cartilaginous disk, plane or somewhat depressed at the center, scarred by large circular excavations after the fall of the nutlets; style arising directly from the center of the discoid gynobase, shorter than the nutlets; stigmas 2, as long or longer than broad, vesicular, pallid, swollen, terminal, separated across the apex of the style by a narrow band of sterile stylar tissue but the two stigmas always evidently projecting above it; nutlets 1–4, usually only one maturing, ovoid, abundantly verrucose and tumulose, gray, reddish or brownish, ascending, supported on a short stout vertical laterally affixed stipe; axial edge of nutlet obtusely angulate, straight and vertical or nearly so, formed above the middle by the short low ventral keel on the nutlet-body and below the middle by the ventral side of the stipe, traversed from apex of nutlet to base of stipe by the closed and completely fused ventral suture; seminiferous body of the nutlet ovoid, inclined at an angle of about 60°, its pointed apex held high above nutlet-attachment and its rounded base held directly abaxial to the attachment; stipe stout, solid, smooth on sides, bearing the convex attachment-scar on its horizontal lower end, attached to the body of the nutlet on the sloping underside of the latter just below its middle; funicular canal ascending vertically inside the stipe and entering the seminiferous body of the nutlet just below the middle on the ventral side; seed compressed ovoid with a short radicle, the funicle attached half way up the ventral side of the seed.

A monotypic genus known from Pakistan and adjoining western India.

Sericostoma pauciflora Stocks ex Wight, Icones Pl. Ind. Orient. 4^2: 15, *t. 1377* (1848); Hooker, Icones **9**: *t. 804* (1852) — Type from Baikur near Deesa, Scinde, *Stocks.*

Sericostoma parviflorum Stocks ex Walp. Annal. **3**: 135 (1852), lapsus calami.

Stems numerous, 1–5 dm. long; old stems woody, with rough dark bark, 1 cm. or more thick; leaf-bearing branches 1–2 dm. long, 1–2.5 mm. thick, bearing straight, closely appressed hairs 0.2–0.6 mm. long; leaves all cauline, numerous, 5–35 mm. long, 2–10 mm. broad, strigose on both surfaces (hairs closely appressed 0.2–0.6 mm. long, most of them arising from discoid, mineralized bases), lowest leaves on the shoot and branches always forming 1–2 opposite pairs; cymes not scorpioid, usually about 4-flowered, at first glomerate and ca. 5 mm. in diameter, in age more loosely flowered on an axis 5–12 mm. long; bracts 1–2, inconspicuous, 1–3 mm. long; calyx strigose outside, inner surface glabrous, at anthesis 2.5–3 mm. long, with a short broad base, subsessile, lobes 0.7–1.2 mm. long; calyx at maturity having weakly accrescent lobes but an enlarged base, tending to become nutant and at extreme maturity to disarticulate from the inflorescence and to fall away with the nutlet still embraced by the connivent lobes, calyx-base thickened, angulate, elongate and frequently more or less pedicellate; corolla rotate, usually about 5 mm. diameter; lobes 1.5–2 mm. long, 1–1.7

mm. broad, usually with conspicuous dichotomous veins; tube 1.2–1.8 mm. long, 0.8–1.2 mm. thick, gradually but weakly ampliate from the base upward, upper half of tube (i.e. the throat) densely and conspicuously white-villous inside, below the middle of the tube glabrous inside except for a narrow inconspicuous villulose band (marking the site of the undeveloped annulus) ca. 0.2 mm. above the coralla-base; filaments 0.8–1 mm. long; anthers 0.8–1 mm. long, erect; gynobase ca. 1 mm. broad at anthesis, becoming 1.5–2 mm. broad when maturing all four nutlets, scar left by the detached nutlet a shallow excavation ca. 0.5 mm. diameter; style 1–1.3 mm. long, sterile apex surpassed by at least one-fourth of the length of the stigmas; nutlets 2–2.4 mm. long, ca. 1.5 mm. broad, ovoid, usually somewhat lustrous, with a rounded base, a convex dorsum and a broadly acute apex, body of nutlet supported on the sloping ventral under side by a stout vertical stipe 0.5 mm. long and almost 0.5 mm. in diameter; attachment-scar of nutlet on the base of the stipe, rough, convex, situated in the same horizontal plane as the base of the nutlet-body and adjacent to the latter and adaxial to it.

Dunes and other sandy places, chiefly in desert areas and along the coast, in southern Pakistan and in adjacent westernmost India.

SPECIMENS STUDIED: Scinde, *Stocks in Hook. & Thomson, Herb. Ind. Orient.* (G); Southeast Punjab, 1886, *J. R. Drummond 25988* (K); Punjab, *J. R. Drummond 25987* (K); Baikur near Deesa, *J. E. Stocks 61* (K); coast of Kathiawar, plentiful low-spreading shrub, *Dalzell* (K); Nargol, open formations in sand along sea, Feb. 24, 1912, *H. M. Chibber* (K); without locality, *V. Jacquemont 59* (G).

As here redefined, *Sericostoma* is reduced to its original species from Pakistan. Plants of Persia, Arabia, and Somalia previously assigned to this genus are now referred to *Echiochilon*. The two genera, although separable by characters of fundamental importance, are close relations, sharing such distinctive features as bicolpate pollen, vescicular stigmatic tissue, villose corolla-throat, and opposite lowermost leaves. In both the anthers are supramedially affixed and have the inner surfaces of the theca pallid, sparsely and very minutely strigose and eventually explanate. Formerly only plants with excessively zygomorphic corollas were referred to *Echiochilon*. Plants with radially symmetric or with only obscurely zygomorphic corollas were referred to *Sericostoma*. The separation of the two genera on this basis, however, can be supported by no other character and is obviously artificial. As now circumscribed, the monotypic genus *Sericostoma* has numerous characters of fundamental importance. Its nutlets are stiped and are borne on a plane, discoid gynobase. The ventral suture on its nutlets is completely closed and the margins fused all the way from the apex of the nutlet-body down to the nutlet-attachment at the base of its stipe. The style arises directly from the center of the discoid gynobase. Its sterile apex is not prolonged upward above the apices of the stigmas. The stigmas are distinct and are as long or longer than broad. They are not laterally prolonged and together do not form a stigmatic band around the style just beneath its sterile apex. The stamens are borne at the top of the throat directly beneath the base of the corolla-sinus and are almost completely exserted. The calyx has obviously imbricate lobes and eventually is deciduous while still embracing the mature fruit.

III. **Echiochilon** Desf. Fl. Atlant. 1: 166, *t. 47* (1798). — Type species: *E. fruticosum* Desf.

Chilochium Raf. Ann. Gen. Sci. Phys. 8: 269 (1821). — A proposed substitute name for *Echiochilon* Desf. (1798).

Exioxylon Raf. Fl. Tellur. 4: 85 (1838). — Apparently based upon *Echiochilon* Desf. (1798).

Leurocline Moore, Jour. Bot. 39: 257, *t. 424* (1901). — Type species: *L. lithospermoides* Moore.

Echiochilopsis Caballero, Trab. Mus. Nac. Cien. Nat. Madrid, Bot. 30: 10, *t. 2* (1935). — Type species: *E. coerulea* Cab. (= *Echiochilon chazaliei* (Boiss.) Johnston).

Tetraedrocarpus O. Schwartz, Mitt. Inst. allgem. Bot. Hamburg 10: 212 (1939). — Type species: *T. arabicus* O. Schwartz.

Plant usually perennial, with widely spreading erectly or ascendingly branched frutescent old stems, herbaceous and annual in one species only, bearing sparse to abundant strongly to loosely appressed hairs on stems and leaves and usually a few spreading hairs on the leaf margins, the hairs on the leaves frequently arising from well developed mineralized discoid bases, surface of the herbage glaucescent in a few species and bearing abundant minute stiped glands in two others; leaves all cauline and prevailingly alternate, the lowest on the shoot smaller than those directly above and always opposite, leaves all opposite only in one species; leaves thickish, firm or somewhat succulent, narrow and elongate and usually without visible veins or midrib, tending to be loosely conduplicate or have the margins somewhat involute, inflorescence few- to many-flowered, bracteate throughout, consisting of flowers interspersed among the leaves along the outer half of the leafy shoot or of flowers aggregated into an erect, elongating, racemose cluster terminating the leafy stems and branches, never developing a distinctly scorpioid apex; calyx 5-fid, subsessile or with a short stout strict pedicel; lobes erect, usually elongate, oblong to lanceolate or oblanceolate, all similar or nearly so or in a few species very unequal, distinct or rarely united at the very base to form a very short tube, when unequal the smallest lobe always adaxial and the largest lobe always one of the abaxial pair; corolla white, lilac, blue or reddish purple, in some species light colored at anthesis and then changing to blue or purple in age, short to elongate, hypocrateriform, funnelform or funnelform-tubular, small to moderately large, radially symmetric to very strongly zygomorphic, outside commonly strigulose or villulose but sometimes glabrous or bearing only minute stipitate glands; corolla-limb horizontal (i.e., on all sides diverging at 90° from the long axis of the corolla) or weakly to extremely oblique (i.e., highest on the adaxial side and sloping downward, gently to very steeply, towards the low abaxial side), in zygomorphic corollas the 2-lobed adaxial side always best developed and its lobes always erect, the forward lip in zygomorphic corollas usually spreading or loosely decurved and evidently 3-lobed but in one species reduced to a very narrow recurved unlobed rim; corolla lobes rounded, obovate to ovate or semicircular, all similar or differing more or less in size and shape, sometimes with conspicuous dichotomous veining or with crisped margins, in radially symmetric corollas the lobes all similar and equally spreading or sometimes the 2 adaxial lobes less widely spreading than the other three, in distinctly zygomorphic corollas the 2 erect adaxial lobes the largest, the medial abaxial lobe the smallest, and the 2 anterior laterals intermediate in size; corolla-throat densely villose inside with white or yellow hairs, bearing neither appendages nor glands, gradually expanding or campanulate, usually about as long as the tube, in zygomorphic corollas most prolonged on the adaxial side, most swollen on the abaxial side, and the upper margin evidently oblique; corolla tube without a well developed annulus, the latter absent or represented by an indistinct broad, very low-convex annular ridge which is either glabrous or inconspicuously villulose; stamens 5, arising from among the abundant hairs deep in the throat, all borne at the same distance above the corolla-base or with the adaxial stamen highest, the forward abaxial pair lowest, and the abaxial lateral pair at an intermediate level; filaments equal or unequal, from very short (merely unguiculate) to almost as long as the anther; anthers affixed above the middle, included or short-exserted, elongate, narrowly oblong with rounded summit, base rounded with short sinus, connective very narrow and inconspicuous; thecae becoming explanate and reflexed after dehiscence, the backs of the open thecae juxtaposed and the flattened pallid inner surfaces of the thecae parallel and facing in diametrically opposite directions, the empty anthers accordingly very pale, very strongly compressed laterally and bearing the filament-attachment in a deep cleft on the narrow dorsal side; pollen usually 2-colpate, and commonly more or less bilateral, 13–21 μ high and 15–24 μ broad, subcylindric and commonly broader than long, polar profile circular to elliptic or rhombic, lateral profile quadrate to transversely oblong; pollen rarely 3-colpate, 13–16 μ high, 15–23 μ broad, polar profile circular or 3-sided, lateral profile transversely ovate or elliptic; gynobase from a broad base medially and abruptly narrowed into a usually 4-sided slender attenuate upward prolongation (usually equalling the nutlet in height), the central upward prolongation commonly buttressed below the middle by 4 triangular wings, the nutlets usually attached in the (frequently excavated) angle between the wings of the gynobase and higher up along the usually sulcate side of the upward prolongation of the gynobase, in one species the nutlet not attached between the buttresses of the gynobase but only along the crest of the buttresses and, higher up, along the sides of the central upward prolongation; style short to moderately elongate, usually extending up only to the base of the corolla-throat, never exserted, terminating the central upward prolongation of the gynobase, slender, entire or, in one species, very shortly bilobed at the apex, cylindric and equally thick throughout or sometimes slightly thickened just below the summit, bearing the stigmas always below the variously modified sterile summit; on simple styles which bear horizontal stigmas the sterile apex of the style low-convex to domed or short-cylindric, entire or centrally depressed or more commonly somewhat bilobed, in one species the sterile apex of style divided into two unequal erect attenuate lobes; on styles apically bilobed each stylar lobe bearing a subterminal stigma and each lobe terminated in a short rounded sterile apex; on styles having oblique stigmas the sterile apex of the style 2-parted, consisting of two paralleling, anterior-posteriorly prolonged ridges which are either low-convex and inconspicuous or are elevated and conspicuous and most prominent over the high anterior side of the stigmas; stigmas 2, subapical, vescicular, transversely very elongate, slightly sinuous, distinct or imperfectly united at the ends, usually arranged end to end around the style just below the sterile apex to form a slightly sinuous swollen vescicular band, rarely separated on short lobes of the style and remaining evidently distinct, usually horizontal, less commonly distinctly oblique and highest above the style-base on the abaxial side; nutlets 1–4 maturing, gray to reddish, geminate or all alike, verrucose, tuberculate or tumulose or (less commonly) nearly smooth especially below the middle, broadly lanceolate, ovate or cordate in dorsal outline, back convex or obtuse without a medio-longitudinal ridge or the latter rare and imperfectly developed, venter obtuse or medially carinate, the medial suture open to form a lineate or attenuate sulcus or, when closed, having the margins merely touching or very narrowly overlapping, the margins of the suture coalescent, if at all, only near the nutlet-apex; attachment of nutlet completely lateral and vertical or below the middle partially oblique and suprabasal or rarely even partially basal, consisting of a lineate or a slenderly attenuate sulcus which extends upward along the vertical ventral keel usually almost to the nutlet-apex and downward into an abruptly expanded triangular or ovate areola, only in one species is the attachment a narrow lineate sulcus that is widely forked below the middle and equally wide for its entire length and nowhere expanded into an areola; the attachment-areola, frequently green and not uncommonly prominent, usually borne above the nutlet-base at the lower end of the ventral keel and usually in the same plane as the latter and hence, like the keel, usually vertical as well as distinctly lateral, much less commonly the areola is borne on the sloping inner side of the nutlet below the end of the ventral keel and hence oblique in its relation to the vertical keel, only in one species is the areola borne on the base of the nutlet and nearly horizontal.

As here defined, *Echiochilon* is amplified to include most of the species formerly referred to *Sericostoma.* These latter species have small, regular or only moderately irregular corollas. They differ from the older members of *Echiochilon* only in size of corolla and in degree of zygomorphy and are obviously very much more closely related to them than to the single original species of *Sericostoma* with which, until now, they have been unnaturally associated. *Echiochilon* as redefined is distinguished from the monotypic *Sericostoma* by the form and position of the stigmas, the form of nutlet-attachment, form of gynobase, valvate rather than imbricate sepals, position of stamen-attachment, etc., characters certainly much more significant than those involving the relative size of corolla and the degree of zygomorphy which alone distinguished the two genera before redefinition.

The corollas of *Echiochilon* may have a pronounced bilateral symmetry or may show little or no departure from the radial symmetry that prevails in the flowers of most Boraginaceae. In four species of the genus, *E. longiflorum*, *E. lithospermoides*, *E. chazaliei*, and *E. fruticosum*, the corollas are very strongly zygomorphic, being conspicuously prolonged dorsally and having an excessively oblique limb. In all these species the stamens are affixed in three superposed levels within the irregular corolla. The most extreme zygomorphy is that of *E. longiflorum*. Whereas the other species have the forward (abaxial) lip of the corolla more or less evidently 3-lobed, *E. longiflorum* has only the two rear corolla lobes well developed, the forward lip of the corolla being represented only by an inconspicuous, narrow, recurving, unlobed margin.

In contrast to the four just discussed, such species as *E. collenettei, E. arenarium, E. jugatum, E. vatkei, E. albidum, E. nubicum, E. verrucosum,* and *E. thesingeri* have corollas that are actinomorphic or practically so. Among this group of species only *E. verrucosum* has stamens that arise at different levels within the corolla. All the others have stamens arising from the wall of the throat all at the same level above the corolla-base. Their flowers have radial symmetry, not only in form of corolla but also as to size and attachment of the members of the androecium.

The remaining species of *Echiochilon* have corollas transitional in various degrees between the strongly bilateral and the radially symmetric corollas just mentioned. The corollas of *E. kotschyi, E. strigosum, E. persicum,* and *E. arabicum* have only inconspicuously zygomorphic corollas. These deviate from radial symmetry only in having the two adaxial lobes somewhat larger and less spreading than the other three lobes. The stamens are borne on the corolla in three superposed levels in all four species. More pronounced zygomorphy is present in the corollas of *E. adenophorum*. In that species the corolla-limb is distinctly oblique, but not so extremely so as in *E. longiflorum* and its relatives. The two lobes of the adaxial lip are large and erect and evidently larger than the three spreading, evidently smaller lobes of the anterior lip. The stamens are affixed at unequal heights within the corolla-throat.

Past authors have repeatedly compared the irregular corollas of *Echiochilon* with those of *Echium* and, indeed, have frequently classified the two genera together because of their zygomorphy. Though the corollas in these genera are both irregular, they are organized with fundamentally different planes of symmetry, cf. Jour. Arn. Arb. **35: 165 (1954).**

The orientation of the strongly zygomorphic corollas of *Echiochilon longiflorum, E. lithospermoides, E. chazaliei,* and *E. fruticosum* can be established readily and with accuracy by reference to identifiable lobes of the calyx. In the species mentioned the calyx-lobes are extremely unequal with the shortest lobes always having the adaxial position and the largest lobe always being one of the two abaxial lobes. Following the system of numbering adopted by Eichler, the largest lobe is No. 1, the smallest lobe is No. 2 and lobe No. 3 is the companion of No. 1 on the abaxial side of the calyx. A close examination of the flower shows very clearly that the medial plane of symmetry in the flower passes through calyx-lobe No. 2 and between calyx-lobes Nos. 1 and 3, and also between the two rear (adaxial) corolla-lobes and through the middle lobe of the three-lobed forward lip of the corolla. The corolla of *Echiochilon* is not resupinate as in *Echium* cf. Jour. Arnold Arb. **34**: 287 (1953), and its rear (adaxial) lip is bilobed rather than trilobed. The stamens, when borne at differing altitudes within the corolla, always have the odd, unpaired member borne on the adaxial side and always affixed higher above the corolla-base than the other four stamens. In *Echium*, although the stamens are also borne at unequal heights in the corolla-throat, the odd, unpaired stamen is borne not on the adaxial but on the abaxial side of the corolla and is the lowest rather than the highest of the five stamens. The differences between the corollas of *Echiochilon* and *Echium* are more significant than are the similarities. This is perhaps not surprising, for if one considers all characters in corolla, stamens, pollen, stigmas and nutlets, it seems impossible that the two genera could be immediately or even closely related.

Characteristic of the genus is 2-colpate, bilaterally symmetric pollen. This anomalous form of pollen has been observed in every species of the genus. Usually it is the only type of pollen produced, but in a few species it may be observed mixed in various proportions with 3-colpate pollen and even in mixtures in which the 3-colpate type may overwhelmingly predominate. Among the sixty-two samples of pollen studied, the largest quantity of 3-colpate grains has been observed in the samples representing *E. jugatum*, *E. persicum*, and *E. thesigeri*. Occasional 3-colpate grains were found intermixed with the almost exclusively 2-colpate pollen of *E. kotschyi* and *E. vatkei*. Only 2-colpate pollen was noted in the other species of the genus. Similar 2-colpate pollen occurs in *Sericostoma*, but is known from no other genus of the Boraginaceae.

The bicolpate bilaterally symmetric pollen of the genus is elliptic, rhombic-elliptic or nearly circular in polar profile. A slight prominence or roughening in the periphery usually marks clearly the location of the two colpi. The colpi are diametrically opposite when the silhouette is circular and usually located at the far ends when elliptic or rhombic. Only in the elongate grains of *E. lithospermoides*, *E. longiflorum*, and *E. fruticosum* are the colpi borne at the middle of the broad side and not at the far ends of the grains.

In lateral profile the grains are quadrate or rectangular and tend to be broader than high. The upper and lower edges in lateral profile are usually straight and parallel, which indicates that the grains are truncate and plane on top and bottom. The vertical edges of the quadrate or rectangular lateral silhouette differ from the top and bottom edges in being very moderately but still distinctly convex. The two colpi are short, vertical and equatorial and are borne on opposite sides of the usually bilaterally symmetric grain.

The grain as a three-dimensional object can be described as subcylindric, flattened on the upper and lower ends and as broad as long or slightly broader than long. The grains are usually swollen laterally in the vicinity of the two colpi and, accordingly, are usually broader along the diameter connecting the two colpiferous faces than along the diameter between the non-colpiferous faces. Because of this, the polar profile of the grain may vary from nearly circular to elliptic or somewhat rhombic in outline. Furthermore, as a result of the described modifications the grains may lose their basic radial organization and assume a moderate but very definite bilateral symmetry.

The bilaterally symmetric bicolpate grains appear to be a modification of the tri-colpate. In polar profile the 3-colpate grains of *Echiochilon* may appear circular with the location of the colpi weakly marked on the periphery or it can be distinctly three-sided with the colpi evident on each of the three angles. In lateral outline the 3-colpate grains are transversely ovate or elliptic and are accordingly broader than high. The grain, as a three-dimensional figure, accordingly, is broader than high and is more or less convex on the upper and lower surfaces. The three colpi are vertical and equatorial. The pollen consists of three equivalent radial sectors. By the suppression of one of these sectors the bicolpate pollen of *Echiochilon* and *Sericostoma* has been formed.

The bicolpate grains in *Echiochilon* when expanded in lactic acid have quadrate or rectangular colpiferous faces, in most species, measuring 16–19 μ in width and 13–16 μ in height. The maximum size occurs in the grains of *E. chazaliei* in which the colpiferous face measures 22–24 μ wide and 18–21 μ high. In the small grains of *E. strigosum* the face is 15–16 μ wide and 13–15 μ high.

In polar profile the grains may be circular or nearly so and 14–16 μ in diameter or be elliptic or rhombic and measure 16–21 μ long and 14–16 μ wide. The grains of *E. chazaliei*, the largest in the genus, have a polar profile 24–28 μ long and 21–24 μ wide.

Tricolpate grains have the lateral silhouette transversely ovate or elliptic and measuring 16–19 μ wide and 13–16 μ high. The polar profile, three-sided or nearly circular, is 15–23 μ broad.

The stigmas of *Echiochilon* are unusual among the Boraginoideae, being transversely prolonged and usually forming a band about the style just below its apex. In *Sericostoma* the two stigmas are subglobose or short-oblong and as long as broad or longer than broad. They always project upward well above the sterile tip of the style. In *Echiochilon* the two stigmas are transversely elongate, being 3–6 times broader than long. The two stigmas usually have their ends touching and sometimes partially confluent. Together they form a narrow, usually slightly sinuous, pallid swollen vescicular band around the style just below its apex. These stigmas unquestionably have a lateral and subapical position on the stylar column. The sterile apex of the style, in a variety of forms, is evidently prolonged above the stigmatic band. In one species the style is bilobed at the apex and a stigma partially encircles each of the short lobes just below the short, convex, sterile apex. The stigmas remain distinct.

In most of the small-flowered species (Nos. 8–17), the tip of the style is broad and low-convex and usually projects above the stigmas for a height equal to about half the width of the stigmatic band. This sterile summit may be simply convex or may be obscurely bilobed. In *E. collenettei*, the apex is most prolonged, being short-cylindric and entire, or sometimes bilobed. In *E. chazaliei* the apex is high convex, being at least hemispheric, and usually bears a small terminal depression at the very summit. In *E. arenarium* the stylar apex is divided into a pair of erect, usually very slightly unequal, attenuate lobes having a length equalling several times the width of the stigmatic ring. The elongate sterile tips of the style, prolonged well beyond the annular stigmas, combine in *E. arenarium* and *E. collenettei* to produce a structure very suggestive of the stigmatic head developed in *Heliotropium*. The condition has its closest parallel among the Boraginoideae in *Buglossoides*, cf. Jour. Arnold Arb. **35**: 40 (1954) and **35**: 161 (1954).

The style and stigmas of *E. longiflorum*, *E. lithospermoides* and *E. adenophorum* are the most specialized in the genus. The summit of the style, encircled by the stigmas, is enlarged, very oblique and bilaterally symmetric. The style just below its summit abruptly increases in diameter two- or rarely three-fold and is there encircled by the stigmas. The style with its abruptly thickened summit is somewhat suggestive of a nail with a broad head. The "head" of the style, however, differs from that of a nail in being oblique rather than horizontal. From the low rear (adaxial) margin its slope upward at an angle of 30°–60° towards the high forward (abaxial) margin. The band of stigmatic tissue on the margin of the "head" is also oblique. On the broad, decidedly sloping summit of the stylar head are borne a pair of sterile stylar apices of unusual form. Viewed from above the two apices are separate and parallel and lanceolate or ovate in outline. Together they are frequently very suggestive of the hoof of a goat. Viewed from the side they increase in height as they extend across the stylar head from the rear towards the forward margin. They are most conspicuous on the high forward side of the stylar head and broadest and tallest there. They are moderately developed in *E. adenophorum* and best developed in *E. longiflorum* and *E. lithospermoides*. These three species all have very strongly zygomorphic corollas. The asymmetric and oblique heads of the style, however, are not an invariable accompaniment of strong zygomorphy. Although the corolla of *E. chazaliei* is very oblique and zygomorphic, its style is not enlarged at the apex, its stigmas form a horizontal band, and the style has a simple, high-domed apex.

The style and stigmas of *E. fruticosum* have unique features. Differing from other species in the genus, *E. fruticosum* has a style which is distinctly bilobed. Each of the very short stout lobes is partially embraced by a transversely elongate stigma borne laterally just beneath the rounded apex of the lobe. Separated on lobes of the style that tend to diverge in age, the stigmas of *E. fruticosum* remain evidently distinct and give no appearance of being joined to form a continuous stigmatic band entirely surrounding the style as do the stigmas in other species of the genus. They are somewhat suggestive of the stigmas in the genus *Sericostoma* but are borne lateral and subapical and not terminal on the style as in that genus.

The nutlets of most of the species of *Echiochilon* are broadly lanceolate to ovate in dorsal outline and most of them are rather plump. In many of the species they are paired, being bent either left or right, so that, of adjacent nutlets, one is the mirror image of the other.

The attachment of the nutlets is essentially lateral. The gynobase is usually about as long as the nutlet. The nutlet has its principal area of attachment in a broad, usually more or less triangular areola which is borne on the ventral side of the nutlet-base at the lower end of the vertical ventral keel, sometimes below and oblique to the keel but usually in the same plane as the keel. Only in *E. chazaliei* and *E. adenophorum* is the attachment-areola so excessively oblique as to become almost basal on the nutlet and even nearly horizontal. From the attachment-areola a linear or attenuate sulcus is usually prolonged up the center of the nutlet along the crest of the ventral angle of the nutlet. This sulcus is the open ventral suture of the nutlet. The margins of the suture are concrescent only near the nutlet apex. In most species the suture is open to well above the middle of the nutlet body and frequently open almost all the way to the nutlet apex. In a few species such as *E. chazaliei*, *E. adenophorum* and *E. arenarium*, however, it may be closed for much of its length, but closed only by having the margins of the suture merely touching or shortly overlapped, and very definitely not by the fusion of the margins.

The pit which represents the end of the broken funicular canal is located in the attachment areola, usually in or near the upper corner of the areola and consequently beneath the lower end of the ventral keel. The course of the canal as it leaves the nutlet is vertical and usually more or less in line with the crest of the ventral keel above it.

Only two species develop nutlets especially noteworthy as to form. The eastern variety of *E. fruticosum* has plump, lanceolate nutlets. In the typical phase of the species from North Africa, however, the nutlets are not straight, erect and lanceolate. They are bent and have their broad lower half diverging from the vertical ventral sulcus and the gynobase at an angle of almost 90°. The back of the nutlet is incurved and saddle-like in lateral outline. I know of no other borage having nutlets which are bent 90° at the middle and which have the upper half vertical and affixed to the slender gynobase while the lower half is spreading and divergent from the floral axis. Bent nutlets occur in the Lithospermeae, cf. Jour. Arnold Arb. **35**: 161 (1954), but among these plants it is the lower half of the nutlet which is vertical. Furthermore, the bending of the nutlet in the Lithospermeae is inward over the floral axis and not outward and away from it as in *E. fruticosum*.

The nutlet of *E. longiflorum* has a number of unusual features. The broad base of the nutlet is shortly bilobed, has a deep medial sinus and is definitely cordate in outline. The nutlets viewed dorsally are decidedly heart-shaped. So deep is the basal sinus that the seed inside the nutlet has bilobed cotyledons. The broad nutlet has no large attachment-areola. It is attached to the slender erect gynobase only along a lineate sulcus. This groove, an open suture, extends down the vertical ventral keel to above the sinus on the nutlet-base where it abruptly and widely forks. The branches of the sulcus are at first divaricate but promptly decurve on the oblique lower surfaces of the nutlet venter and finally end low down on the oblique side of the two basal lobes of the nutlet. In most species of the genus the nutlet-areole is attached in the angle at the base of the gynobase between the wings buttressing the base. In *E. longiflorum*, however, the attachment sulcus is affixed to the sides of the subulate gynobase and, below the fork, along the crests of the buttressing wings and not at all in the angle between them.

KEY TO THE SPECIES OF ECHIOCHILON

Corolla glabrous on outer surface; foliage tending to be succulent and glaucescent.

  Plant annual; nutlets cordate, having a pronounced basal sinus. .... 1. *E. longiflorum.*

  Plants perennial, frutescent; nutlets ovoid, not cordate.

    Leaves, bracts and calyx-lobes with a midrib; leaves lanceolate, apex attenuate, margin hispid-ciliate; stigmas decidedly oblique, surmounted by a bilobed tip of the style. .... 2. *E. lithospermoides.*

    Leaves, bracts and calyx-lobes not costate; leaves thick, obovate to spathulate, apex obtuse or rounded, margins not ciliate; stigmas horizontal, surrounding the domed sterile apex of the style. ... 3. *E. chazaliei.*

Corolla evidently hairy outside or bearing minute stipitate glands.

  Herbage bearing abundant minute stipitate glands; corolla glanduliferous outside, not hairy.

    Corolla zygomorphic, limb oblique and bilabiate, filaments borne at unequal heights in the corolla-throat; stigmas very oblique, sterile tip of style inconspicuous, extremely short; nutlets with basal and horizontal attachment-scar. .... 4. *E. adenophorum.*

    Corolla regular, limb not oblique, filaments all arising at the same distance above the corolla-base; stigmas horizontal, surmounted by the evident, somewhat cylindric sterile tip of the style; nutlets with the attachment-scar distinctly lateral and vertical. .... 5. *E. collenettei.*

  Herbage not distinctly glanduliferous; corolla villulose or strigulose outside, not glanduliferous.

    Calyx-lobes conspicuously unequal in length, commonly with blue margins; corolla 8–12 mm. long, strongly zygomorphic with a conspicuously oblique limb; style 2.5–3.5 mm. long; stigmas distinctly oblique; North Africa, Sinai and Palestine. .... 6. *E. fruticosum.*

Calyx-lobes equal in length or practically so, without colored margins; corolla 3–6 mm. long, radially symmetric or only very moderately zygomorphic, limb not at all oblique or only very moderately so; stigmas horizontal or somewhat oblique only in No. 7.

Style 1–3.5 mm. long, terminated in a pair of subulate sterile tips 0.2–0.5 mm. long; calyx with lobes united at the base into a short tube; coast of Italian Somaliland. .... 7. *E. arenarium.*

Style 0.5–1.5 mm. long, abruptly contracted into a very short broad usually merely convex sterile tip barely surpassing the stigmas; calyx-lobes not united into a short tube.

Flowers borne along the leafy stems interspersed among developed leaves, the inflorescence hence interrupted, not distinctly racemose nor unilateral.

Leaves all opposite, only the bracts alternate and these usually opposing a flower; plant silvery strigose, and indument smooth and dense; corolla 5–6 mm. long, regular; eastern and southern Arabia. .... 8. *E. jugatum.*

Leaves mostly alternate, only the several lowermost pairs of leaves on the shoot opposite.

Plant generously strigose, whitish or gray; corolla 5.5–6 mm. long, zygomorphic, the 2 adaxial lobes prolonged, the limb somewhat oblique and the filaments affixed at unequal heights on the corolla; style 1.5–1.7 mm. long; nutlets obscurely roughened or nearly smooth; islands of the Persian Gulf. .... 9. *E. kotschyi.*

Plant with sparse appressed grayish hairs, greenish; corolla 3.5–4 mm. long, the limb regular and the filaments affixed at equal heights on the corolla; style 0.5–0.7 mm. long; nutlets prominently and densely verrucose; eastern British Somaliland. .... 10. *E. vatkei.*

Flowers borne in elongating unilateral racemose cymes; inflorescence terminating the leafy twig, bearing small bracts but not interrupted by well developed leaves.

Leaves lustrous, white, densely clad with abundant appressed snowy or silvery white hairs; northeastern Somaliland. 11. *E. albidum.*

Leaves greenish or cinereous, if distinctly pallid not clad in abundant lustrous white hairs.

Corolla distinctly prolonged on the adaxial side, the axial pair of lobes largest and the limb oblique.

Leaves small (1–6 mm. long, 0.5–1 mm. broad), becoming recurved; corolla small, 3–4 mm. long; southern Arabia. .... 12. *E. strigosum.*

Leaves larger (3–15 mm. long, 1–3 mm. broad), spreading or ascending.

Plant pallid, clothed with abundant appressed white or gray hairs; corolla 4.5–6 mm. long; southern Iran and Baluchistan. .... 13. *E. persicum.*

Plant greenish, clothed with fewer hairs and usually hispid; corolla 5–8 mm. long; southern Arabia and middle northern British Somaliland. .... 14. *E. arabicum.*

Corolla not prolonged on adaxial side or at most only very obscurely so; corolla limb not oblique and the lobes equal or nearly so.

Plant whitish, densely clad with pallid hairs; calyx at anthesis 2–2.5 mm. long, sessile or subsessile at maturity; style very short 0.5–0.8 mm. long; Sudan coast of Red Sea. .... 15. *E. nubicum.*

Plant grayish green, only moderately hairy; calyx at anthesis 2.5–3 mm. long, developing a stout strict pedicel 0.5–1.5 mm. long at maturity; style 1–1.4 mm. long.

Filaments arising from the corolla at unequal distances above the corolla-base; western Brit. Somaliland. .... 16. *E. verrucosum.*

Filaments within the corolla all arising at the same distance above the corolla-base; eastern and southern Arabia. .... 17. *E. thesigeri.*

1. **Echiochilon longiflorum** Benth. in Hook. Icones Pl. 13: 60, *t. 1277* (1879) — near Aden, *Wykeham Perry.*

Lobostemon somalensis Franchet, Sert. Somal. 44 (1882) — pays des Çomalis, *George Revoil 78.*
Leurocline somalensis (Franch.) S. Moore, Jour. Bot. **39**: 258 (1901).
Echiochilon somalense (Franch.) Johnston, Contr. Gray Herb. 73: 50 (1924).

Annual herb, erect with ascending branches, glaucous, 5–40 cm. tall; cotyledons persisting (sometimes even on the flowering plant), 6–10 mm. long, from a slender petiole 3–5 mm. long expanding into a blade 4–7 mm. wide, coarsely and conspicuously emarginate at apex, the terminal sinus 1-2 mm. deep and usually as broad, usually rounded at the base; leaves alternate or only the lowermost opposite, somewhat succulent, lanceolate, usually acute, 1–4 cm. long, 2–6 mm. broad, upper surface glabrous, lower surface bearing scattered coarse mineralized disks from which may arise short usually appressed hairs, midrib usually evident on lower surface; stems and branches terminating into elongate unilateral racemose cymes; cymes not at all scorpioid, erect, many-flowered; bracts numerous, foliaceous, gradually reduced in size upwards along the cyme; calyx with very unequal lobes, at anthesis 4–6 mm. long, borne on a pedicel 1–3 mm. long, smallest lobe adaxial, linear, 1.5–2 mm. long, 0.2–0.5 mm. wide, largest lobe abaxial 5–6 mm. long, 1–2 mm. broad; corolla lilac or pale blue, glabrous, texture not firm, 12–18 mm. long, densely white villose inside throat; limb of corolla very oblique ca. 10 mm. long, the adaxial lip prolonged, loosely recurving above the middle, its lobes 2–2.5 mm. long, the three abaxial lobes small, crowded to form the poorly developed weakly 3-lobed recurving abaxial lip of the corolla; corolla-tube 4.5–5.5 mm. long, broadest (ca. 1.3 mm. thick) 1–1.5 mm. above the base, at summit expanding into an evident funnelform oblique throat which is 2–3.5 mm. thick; stamens borne at base of throat just above the narrowest part of the tube, with filaments of unequal lengths and affixed at unequal heights above the corolla-base; anthers 0.8–1 mm. long; adaxial medial filament as much as 0.8 mm. long and borne 7 mm. above corolla-base; abaxial pair of stamens with filaments 0.2 mm. long and affixed 5.5 mm. above corolla-base; lateral stamens with filaments 0.7–0.8 mm. long and affixed 6 mm. above base of corolla; gynobase with a small horizontal base (1–1.3 mm. wide) from the center of which arises a slender 4-sided vertical upward prolongation ca. 2.5 mm. long and ca. 0.25 mm. thick, terminated by a style 4–5 mm. long; stigmas strongly oblique, highest on abaxial side, surmounted by 2 prominent sterile terminal lobes (0.1–0.2 mm. long) of the style; nutlets 2.3–3 mm. long, reddish to gray-brown, usually four developing, 1.8–2 mm. broad just above the base, verrucose or irregularly tuberculate, the base broad, deeply and conspicuously cordate, the apex coarsely rostrate, venter evidently sulcate, the groove extending down from near the nutlet-tip almost to the nutlet-base, lateral and vertical, above the base very widely forked and oblique on the basal lobes of the nutlet.

ADEN: Aden, received Aug. 1900, *Dr. T. Cooke*, (K); "Aden or Perim," *J. V. Lester-Garland* (K); Aden, Feb. 19, 1900, *W. S. Birdwood* (K); Aden, 1884, *H. R. Beevor 103* (K); Aden, only one specimen found, ca. 1 ft. tall, corolla light blue, stems and branches smooth, March 1878, *W. Wykeham Perry 9* (Type of *E. longiflorum*, Kew).

SOMALILAND: Wardere Well, 6–10 in. tall, fl. lilac, Nov. 23, 1944, "Kabaageye," *Glover & Gilliland 302* (K); Dubriat Mt., lat. 10°22'N., long. 45°10'E., throat and tube of corolla bright pale blue, limb pale lilac, bed of torrent, limestone, 700 ft. alt., Jan. 3, 1933, *J. B. Gillett 4787* (K); Djibouti, 1895, *Dr. Jousseaume* (P); pays des Çomalis, *Geo. Revoil 78* (Type of *L. somalensis*, Paris).

Distinguished from all other members of the genus both by its annual habit and its cordate nutlets. The nutlets of *E. longiflorum* constitute one of the bizarre extreme variants of the boraginaceous fruit. As to their cordate body, they have a parallel only in the fruit of the unrelated *Arnebia tetrastigma* Forsk. The closest relation of our species, however, appears to be with *E. lithospermoides*. Interestingly, in that species the base of the nutlets may be obscurely depressed and hence is suggestive of an incipient state of a type of variation that could be elaborated to form a deep basal sinus such as is present on the nutlets of *E. longiflorum*. I have seen both the type of *E. longiflorum* and of *Lobostemon somalensis*. They are representative of the same species without doubt. The plant is a desert annual which is not only rare but also one that has been encountered only in very limited quantity.

2. **Echiochilon lithospermoides** (S. Moore) Johnston, Contr. Gray Herb. **73**: 50 (1924).

Leurocline lithospermoides S. Moore, Jour. Bot. **39**: 257, *t. 424, f. 1* (1901) — Brit. East Africa: Leikipia, June 1893, *J. W. Gregory*; Gof at 3800 ft. and between Lé and Tocha, 1898, *Lord Delamere*.

Lobostemon lithospermoides (S. Moore) Baker, Fl. Trop. Africa **4**^{2}: 60 (1905).

Plant suffrutescent, perennial, 1–4 dm. tall, freely and ascendingly branched; stems 1–10 dm. long, becoming shrubby and decumbent in age; herbage glaucous; leaves lanceolate, 1–3 cm. long, 2–5 mm. wide, broadest above the sessile base and gradually narrowed to the sharply acute or acuminate apex, upper surface usually glabrous, lower surface with mineralized pustules or short stout spreading hairs arising from bulbose bases, usually more or less evidently costate, margin usually coarsely hispid-ciliate; inflorescence an erect unilateral racemose cyme, elongating in age, 1–3 dm. long, 10–50-flowered, terminating the stem and branches, bracts numerous, evident, foliose, lowermost similar to the uppermost leaves, very gradually reduced upward along the cyme; calyx subsessile or in age with strict pedicel 1–2 mm. long, with very unequal lobes; lobes distinct, hispid-ciliate, largest lobe abaxial, lanceolate, attenuate, ca. 8 mm. long and ca. 1.3 mm. broad above the base, becoming twice as large and costate at maturity; smallest lobe adaxial, ca. 4 mm. long and 0.4–0.5 mm. broad, twice as large at maturity; inner surface of calyx lobes glabrous, outer surface pustulate or bearing some stout hairs arising from bulbose bases; corolla reddish purple, 12–15 mm. long, strongly zygomorphic, glabrous outside, below the middle tubular and above the middle expanding into an extremely oblique funnelform throat and limb; corolla-tube usually ca. 2 mm. in diameter at the very base, constricted (to 1.3–1.5 mm. thick) 4.5–6 mm. above the base and then expanding into the throat; limb 7–9 mm. in diameter; corolla-lobes rounded, the two adaxial lobes vertical, erect, 2.5 mm. broad, the three other lobes less well developed, the single anterior lobe horizontal; inside of corolla densely villulose in a zone usually extending from 4 to 6.5 mm. above the corolla base, hairs 0.2–0.3 mm. long, white or slightly yellowish; inside of corolla-throat bearing only scattered hairs which may be 0.3–0.4 mm. long, base of tube without annulus and glabrous; anthers 1–1.3 mm. long, elongate, slightly arcuate, emarginate at base, borne at unequal heights just above the narrowest part of the corolla at the base of the throat; adaxial anther borne on a filament 0.6–0.7 mm. long arising ca. 6.5 mm. above the corolla-base; adaxial lateral pair of anthers borne on filaments 0.3–0.4 mm. long arising ca. 5.5 mm. above corolla-base; abaxial pairs of anthers borne on filaments 0.2–0.3 mm. long arising only 5 mm. above corolla-base; gynobase at maturity 1.5–2 mm. tall, pyramidal, 1–1.3 mm. broad at base, sides usually excavated; style 3–4 mm. long at anthesis, stigmas oblique, surmounted by 2 laterally compressed sterile tips of the style which are usually most prominent on the high abaxial side of the stigma; nutlets 1–4 developing, 2–2.4 mm. long and nearly as broad, plump, reddish, back usually tuberculate and more or less tumulose, venter angulate, bearing a triangular areole (ca. 1 mm.

wide) which contracts into a linear or (more commonly) attenuate sulcus that extends upward almost to the nutlet-apex; areola ventral, usually with prominent scar-tissue, more or less oblique.

KENYA: Banaisa, North Frontier dist., fl. red, June 27, 1951, *Kirrika 92* (G, K); Rumuruti, K. 3, *Coryndon 6865* (K); Rumuruti, northeast slope of Aberdares, 7000 ft. alt., fl. pink or red, *W. J. Dowson 551, 554* (K); Rumuruti, common locally, grassland with scattered trees, Aug. 12, 1952, *Bogdan 3519* (K); 50 miles southeast of Nairobe, dry soil in shade, fl. "aster purple," leaves "bice green," 5000–7000 ft. alt., July 13, 1923, *A. G. Curtis 757* (G); Mile 20, between Laitokitak and Kijiado, N. Kilimanjaro, tufted grassland, shallow red soil above limestone, plant tufted, about 2 ft. tall and 2 ft. in diameter, Sept. 1952, *P. R. O. Bally 8323* (K, Fl).
ETHIOPIA (Boran): Road between Moyale and Mega, 30°44′N, 38°50′E, open scrub in red sandy loam, spreading shrublet 40 cm. tall, corolla reddish purple fading to blue-purple, 4200 ft. alt., Nov. 10, 1952, *J. B. Gillett 14191* (G, K); in deserto Banas, July 14, 1893, *Ruspoli & Riva 1634 (882)* (Fl); between Mega and Malca Guba, April 26, 1939, *R. Corradi 6206* (Fl); Mega, April and Sept. 1939, *R. Corradi 6389, 6399, 6401* (Fl); Javello diclivi de Quota Littorio, fl. atropurpurei, April 18, 1937, *G. Cufodontis 479* (Fl); Foresta de Neghelli, Aug. 23, 1937, *A. Vàtova 231* (Fl); Foresta di Neghelli, Sept. 27, 1939, *R. Corradi 8237* (Fl); Neghelli, Sept. 10–29, 1939, *R. Corradi 6230, 6284* (Fl).

A plant of desert grasslands which ranges from southern Ethiopia south through northern and eastern Kenya. It is known from a few stations south of the equator and accordingly is the most southerly ranging member of its genus. The species is readily recognizable and very distinct. It appears to have close relations only with *E. chazaliei* and *E. longiflorum*. In having relatively large, plump, dark reddish nutlets and sharply acute or acuminate, usually costate, leaves, bracts, and calyx-lobes, it is distinguishable from all other members of the genus.

3. **Echiochilon chazaliei** (Boiss.) Johnston, Contr. Gray Herb. 73: 50 (1924).

Lithospermum chazaliei Boiss. Jour. de Bot. **10:** 220 (1896) — Cape Blanc, May 1895, *M. de Dalmas.*
Leurocline chazaliei (Boiss.) Bonnet, Bull. Soc. Bot. France **58:** 38 (1911).
Leurocline mauritanica Bonnet, Bull. Mus. Hist. Nat. Paris **14:** 403 (1908) — near Port Etienne, 1908, *R. Chudeau.*
Echiochilopsis coerulea A. Caballero, Trab. Mus. Nac. Cien. Nat. Madrid, Bot. **30:** 10, *t. 2* (1935) — inter ora fl. *Tazarut* et promintorio *Non* dictis, July 11, 1934, et ad oram fl. *Assaka* dicto, July 13, 1934, *Caballero.*

Plant fruticose, perennial; stems 5–35 cm. long, erect or ascending or decumbent, loosely and dichotomously branched, 1–5 mm. thick, sparsely strigose or nearly glabrous, in age albescent and eventually decorticating; leaves mostly alternate, only the lowest ones on the shoot opposite, oblanceolate or oblance-obovate, fleshy, glaucous, bearing scattered coarse short appressed hairs arising from discoid bases, 4–18 mm. long, 2–5 mm. broad, apex rounded, base cuneate, without evident midrib or nerves; cymes 3–8 -flowered, leafy bracted, erect, terminating the leafy branches; calyx 5-parted, 6–8 mm. long at anthesis, becoming 8–15 mm. long at maturity; calyx-lobes extremely unequal, oblong or oblanceolate, not costate, bearing scattered appressed hairs with discoid bases, tip rounded; smallest calyx lobe adaxial, 2–4 mm. long, ca. 0.5 mm. broad, largest lobes abaxial 7–13 mm. long, 1–2.5 mm. broad; pedicel stout, 1–4 mm. long; corolla violaceous or mauve, outside glabrous, 11–21 mm. long, limb very strongly oblique, 10–20 mm. long, margin frequently crisped, two rear corolla-lobes erect 3–5 mm. long and 2.5–5.5 mm. broad, forward middle lobe 2.5–5.5 mm. long and 2.5–5 mm. broad, throat oblique, narrowly funnelform, corolla-tube 6–8 mm. long 2.5–3 mm. thick, inside densely hairy above the middle, hairs in the tube and throat white; anthers 1.2–1.5 mm. long; filament of medial adaxial stamen 1.4 mm. long, affixed 6–8 mm. above corolla-base, filaments of dorsal lateral stamens 0.8–1 mm. long, affixed 5–6 mm. above corolla-base, filament of forward lateral stamens 0.8–1 mm. long affixed 4–4.5 mm. above base of corolla; gynobase very narrowly pyramidal, 3–3.5 mm. long, ca. 1 mm. thick at base; style 3–5 mm. long, sterile apex domed, high convex with a central depression, not oblique, surrounded at the base by the horizontal stigmatic band; nutlets 1–4 maturing, gray, erect, acute, 3–4 mm. long, 2–2.5 mm. broad, dorsum convex sparsely tuberculate or tumulose or somewhat lobulate-tuberculate, especially above the middle, venter obtuse, for most of its length bearing a lineate groove, attachment-areole basal, very broadly flabelliform, horizontal or oblique, its ventral angle prolonged to form a lineate sulcus which extends upward nearly to the nutlet-apex.

Spanish Sahara: Aguerguer, north of Cape Blanc, Jan. 22, 1937, *Murat 1907* (G); between mouth of Rio Tazarut and Cabo Non, July 11, 1934, *Caballero* (G, Isotype of *E. coerulea*). Morocco: falaises du littoral de l'Ocean a l'embouchure de l'Oued Aourioura, lat. 28°50'N, March 31, 1937, *Maire* (G).

Known only from northwestern Africa were it occurs on dunes along the coast, between lat. 20° and 30°N, in Ifni, in extreme southwestern Morocco, in Spanish Sahara and in that part of Mauritania near Port Etienne. It is the most westerly ranging member of its genus. The species is a very distinct one. The closest relation is *E. lithospermoides* of east Africa. Unlike other congeners having a strongly zygomorphic corolla with an oblique limb, *E. chazaliei* has horizontal rather than oblique stigmas. The nutlets of our species are roughened principally on the back above the middle with tuberculations and papillae of unusual form. These latter are strict and have a decurrent base. A new description and illustration of the plant has been recently published by Sauvage & Vindt, Fl. du Maroc 2: 116, *f. 2460* (1954). It is to be noted that the species is named not for its collector but for the yacht *Chazalie,* owned by the collector, the Count de Dalmas.

4. **Echiochilon adenophorum,** sp. nov.

Planta fruticosa 1–3 dm. alta laxe ramosa; ramis vetustioribus cortice alba decorticanti donatis; ramulis hornotinis foliosis 4–6 cm. longis 1–2 mm. crassis; internodiis 1–5 mm. longis; foliis ascendentibus alternatis (vel solum imam ad basim ramuli oppositis) glandulas minutas stipitatas abundantis proferentibus lineari-oblanceolatis laxe valdeque involutis ergo saepe plus minusve teretibus 10–25 mm. longis 1–2 mm. crassis, facie interiore glabris, facie exteriore glanduliferis sparse hispidulis (pilis rigidis 0.5–0.8 mm. longis ascendentibus vel appressis basibus discoideis praeditis); inflorescentia racemosa 5–15-flora 3–5 cm. longa; floribus congestis biseriatis bracteatis; calyce subanthesi 4 mm. longo, maturitate accrescenti 5–6 mm. longo, lobis acutis valde inaequalibus, maturitate margine incrassato et costa plus minusve incrassata donatis; pedicello 1–2 mm. longo; corolla alba elongata 10–13 mm. longa extus sparse glandulifera, tubo 5–6 mm. longo a basi imo 1–1.5 mm. crasso sursum ampliato, 1–1.5 mm. supra basim crassissime (1.7–2 mm.) deinde sursum gradatim contracto, summum ad apicem 1 mm. crasso; faucibus infundibuliformibus 4–5 mm. longis margine superiore satis obliquis 3.5–4 mm. diametro, intus pilis albis vestitis; lobis inaequalibus integris rotundis, duobus adaxialibus erectis 1.8 mm. longis late ovatis, tribus anterioribus patentibus 1 mm. longis 1.5–1.8 mm. latis; antheris ca. 1.8 mm. longis inclusis; filamentis 0.1–0.2 mm. longis aequilongis; filamento postico ca. 6.5 mm. supra basim corollae affixo; filamento duobus anticis ca. 5.5 mm. supra basim corollae affixis; filamentis duobus lateralibus intermediis 6 mm. supra basim affixis; gynobasi 1.5–1.7 mm. alto a basi 1 mm. lato sursum abrupte attenuato; stylo 4–5 mm. longo supra stigmata valde obliqua apicibus sterilibus inconspicuis latis sed perbrevibus donato; nuculis saepe solum 1–2 maturantibus erectis vel parce incurvatis ca. 2 mm. longis et 1.4 mm. latis pallide rubescentibus vetustioribus plus minusve cinereis, supra medium crasse rostratis, infra medium satis compressis, dorse supra medium evidenter tuberculatis et tumulosis, infra medium conspicue laevioribus inconspicue tuberculatis et tumulosis subplanis; ventre nuculae late obtuso sulcum lineatum angustum medio-longitudinalem haud crassi-marginatum proferenti; cicatrice nuculae basali fere horizontali 1 mm. lata.

British Somaliland: rocky slopes of Goldither at 400 ft., behind Karin near Berbera, Berbera District, limestone, woody herb up to 1 ft., "sintar," April 24, 1945, *P. E. Glover & H. B. Gilliland 1181* (Type, Brit. Mus.; Isotype, Kew).

A very distinct species which is notable for its elongate, very strongly involute leaves, its glanduliferous herbage and its elongate, moderately but distinctly zygomorphic corollas. Along with *E. collenettei*, the species seems transitional between the group of species with very strongly zygomorphic, extremely oblique, usually elongate corollas and that with short, inconspicuously oblique, or more or less perfectly symmetric, relatively short corollas. In *E. adenophorum* the summit of the throat is less than 1 mm. longer on the adaxial side than on its forward side. The throat, accordingly, is very much less oblique than in the corollas of such species as *E. longiflorum*, *E. lithospermoides*, *E. chazaliei* and *E. fruticosum*. Externally the zygomorphy in our plant is manifest most by the dorsal swelling of the throat and in the enlargement of the two adaxial lobes.

Though certainly very distinct, *E. adenophorum* appears to be most closely related to *E. collenettei*. It differs from the latter species in having strongly involute leaves which are usually terete and have the upper leaf-surface completely hidden by the inrolled margins of the leaves. The corolla of *E. adenophorum* also differs in being glanduliferous but not hairy outside and in being distinctly zygomorphic with the limb oblique, the corolla lobes unequal and the stamens affixed at unequal heights in the throat. The style also differs in having very poorly developed sterile tips surmounting the very strongly oblique stigmas. The nutlets differ also in being basifixed.

According to the label, the plant is said to come from "Karin near Berbera." Perhaps Karin or Karrin on the coast 100 km. east of Berbera is intended, being designated as "near Berbera" to distinguish it from Karin or Carin, a well-known locality just east of the eastern boundary of British Somaliland, which is located nearly 500 km. east of Berbera.

5. **Echiochilon collenettei**, sp. nov.

Planta frutescens ascendenter ramosa 25 cm. alta; ramis annotinis albis vetustioribus decorticatis; ramulis hornotinis 0.5–1.5 mm. crassis foliis congestis ascendentibus vestitis; foliis alternis crassiusculis 5–10 mm. longis 0.8–1.2 mm. latis oblanceolatis haud costatis subplanis vel satis conduplicatis utrinque glandulas stipitatas abundantis gerentibus, subtus basim versus cuticula calcarea alba donatis alibi pilos rigidos e basi discoideo erumpentis 0.5–0.9 mm. longos haud abundantis ascendentis vel appressos gerentibus; inflorescentia pauciflora, floribus 1–5 apicem versus ramulorum inter folia gestis; calyce sub anthesi 4.5 mm. longo mox 6 mm. longo, lobis subaequalibus 1–1.5 mm. latis glanduliferis pilos paucos e basi discoideo erumpentis proferentibus vetuste costatis; corolla alba elongata sub hypocrateriformi 13–15 mm. longa radialiter symmetrica, tubo 5–6 mm. longo extus glandulifero intus fere ad basim minutissime villuloso, faucibus infundibuliformibus 5–6 mm. longis ca. 3 mm. crassis intus flavo-villosis, limbo horizontaliter patenti haud obliquo, lobis subhomomorphis triangulari-ovatis 2–3 mm. longis utrinque albo-villulosis margine crispatis; antheris 1.2–1.4 mm. longis; filamentis aequalibus 0.1–0.2 mm. longis 7.5–8 mm. supra basim corollae affixis; gynobasi pyramidali 1.1–1.5 mm. alta basi 1.1–1.3 mm. lato; stylo 3.5–4.5 mm. longo supra stigmata horizontalia apicem sterilem breviter cylindraceum truncatum vel plus minusve bilobatum 0.1–0.2 mm. longum 0.1–0.15 mm. crassum gerente, nuculis verrucosis 2 mm. longis 1.5 mm. latis dorse convexis ventre obtusis carinatis, cicatrice laterali verticali triangulari ca. 0.6 mm. lata prominenti sursum in sulcum crasse marginatum attenuatum abrupte producta.

ITALIAN SOMALILAND: Karin, lat. 10°57′N., long. 49°24′E., stony ground in dry stream bed, 900 ft. alt., plant 9 in. tall, fl. white, scarce, Oct. 29, 1929, *C. N. Collenette 196* (Type, Kew).

This very well-marked species is known only from a single collection originating in northernmost Italian Somaliland just east of the British Somaliland boundary, cf. Collenette, Kew Bull. **1931**: 403, 410 (1931). Unhappily, only a single corolla has been available for dissection. The stamens are borne on filaments of equal length which are all affixed at the same distance above the corolla-base. The corolla is regular or practically so, at most having the lobes differing very slightly in size. The relationships of the plant are probably closest with the very distinct *E. adenophorum* of northern middle British Somaliland. Both species have glanduliferous herbage and an elongate, somewhat trumpet-shaped corolla. Our plant differs, however, in having regular, non-zygomorphic corollas, as well as stouter, more plump nutlets, a lateral rather than basal nutlet-attachment, nearly equal calyx-lobes, smaller, nearly flat leaves, etc. The nutlets are very similar to those of *E. verrucosum.*

6. **Echiochilon fruticosum** Desf. Fl. Atlant. **1**: 167, *t. 47* (1798) — habitat prope Kerwan in regno Tunetano.

Echiochilon fruticosum var. *marginatum* F. Buxb. Verhandl. Zoo.-Bot. Ges. Wien **76**: 61 (1927) — Aïn Ghrasesia, Tunisia, 1913, *Janchen & Vierhapper.*

Plant fruticose, pale; stems slender, decumbent, loosely branched, leafy branchlets 1–2 mm. thick, bearing appressed hairs ca. 0.5 mm. long; leaves all cauline, numerous, lanceolate, small, 2–10 mm. long and 0.5–2 mm. broad, acute, lacking evident midrib or veins, bearing appressed hairs on both surfaces; lowermost leaves opposite; cymes racemose, slender, erect, not at all scorpioid, 5–15 cm. long; bracts numerous, foliaceous, frequently with blue margins; calyx 4.5–5 mm. long, subsessile; calyx-lobes very unequal, lanceolate, frequently with blue margins, shortest lobe adaxial, 2–3.5 mm. long and 0.5 mm. wide, largest lobe 3.5–4.5 mm. long and 1 mm. wide; corolla blue, strongly zygomorphic, 8–12 mm. long, conspicuously hairy outside; limb very oblique, 8–10 mm. long and 4–6 mm. broad, with a spreading crisped margin 1–2 mm. wide, upper adaxial end of limb evidently 2-lobed (lobes erect 1.5–2.5 mm. long and broad) but less evidently lobed on the lower abaxial lip; tube and throat together 4.5–6 mm. long, 0.8–1 mm. thick at base, ampliate upwards and becoming 1.5–1.8 mm. thick (1–1.5 mm. above base of tube) and then constricted to 0.9–1.3 mm. thick (at 2.5–3 mm. above base) and finally swelling to 2.3 mm. (at 4–4.5 mm. above the base) at the level of the base of the forward corolla-lip; inside of corolla with an abundance of white or gray hairs just above the constriction of the corolla-tube, sparingly hairy in the throat and on the limb; anthers 1–1.2 mm. long; adaxial filament longest and borne highest in the throat, 0.4–0.6 mm. long, affixed 4.5 mm. above corolla-base; adaxial lateral pair of filaments borne 0.3–0.5 mm. below upper filament, 0.1–0.3

mm. long; forward pair of filaments borne 3.5–4 mm. above corolla-base, 0.1 mm. long; gynobase ca. 1 mm. tall, pyramidal below the middle and attenuate above the middle, terminated by a style 2.5–3.5 mm. long; style shortly bilobed at the apex, each lobe bearing a subterminal stigma; stigmas somewhat oblique, most prolonged on abaxial side, at anthesis closely juxtaposed and apparently united, in age the short lobes of the style tending to spread and the stigmas to separate, sterile tips of the style-lobes broad convex, scarcely surpassing the stigma; nutlets cinereous or pinkish and frequently somewhat mottled with brown, somewhat verrucose or tumulose, 1.6 mm. long, 1.2 mm. broad, bent near the middle with the beaked upper half erect and paralleling the ventral keel and the broad rounded lower half horizontal and diverging from the ventral keel at an angle of about 90°, ventral edge of nutlet angulate, nearly straight and vertical, dorsal side of nutlet saddle-like, base of nutlet strongly constricted and substipitate bearing an oblique open more or less triangular areola ca. 0.5 mm. broad, areola apically constricted and prolonged as a narrow groove to about the middle of the prominent ventral keel.

Ranging in the deserts from eastern Morocco eastward into Egypt.

ALGERIA: Beni-Mora à Biskra, *C. Schmitt 165* (G); environs d'Aïn-Sefra-Oranais, May 30, 1934, *Faure* (G). TUNISIA: Zarzis, May 1884, *Letourneux* (G); Oued Chaffar entre Ifax et Gafsa, 1904, *Romieux 122* (G); Gabes (Kauzeria), in desertis, *Petard 197* (G). TRIPOLITANIA: Souk-el-Djemâa, 1939, *Maire & Weiller 1054* (G); Tripoli in sand near Tadjura, *Bornmüller 824* (G); ad Sabratha, *Bornmüller 823* (G); Tripoli near Gargaresik, *Bornmüller 922* and *8246* (G). EGYPT: near Alexandria, Ramleh, *H. A. Hurst* (K).

6a. **Echiochilon fruticosum** var. **sieberi**, nom. nov.

Lithospermum divaricatum Sieber ex. Spreng. Syst. **1**: 543 (1825) — Ascalona, Palestine, *Sieber*.

Nutlets lance-ovoid, about twice as long as broad, 2–2.2 mm. long, 1–1.3 mm. thick, broadest above the rounded base and gradually narrowed towards the apex, back not saddle-like, venter angulate, nearly straight, vertical, bearing an ovate-lanceolate areola ca. 0.5 mm. broad on the ventral side of the rounded base, the apex of the areola gradually narrowing and prolonged upward along the ventral angle to above the middle of the nutlet.

Known only from Sinai, Palestine and Lebanon, on sands near the coast.

LEBANON: Jaffa, sables maritimes, Nov. 1832, *Bové 224* (K), *428* (G, K); ISRAEL: Khan-Yunis, March 12, 1926, *S. Fishelsohn 350* (K); Ascalona, in collibus arenosis, *Sieber s.n.* (Isotype, G, K); in planitie Philistaea at Chan-Junis (ad fines Aegypt.), May 27, 1897, *Bornmüller 1171* (G, K). EGYPT: Sinai Desert, May 1916, *M. F. White* (K).

The oldest and best known species of the genus. It has been collected repeatedly in the deserts of North Africa, in all the states from Morocco to Egypt. For a widely distributed plant it is surprisingly constant. The most conspicuous variation concerns the coloration of the calyx-lobes and the bracts of the inflorescence. These may be entirely green but usually tend to have a blue margin and because of their coloration can become very conspicuous. A form in which the blue calyx-lobes and bracts are margined with carmine red, thus giving the inflorescence a distinct reddish tonality, has been described from Tunis as the var. *marginata*.

The most important variation detected within *E. fruticosum* involves the shape of the nutlets. In plants ranging from Sinai northward along the Palestine coast, the var. *sieberi*, the nutlets are always lance-ovoid. The African plants, typical *E. fruticosum*, have bent nutlets. The longitudinal axis of the nutlet is not straight and vertical as in the nutlet of the Palestinian var. *sieberi*. It is medially bent 90° with the upper half vertical and the lower half horizontal and directed away from the axis of the fruit. In lateral outline the nutlets of typical *fruticosum* are sway-backed. The dorsal edge is not straight above the rounded base as in var. *sieberi* but incurving, sagging inward near the middle and suggesting a saddle in silhouette. In various genera of the family the nutlets have the body bent ventrally, towards the floral axis, cf. Jour. Arnold Arb. **35**: 161 (1954), but dorsal bending, away from the axis, is rare and generally weak. The strong dorsally bent nutlets of *E. fruticosum* are perhaps unique in the family.

A careful description of the minor details of corolla structure is needed and should be prepared by someone with access to fresh material. On some corollas, below the middle of the large upper lip, I have observed a light-colored area upon which sand is usually found adhering. The area seems to bear numerous minute stipitate glands.

7. **Echiochilon arenarium** (Vatke), comb. nov.

Heliotropium arenarium Vatke, Linnaea **43**: 319 (1882) — Type from Brava, Ital. Somaliland, *Hildebrandt 1314*. Not *H. arenarium* F. v.M. (1867–68).
Sericostoma arenarium (Vatke) Johnston, Contr. Gray Herb. **92**: 92 (1930).

Plant fruticose with numerous very leafy much-branched prostrate or widely spreading stems 5–25 cm. long; foliage and new growth somewhat succulent, bearing loosely to closely appressed, uncrowded hairs 0.3–0.9 mm. long which usually arise from mineralized discoid bases; leafy branches 1–10 cm. long, internodes 1–10 mm. long; leaves numerous, oblanceolate, 2–20 mm. long, thickish, more or less conduplicate and having involute margins, upper surface concave or frequently hidden by the infolded margins, lower surface convex, not costate, apex obtuse or rounded; inflorescence multiflorous, terminating the leafy branchlets, usually a short dense unilateral and biseriate racemose cyme, commonly 1–2 cm. long but sometimes short and glomerate; calyx at anthesis 2–3 mm. long, subsessile or with a stout pedicel 0.5 mm. long, lobes about equally long or moderately unequal, thick, united towards the base, bearing loosely appressed hairs arising from thickened bases, not costate, abaxial lobe usually tending to be broadest and even the longest; calyx in fruit 3–5 mm.

long, lobes usually thick; corolla apparently white, funnelform, 3–6 mm. long (usually 3–4 mm. long and only shortly surpassing the calyx), subcylindric below the middle, outer surface glabrous or sparsely hairy only on the lobes, limb 1.5–3(–4.5) mm. broad; lobes ascending, equal or nearly so; throat inside bearing abundant white hairs; anthers 0.5–1 mm. long, usually included; filaments very short, equal, affixed at equal distances above the base of the corolla; gynobase pyramidal; style 1–3.2 mm. long, terminated by a pair of sterile attenuate lobes, lobes erect juxtaposed parallel slightly unequal in length, 0.2–0.5 mm. long; stigmas 2, forming the discrete halves of a pale, swollen, sometimes oblique, vescicular ring borne about the base of the bilobed sterile tip of the style; nutlets 1.2–2 mm. long, 1.0–1.7 mm. broad, thick, ovate in dorsal outline, obscurely tuberculate, back convex, venter obtusely angled, areole evident, obliquely basal, triangular or transversely elongate, abruptly contracted into a narrow lateral groove which is prolonged upward to above the middle of the nutlet.

Coastal dunes along middle and southern Italian Somaliland.

ITALIAN SOMALILAND: sand hills near Brava, March 1874, *Hildebrandt 1314* (frag. of Type, G; Isotype, BM); Mogadiscio, dune stabile, Aug. 8–9, 1929, *L. Senni 575*, *596* (Fl); dintorni di Mogadiscio, *Ciferri 66* (Florence); spiaggia di Mogadiscio, May 17, 1913, *G. Paoli 5*, *10* (Fl); Mogadiscio, nelle vicinanze del campo avicezione, April 9, 1939, *R. Corradi 6335* (Fl); littorale di Ras Mallen, 1890, *R. Bricchetti 512* (Fl); duna tra Magangib e Obbia, April 18–19, 1924, *Puccioni & Stefanini 369*, *382* (Fl).

A very distinct species with salient characters in the prolonged sterile tip of its style, the short tube of the calyx, the white faucal hairs in the corolla and the short not abundantly flowered inflorescences. The plant is a small shrub with succulent herbage. It frequents dunes along the coast of Italian Somaliland. The prolonged sterile bilobed tip of its style is of some interest, since the sterile tip and the stigma together form an aggregate which is very suggestive of the stigmatic head in *Heliotropium*. Indeed, because of this similarity the species was originally proposed as a species of *Heliotropium* and some recent authors have been content to continue to treat it so. A comparison of the style of *E. arenarium* with that of other species of the genus makes it very clear that these are all similar in structure and organization. In the present species the sterile tips of the style are simply more generously developed and more prolonged than in other congeners. The similarity to the stigmatic head in *Heliotropium* is superficial. The closest homologies, outside *Echiochilon*, are to be found not in *Heliotropium* but rather in *Buglossoides* and *Lithospermum*, cf. Jour. Arnold Arb. **35**: 161 (1954).

I have found abnormal flowers frequently developed on the herbarium specimens available to me. These flowers have corollas 6–9 mm. long. The tube, 4–6 mm. long and 1–1.5 mm. thick, is gradually narrowed upwards and then abruptly expanded into a campanulate or even hemispheric throat, 2.5–4 mm. long and 3–4 mm. thick. The corolla lobes are thick, erect, rounded and 1.5–2 mm. long. The tissue of the tube and throat is heavily mineralized. Examination shows that such corollas are, or have been, inhabited by a hymenopterous (?chalcid) larva and are gall-like hypertrophies. They are especially well developed on ***Hildebrandt 1314***, the original collection of the species. Monstrous flowers of similar nature have been observed in only one other species of *Echiochilon*, in *E. strigosum*, and then only in very limited numbers.

8. **Echiochilon jugatum**, sp. nov.

Herba perennis pilis abundantibus rectis valde appressis 0.2–0.5 mm. longis pallidis indumentum levum argentaceum formantibus vestita; caulibus numerosis decumbentibus ascendenter ramosis 1–5 dm. longis 1–2.5 mm. crassis, internodiis 2–5 (–10) mm. longis; foliis numerosis omnino oppositis decussatis ascendentibus vel supra medium plus minusve recurvatis carnosis concavo-convexis 1.5–6 mm. longis utrinque dense strigosis nullo modo costatis, basi 1.5–3 mm. latis anguste 0.5–1.5 mm. lateque connatis; floribus oppositifoliis vel rariter axillaribus dissitis paucis apicem versus caulis ramorumque inter paria foliorum oppositorum gestis; calyce sessili sub anthesi 3.5–4.5 mm. longo, fructiferi ad 5 mm. longo, lobis saepe subaequilongis lanceolatis; corolla 5–6 mm. longa; limbo haud obliquo 5.5–7 mm. diametro; tubo (faucibus subcylindraceis incluso) 3–4 mm. longo, intus basim versus inconspicue minutissimeque pubescenti; lobis patentibus aequalibus obtusis 2 mm. longis basim versus 2.5 mm. latis in faciebus utrinque albo-villulosis margine erosis; faucibus intus flavo-villosis; antheris exsertis 1.3–1.9 mm. longis; filamentis 0.8–1 mm. longis, omnibus ca. 3 mm. supra basim tubi orientibus; gynobasi pyramidali 2–2.5 mm. longa basim versus ad 1.5 mm. lata; stylo 1.5 mm. longo apicem sterilem inconspicuum latum convexum stigmata horizontalia vix superantem proferente; nuculis ca. 3 mm. longis, 2 mm. latis, sublaevibus vel sparse verrucosis, cinereis vel rosaceis; cicatrice laterali verticali basi ad 1.5 mm. lata supra basim sursum abrupte deinde gradatim contracta.

Eastern Arabia, near the coast, from Bahrain Island south to Dhofar.

ARABIA: Bahrain Island, sandy desert at northwest end of pipeline, March 11, 1950, *Ronald Good 224* (BM, K); Dubai, Trucial Oman, sand on limestone near sea level, plant 11–18 inches tall, leaves gray green, fl. pale yellow, March 22, 1937, *Mrs. F. Holmes 351* (BM, K); Near Ras al Hadd, Gulf of Oman, sand dunes, Nov. 5, 1933, *H. Carry Gilson K 10* (K); near Jazir, Wadi Ghudun, long. 56°45′E, "Halmit," Feb. 9, 1947, *W. Thesiger* (BM); Wadi Shibun, long. 56°00′E, "Halmit," Feb. 11, 1947, *W. Thesiger* (BM); Dhofar Mountains, Marbat, coast, 1895, *Mrs. J. T. Bent 21* (Type, Kew); Red Sea, *Dr. Nimmo* (K).

The opposite leaves in *Echiochilon jugatum* are narrowly connate and accordingly arise from a short tight vaginate base. The flowers, usually borne opposite foliaceous bracts, occur along the terminal portion of the stems and branches and are usually separated by one to several pairs of leaves. There is no crowding of the flowers to form a differentiated racemose inflorescence. In other species of *Echiochilon* only the lowest leaves on the stem and branches are opposite, most of the leaves being alternate. In *E. jugatum* all the leaves are opposite. As to general facies I find the present species more suggestive of a member of the Caryophyllaceae or Chenopodiaceae than of the Boraginaceae. Among the members of *Echiochilon* the species most closely approaches *E. kotschyi* in habit as well as in other characters.

The collection from the "Red Sea" by Dr. Nimmo, cited above, is one of a number with such data contained in the Hooker Herbarium at Kew. J. B. Balfour, Bot. Socotra pg. xvi (1888), believes that some of these actually originated on Socotra. Indeed on most of Dr. Nimmo's collections from the "Red Sea," a definite locality "Socotra" has been added in pencil by some person unknown. I do not believe that Nimmo's material of *E. jugatum* came from either the Red Sea or the island of Socotra. The plant is definitely known only from Bahrain Island and from other localities in southeastern Arabia not far from the coast in Trucial Oman and in Oman. Nimmo also has a collection of *E. thesigeri*, a species that has been found in this same section of Arabia. Of special interest is a collection of *Cynoglossum* at the British Museum from Jabal Qara, Dhofar (*D. Vesey Fitzgerald 12448–4*) which without doubt is conspecific with a collection of Nimmo (from "Red Sea") in the Kew Herbarium. Although at first I believed an undescribed species was involved, much to my surprise I find that the Arabian plant is indistinguishable from *Cynoglossum coelestinum* Lindl. of the mountains of Bombay State, India. For the matter at hand the important fact is that this very distinct *Cynoglossum*, long ago found by Nimmo, has recently been localized in Arabia where it appears to be native. The locality in the mountains overlooking the Dhofar Coast is in the same general area as that in which Bent collected *E. jugatum*. From what is known of the distribution of *E. thesigeri*, that species can be expected eventually to be found also within this same general area. It is quite possible that Dr. Nimmo collected all three of the Boraginaceae mentioned during a visit to Dhofar, probably while his ship was at anchor at Marbat.

9. **Echiochilon kotschyi** (Boiss.), comb. nov.

Lithospermum kotschyi Boiss. & Hohenack. ex Boiss. Diag. Pl. Orient. Nov. **4**: 49 (1844); Boiss. Fl. Orient **4**: 219 (1875) — Type from Karrak Island, Persian Gulf, *Kotschy 15*.

Sericostoma kotschyi (Boiss.) Franchet in Révoil, Fauna et Flore Pays Çomalis (Sertulum Somalense) 46 (1882).

Plant suffruticose, pale strigose; hairs of indument white, rigid, abundant, strongly appressed, 0.5–1 mm. long; stems becoming 3 dm. long, at base 3 mm. thick; leafy branchlets numerous, strict, slender, usually ca. 1 mm. thick and 5–10 mm. long, internodes 1–5 mm. long; leaves abundant, 2–4 mm. long, 0.8–1.2 mm. broad, oblong, usually loosely recurving, upper surface concave, lower surface convex, apex obtuse; leaves mostly alternate, only the several lowest pairs of leaves on the shoot opposite;

flowers oppositiflorous, borne interspersed among the leaves above the middle of the leafy branchlets, not aggregated into a well-defined inflorescence; calyx-lobes all about the same length, about 4 mm. long at anthesis, shorter than the corolla-tube; corolla 5.5–6 mm. long, with a moderately oblique limb 4–5 mm. broad, the 2-lobed adaxial side of corolla ca. 0.8 mm. longer than the abaxial side, tube about 1.5 mm. thick at base, ca. 2 mm. long, short-cylindric, expanding into a throat ca. 2.5 mm. broad at the summit; throat inside bearing abundant yellow hairs; corolla-lobes strigulose on both surfaces, broadly triangular-ovate, 1.5 mm. broad, 1.2 mm. long, ascending, medial abaxial lobes slightly smaller than the other four; anthers 1.7 mm. long, only the tip of the adaxial anther exserted; filaments unguiculate, ca. 0.5 mm. long, affixed at unequal heights in the corolla-throat, adaxial one arising ca. 3.5 mm. above corolla-base, dorsal lateral pair ca. 3 mm. above base, and anterior pair ca. 2.5 mm. above corolla-base; style 1.5–1.7 mm. long, with a very short truncate or convex sterile tip surrounded by the two lobed horizontal vescicular stigma; nutlets pinkish, 2–2.3 mm. long, 1.5 mm. broad, nearly smooth, obscurely tumulose, areola lateral and vertical, 1 mm. wide at base, abruptly narrowed into a groove which extends upward almost to nutlet-apex.

IRAN: Korgo (Khargu) Island, Persian Gulf, ca. lat. 29°00′, in arenosis, Jan. 7, 1842, *T. Kotschy 15a* (G, K); Karek (Kharg) Island, Persian Gulf, Jan. 1842, *Kotschy 15* (K, Isotype).

A plant growing in sand and known only from a group of small islands lying about 30 km. off the Iranian shore near the northern end of the Persian Gulf. Its relations are clearly with the Arabian *E. jugatum* and with *E. persicum* of Iran and Baluchistan. As in the species mentioned, the nutlets of *E. kotschyi* are nearly smooth and its indument is pallid. Our plant has noticeably more slender stems and leaves than *E. jugatum* and differs further in having most of its leaves alternate. *Echiochilon kotschyi* differs from *E. persicum* in inflorescence, zygomorphic corollas, small leaves and less roughened nutlets.

10. **Echiochilon vatkei** (Baker), comb. nov.

Heliotropium calcareum Vatke, Linnaea **43**: 318 (1882), not Stocks (1852) — Type from Yafir, Ahl Mountains, Brit. Somaliland, *Hildebrandt 890a.*
Heliotropium vatkei Baker in Thiselton-Dyer, Fl. Trop. Africa 4^2: 39 (1905) — a renaming of *H. calcareum* Vatke (1882), not Stocks (1852).
Sericostoma calcareum (Vatke) Johnston, Contr. Gray Herb. **92**: 92 (1930).
Heliotropium thymoides var., sensu Vatke, Oesterr. Bot. Zeits. **25**: 166 (1875).

Plant suffrutescent, 15 cm. tall; stems slender, numerous, ascendingly branched; leafy branchlets 1–5 cm. long, ca. 1 mm. thick, scantily strigose with stout straight hairs 0.5–1 mm. long, internodes 1–2 mm. long; leaves oblong to broadly oblanceolate, thickish, not costate, 2–5 mm. long, 0.5–0.9 mm. broad, mostly alternate, only the lowermost on the shoot opposite, bearing inconspicuous scattered stipitate glands, scantily strigose and bearing some spreading hairs along the margin (hairs straight, 0.5–1 mm. long), upper surface concave, lower surface convex, apex rounded or obtusish; flowers borne opposite or lateral to a leaf at irregular intervals along the leafy (sometimes branching) ultimate twigs, not arranged in a well-developed, elongate unilateral inflorescence; calyx at anthesis 2–2.5 mm. long, in fruit becoming 4 mm. long and usually with a pedicel ca. 1 mm. long, lobes subequal, at anthesis ca. 2 mm. long, oblong or broadly spathulate; corolla 3.5–4 mm. long, funnelform, regular, limb 3–3.5 mm. broad, corolla-lobes ascending, 1.5 mm. wide, 1.0 mm. long, outer surface villulose-strigose, tube (including throat) 1–1.8 mm. long, throat densely yellow villulose inside; annulus represented by tufts of minute hairs borne in a band 0.3 mm. above corolla-base; filaments equal, 0.7 mm. long, arising at equal heights in the throat 1.5–1.7 mm. above the corolla-base, anthers 1.3 mm. long; style short, 0.6–0.7 mm. long, with a very short convex sterile tip; stigma 2-lobed; nutlets (only one developing) 2 mm. long, at base 1.5 mm. thick and 1.5–1.7 mm. broad, apex somewhat rostrate, surface somewhat reddish, verrucose; attachment-areole green, lateral, vertical, 0.5 mm. wide at base, abruptly narrowed upwards into a short groove, rarely prolonged above the middle of the nutlet.

British Somaliland: Yafir, Ahl Mts., 2000 m. alt., March 1873, *J. M. Hildebrandt 890a* (G, frag. of Type; BM, Isotype).

In having the flowers borne among the leaves along the outer portion of the leafy twigs and not in a well-defined, many-flowered unilateral racemose inflorescence, the present plant is distinguished from all other species known from British Somaliland. It is most closely related to *E. verrucosum*, from which it differs, in addition to the inflorescence, in having small leaves, a short style, and equal filaments all borne at the same height above the corolla-base.

The species is known only from the type collection obtained about Yafir, a broad pass near the crest of the Ahl Mountains, near long. 48°30′E, about 50 km. east-southeast of Las Gori, in extreme eastern British Somaliland. Under the incorrect name "*Heliotropium thymoides*," it is mentioned by Hildebrandt, Zeitsch. d. Ges. f. Erdkunde, Berlin, **20**: 286 (1875), in the account of his visit to the Ahl Mountains.

11. **Echiochilon albidum** (Franchet), comb. nov.

Sericostoma albidum Franchet in G. Révoil, Fauna et Flora Pays Çomalis (Sertulum Somalense) 46 (1882).

Leaves densely and completely clothed by an abundance of appressed straight clean white somewhat lustrous hairs ca. 1 mm. long; corolla 4 mm. long, apparently regular; filaments equal, ca. 0.5 mm. long, arising ca. 2.5 mm. above the base of the corolla.

Somalia: no locality given, *Geo. Révoil 81* (Paris, Type).

A species known only from the type specimen which was collected at some unrecorded locality in northeastern British Somaliland or in adjoining portions of extreme northern Italian Somaliland. George Révoil worked for a few days near Heis, but during most of his nine months in Somalia he travelled and studied in the area east and southeast of Las Khoreh (Las Gore), and as far eastward as Bargal on the shores of the Indian Ocean. At no time, however, was he ever more than 100 km. south of the shores of the Gulf of Aden, cf. G. Révoil, La Vallée du Darror, pp. 1–388, map, Paris, 1882.

I examined the type of the species at Paris but unhappily, except for the few details recorded above, my notes on the type have been lost. The plant seems to be most closely related to *E. verrucosum* of western British Somaliland. It differs in having a regular corolla with the stamens borne at equal heights on the corolla. Its most distinctive feature, however, is its dense indument of very abundant, very clean and white appressed hairs. A very few collections of *E. verrucosum* (e.g., *Gillett 4026* from Hargesia) have a white indument but none of them has a snow-white or somewhat silvery white indument such as that possessed by the type of *E. albidum*.

Of the six species of the genus known from British Somaliland and adjacent extreme northern Italian Somaliland, only *E. verrucosum* is known from a goodly number of scattered collections. It appears to be widely distributed in the hills over the western half of British Somaliland and is there the only perennial representative of the genus. In the eastern half of British Somaliland and in adjacent Italian Somaliland the genus is represented by a number of apparently local species. Of the five occurring in this latter area (*E. arabicum, E. vatkei, E. collenettei, E. adenophorum* and *E. albidum*), only *E. arabicum* is known from more than a single station or has been collected more than once. The behavior of *Echiochilon* in eastern British Somaliland and in northern Italian Somaliland differs from that elsewhere within the geographic range of the genus. More species are concentrated in this area than in any other of comparable size. Also, the geographic distribution of the species of *Echiochilon* within the area is extremely localized as compared with those occurring elsewhere. Recognizing these facts, it seems wise therefore to accord at least conditional recognition to *E. albidum* until it has been recollected and more is known concerning the plant and its occurrence. If *E. albidum* is not a recognizable local endemic species of extreme eastern British Somaliland or adjacent Italian Somaliland, it may prove to be only a form of *E. verrucosum*. Should this be true, the name "albidum" being older than "verrucosum," the binomial *E. albidum* would become the correct one for the plant I have treated as *E. verrucosum*.

12. **Echiochilon strigosum** (Deflers), comb. nov.

Sericostoma strigosa Deflers, Bull. Soc. Bot. France **43:** 120 (1896) — Type from southwestern Arabia, Bilad Fodhli, ad fauces australes montis el'Areys, 500–600 m. alt. *Deflers 1075*.

Heliotropium deflersii O. Schwartz, Mitt. Inst. allgem. Bot. Hamburg **10:** 212 (1939) — based on *S. strigosa* Deflers (1896).

Plant suffrutescent, apparently prostrate; stems very slender and very loosely branched, 10–20 cm. long; leaf-bearing branchlets 5–12 cm. long, 0.5–1 mm. thick, densely strigulose (hairs 0.1–0.5 mm. long), with internodes 0.2–5 mm. long, bearing very numerous small leaves directly upon the branchlet and also in axillary fascicles; leaves linear or narrowly oblong, sessile, 1–6 mm. long, 0.5–1 mm. broad, becoming loosely but distinctly recurved, usually green, sparsely strigulose (hairs 0.1–0.8 mm. long) and sometimes sparsely ciliate (hairs 0.6–1.2 mm. long) below the middle, mostly alternate, with only the lowest 2–3 pairs on the shoot opposite; leaf-blade thickish, more or less conduplicate, the upper surface mostly hidden and apparently narrowed to a longitudinal groove, lower surface convex, not costate; inflorescence 10–20-flowered, unilateral, becoming loosely racemose, 1–7 cm. long, terminal on the branchlets; bracts small, linear, 1–2 mm. long; calyx at anthesis 1.5–2.5 mm. long, borne on a strict pedicel 0.5–1 mm. long, lobes linear, 1–2 mm. long, equal or nearly so, not costate; corolla 3–4 mm. long, unilaterally prolonged on the adaxial side, densely strigulose outside, limb moderately but distinctly oblique; corolla-lobes about equal, ca. 1 mm. diameter, usually with pale crisped margins, two rear lobes overtopping the other lobes 0.5–1 mm.; corolla-throat with abundant yellow hairs inside; annulus marked only by an indistinct inconspicuous band of minute hairs ca. 0.5 mm. above the corolla-base; anthers 0.7–0.9 mm. long, sometimes exserted; filaments unequal, 0.5–1.5 mm. long, arising at unequal heights above the corolla-base, one 1.5 mm. above the base, two ca. 1.8 mm. above the base and the remaining two 2–2.1 mm. above the corolla-base; gynobase broadly pyramidal; style 0.5–1.2 mm. long, the sterile tip convex, short; stigmas 2; nutlets 1.5–2 mm. long, above the base 1.5 mm. wide and 1.2–1.5 mm. thick, commonly 3–4 developing, back verrucose or somewhat papillate, venter with prominent scar and keel, attachment-scar lateral and vertical (or perhaps sometimes somewhat oblique), ca. 0.5 mm. broad, ovate or broader than long; groove closed or a narrow prolongation of the areola extending up to the middle of the nutlet.

Known only from the western half of the south coast of Arabia.

ARABIA: Montes el'Areys, Bilad Fodhli, 500–600 m. alt., April 28, 1893, *A. Deflers 1075* (Paris, Type; G, fragment); hills near Dobaibah [35–40 mi. east-northeast of Mukalla], Hadhramaut, small plant, flowers pale blue, 3000 ft. alt., Feb. 28, 1894, *W. Lunt 224* (K); between Mukalla and Sai'un, jol along East Road, Hadhramaut, March 30, 1952, *G. Popov 530* (BM).

Among the distinctive features of *E. strigosum* are its very slender and very loosely branched stems, its very short, narrow, usually recurved leaves and its abundant, frequently crowded, axillary fascicles of leaves. On some plants the well-developed leaf-fascicles are so numerous and so crowded as to form a cylindric mass of foliage 7–8 mm. in diameter that completely hides the twig within it. The species is a well-marked one, having its closest relations perhaps in *E. verrucosum* of British Somaliland.

Deflers appears to have collected the type of species in what is now known as Dairi, Fadhli Sultanate, in the Aden Protectorate about 45–50 miles north-northeast of Aden. His collection is unquestionably conspecific with those I have cited from the Hadhramaut.

13. **Echiochilon persicum** (Burmann f.), comb. nov.

Heliotropium fruticosum var. *persicum* Burmann f., Fl. Indica 41, *t. 19, f. 1* (1768) — Persia.

Heliotropium persicum Burmann f. Fl. Indica *t. 19, f. 1* (1768); Lam. Encyc. 3: 94 (1789).

Sericostoma persicum (Burm. f.) B. L. Burtt, Kew Bull. **1949:** 138 (1949).

Lithospermum persicum Gand. Bull. Soc. Bot. France **65:** 62 (1918) — "Persia merid., Laristan ad Bender-Abbas (Bornmüller No. 521!)."

Lithospermum kotschyi var. *brevifolia* Bornmüller, Mitt. Thür. Bot. Vereins n.s. **6:** 59 (1894) — "bei Bender-Abbas am Fusse des Kuh Ghino gesammelt." *J. Bornmüller 522, in pt.*

A decumbent shrub with pallid herbage; old stems lignescent, as much as 8 mm. thick; leafy branchlets 5–15 cm. long, 1–2 mm. thick, simple or ascendingly branched above the middle, pallid strigose (hairs straight 0.5–1 mm. long, closely appressed), internodes 1–10 mm. long; leaves pallid-strigose and usually also more or less coarsely ciliate (hairs straight 0.5–1 mm. long), usually ascending, 3–15 (usually 5–10) mm. long, oblong or oblanceolate, 1–3 mm. broad, thickish, weakly conduplicate or the upper surface merely somewhat concave, lower surface convex, not costate; lowest 2–3 pairs of leaves on the shoot opposite, the others all alternate; inflorescence bracted, unilateral, 10–20-flowered, racemose, 3–8 cm. long, terminating the leafy shoots and their branches; bracts oblong, shorter than the calyx; calyx at anthesis 3.5–4 mm. long; lobes 2.5–3 mm. long, equilong or nearly so; corolla 4.5–6 mm. long, tubular funnelform, abaxial side 1–1.5 mm. shorter than the adaxial side, outer surface minutely villulose; limb 4–6 mm. in diameter, moderately but distinctly oblique; corolla-lobes ascending, 1–1.5 mm. diameter, margins crisped, medial abaxial one slightly but perceptibly the smallest; throat inside bearing abundant yellow hairs; annulus usually marked only by an indistinct band of minute hairs ca. 0.5 mm. above corolla-base; anthers 1.2–1.7 mm. long, usually included; filaments 0.5–0.8 mm. long, unequal, borne at unequal heights (2.3–3 mm.) above the corolla-base; style 0.9–1.5 mm. long, sterile tip very short, low-convex; gynobase 1.5 mm. tall, abruptly narrowed above the broad (ca. 1 mm.) base; nutlets 2–2.3 mm. long, above the base 1.5–1.7 mm. broad and 1.3–1.6 mm. thick, gray or pinkish, usually one or more aborted, back convex, obscurely roughened or tumulose and with a few scattered prominent tuberculations; areola green, vertical (or rarely somewhat oblique), ca. 1 mm. broad, abruptly contracting into a narrow groove extending upward to above middle of the nutlet.

Known only from the coastal areas of southern Iran and Baluchistan.

IRAN: Henjam Island, Strait of Hormuz, *W. Wykeham* (K); sand hills near Bandar Abbas, Jan. 19, 1893, *J. Bornmüller 521* (G); near Gahkum, lat. 28°11′N, long. 55°50′E, woody shrub 2 ft. tall, fl. brownish purple, silty plain, 3000 ft. alt., March 25, 1951, *G. B. Popov 46* (BM, G); Makran (perhaps near Jask, long. 58°), *Aucher-Eloy 5001* (K, P); Tcharbahar (Chahbar), Tiss, long. 60°40′ June 12, 1943, *A. Parsa* (K). PAKISTAN: Hala Range, long. 66°E., *Capt. Vicary* (K).

This species is the oldest in the genus. It was first described and figured nearly two hundred years ago from a plant said to have come from Persia. Unfortunately it was mistakenly identified with *Heliotropium*. Only recently was the true identity established by B. L. Burtt. This plant is the most easterly ranging member of *Echiochilon* and the only one known from the mainland of Iran or from Pakistan to the eastward. Its closest relation appears to be *E. kotschyi* of the islands of the Persian Gulf. The insular species, however, is very distinct, differing from *E. persicum* in its practically smooth nutlets, few-flowered inflorescence, small recurved leaves and its regular, rather than zygomorphic corollas.

14. **Echiochilon arabicum** (Schwartz), comb. nov.

Tetraedrocarpus arabicus O. Schwartz, Mitt. Inst. allgem. Bot. Hamburg **10**: 212 (1939) — southern Arabia (Hadhramaut), near Mukalla, *Wissmann 1241*; on mountainsides behind Mukalla, near Lasb, *Wissmann 1240*; in the Wadi Himen, *Wissmann 1234*.

A small slender-stemmed grayish green shrub 1–5 dm. tall, hispid, loosely or densely branched; leafy branchlets 5–20 cm. long, 1–1.5 mm. thick, internodes 1–10 mm. long; older branches distinctly shrubby, 3–5 mm. thick, usually decorticating; leaves oblanceolate, all alternate or only the lowest pair on the shoot opposite, 5–15(–35) mm. long, from a narrow base gradually broadening and becoming 1–4 mm. broad between the apex and the middle, apex acutish, firm, thickish, weakly conduplicate, lacking midrib and veins, bearing stiff (even pungent) straight hairs 0.7–1.5 mm. long which arise from discoid bases, hairs loosely appressed or those along the leaf-margin more or less spreading; inflorescence elongating, racemose, unilateral, 10–40-flowered, becoming 5–17 cm. long; calyx 2–2.5 mm. long at anthesis, becoming 3–5 mm. long in fruit, base narrowed into a strict pedicel 1–2 mm. long, lobes about equally long but with the abaxial one broadest, without evident midrib; bracts numerous, mostly small and not surpassing the calyx; corolla 5–8 mm. long, funnelform, prolonged on the adaxial side, minutely hispidulous or villulose outside, tube 3–5.5 mm. long and 1–1.5 mm. thick expanding into a throat 2.5–3 mm. broad, limb distinctly, although only moderately oblique, sloping 25°–35° from the horizontal; lobes prominently and dichotomously veined, inner surface sparingly white hairy above the base, the two adaxial lobes largest 2–2.5 mm. broad and 1.5–2 mm. long, medial abaxial lobe 1.5 mm. wide and 1 mm. long, anterior lateral lobes 1.7 mm. broad and 1–1.5 mm. long; corolla-throat bearing yellow hairs inside; anthers 1–1.2 mm. long, included or only shortly exserted; filaments borne at unequal heights above the corolla-base; medial adaxial filament 1–1.2 mm. long, arising 3–4 mm.

above the corolla-base; anterior pair of filaments 0.2–0.5 mm. long, arising 2–3 mm. above corolla-base; gynobase 2 mm. tall, attenuate, abruptly arising from a broad base, 1.5–2 mm. high, ca. 1 mm. wide at base; style 1.2–1.5 mm. long, sterile tip very short and broad, stigma not oblique; nutlets 1.5–2 mm. long, above the base 1.3–1.5 mm. broad and 1–1.5 mm. thick, usually verrucose, gray or somewhat reddish, 1–4 developing; areola green, base broad and more or less oblique, usually triangular (ca. 0.8 mm. broad and 0.4 mm. long), prolonged upward on the vertical ventral angle of the nutlet as an open groove reaching almost to the nutlet-apex.

ARABIA: (Hadhramaut): Mukalla, 1931, *H. v. Wissmann 1241* (G, fragment of Type); Lasb [mountain slope back of Mukalla], May 1931, *H. v. Wissmann 1240* (photo); el Sibeth [ca. 20 mi. north of Mukalla], 600 ft. alt., small straggling plant, flowers pale blue, Dec. 26, 1893, *W. Lunt 94* (BM, K).

BRITISH SOMALILAND: Serrut Mts., inland from Mait, limestone, fl. pale blue, 1800 m. alt., April 1875, *J. M. Hildebrandt 1416* (BM); Daageg delta, Heis, Erigavo Dist., fl. blue, bunch plant with thick taproot, Feb. 18, 1945, *Glover & Gilliland 715* (BM, K); Dubriet Mt., lat. 10°22′N, long. 45°10′E, 500 m. alt., fl. pale blue, open sandy soil, *J. B. Gillett 4776* (K, Fl).

Among the small-flowered members of the genus (spp. no. 7–17) the present one has the corollas which are most evidently zygomorphic and those which attain the largest size. The plant has relatively coarse foliage and has a thin open indument of loosely spaced, stiff, spreading or appressed hairs. It is, accordingly, a gray-green hispid plant and is more scabrous than other congeners. Because of these details I find the plant as to gross aspect very suggestive of the American genus *Cryptantha*.

In Arabia the species has been collected near Mukalla (the type locality) and also north of that port along the road to Wadi Hadhrâmaut. Two congeners have also been found in this general area, *E. strigosum* and *E. thesigeri*. Like *E. longiflorum*, the present species is known from southern Arabia and also from the adjacent African mainland. It occurs in the coastal mountains of middle British Somaliland, in an area in which the genus is otherwise represented only by the very different *E. longiflorum*, *E. adenophorum* and *E. vatkei*.

The present species was based by Schwartz on two collections. Through the kindness of Dr. Walter Domke of the Institut für allegemeine Botanik, Hamburg, I have had available for close study an excellent photograph of the type of the species, as well as a very generous fragment of the cotype. It has been possible, therefore, to identify Schwartz' proposed new genus and species with certainty, an operation impossible had I been forced to depend completely on the rather ambiguous original description.

15. **Echiochilon nubicum**, sp. nov.

Fruticulus decumbens pallidus 10–15 cm. altus e radice lignosa valida palari ad 13 mm. crassa erumpens pilis abundantibus albis ca. 1 mm. longis appressis vestitus; ramis vetustioribus lignosis 2–5 mm. crassis decorticatis prostratis vel laxe ascendentibus; ramulis hornotinis erectis vel ascendentibus 5–15 cm. longis pallide strigosis saepe ascendenter ramosis foliosis 1–2 mm. crassis, internodiis 3–12 mm. longis; foliis oblongis vel saepissime oblanceolatis 7–14 mm. longis, 1–2.5 mm. latis alternis (vel solum eis basim versus ramulorum gestis oppositis) indumento pallido vestitis, supra concavis, subtus convexis haud costatis, margine crassis sparse hispido-ciliatis; inflorescentia ramulos foliosos terminanti 3–9 cm. longa densa unilaterali racemosa 10–20-flora bracteis obovatis vel obovato-oblongis instructa; calyce sub anthesi 2–2.5 mm. longo maturitate 2.5–2.9 mm. longo subsessili vel pedicello ad 0.5 mm. longo donato; lobis aequalibus oblongis maturitate apicem nucularum paullo superante; corolla 3–4 mm. longa extus minute villulosa, limbo ca. 3.5 mm. diametro horizontali, lobis homomorphis patentibus 0.8–1 mm. longis rotundis; faucibus intus flavo-villosis; tubo intus fere ad basim glabro vel annulo villuloso donato; antheris 0.9–1 mm. longis exsertis; filamentis aequalibus 0.3–0.5 mm. longis omnibus pari altitude (2–2.5 mm.) supra basim corollae affixis; gynobasi 1.2–1.5 mm. alta basi 1–1.3 mm. diametro deinde sursum abrupte contracta faciebus excavata; stylo 0.5–0.8 mm. longo supra stigmata horizontalia apicem sterilem inconspicuum perbrevem proferente; nuculis 1.7–1.9 mm. longis 1.5 mm. latis, 1.3–1.5 mm. crassis sparse irregulariterque sed prominenter tumulosis et verrucosis, dorse obtusis carina imperfecta tuberculata donatis; cicatrice laterali prominenti basim versus 0.7–1 mm. lata supra medium nuculae apicem attenuatum producta.

SUDAN: Macaur [= Makawa] Island, Red Sea, lat. 21°, 1864, *G. Schweinfurth 2108* (Type, Kew); Nubia, about lat. 21°, seacoast between 3000 and 4000 ft. alt., 1896, *J. T. Bent* (K).

A plant known only from the middle of the west side of the Red Sea. Because of its pallid indument I find it most suggestive of *Echiochilon persicum* as regards gross aspect. Its relationship, however, seems to be closest with *E. verrucosum* of British Somaliland and perhaps also with *E. thesigeri* of Arabia. Among the features of the plant useful in recognizing it are its white indument, stout sessile or subsessile calyces, small regular corollas, and very short style.

16. **Echiochilon verrucosum** (Beck), comb. nov.

Sericostoma verrucosum Beck in P. Paulitschke, Harar 457, *f. 3–6* (1888) — Type from Wárabot, western Brit. Somaliland, ca. 10 km. south of Zeila, *von Hardegger & Paulitschke.*

Heliotropium albo-hispidum Baker in Thiselton-Dyer, Fl. Trop. Africa 4^2: 39 (1905) — Type from Hammar, Golis Range, Brit. Somaliland, Feb. 9, 1895, *Edith Cole.*

Small usually gray-green shrubby plant; older stems lignescent, prostrate or decumbent, becoming 5 mm. thick; leafy branchlets cinereous, erect, 2–15 cm. long, ca. 1 mm. thick, somewhat strigose (hairs 0.6–1.2 mm. long), simple or ascendingly branched above the middle, internodes 1–10 mm. long; leaves linear or linear-oblanceolate or sometimes oblanceolate, numerous 5–15 (usually 8–12) mm. long, ascending, 0.5–1 or sometimes

1.5 mm. broad, clothed with slender appressed hairs 0.5–1 mm. long, upper surface concave, lower surface convex, margin thick and usually sparsely hispid-ciliate; inflorescence terminating the leafy branchlets, erect, bracted, racemose, unilateral, 10–40-flowered, 5–14 cm. long; calyx at anthesis 2.5–3 mm. long, lobes linear or lanceolate, usually equal or nearly so but sometimes with the abaxial lobe enlarged; calyx in fruit somewhat accrescent, with stout ascending pedicel 0.8–1.5 mm. long; corolla 4–5 mm. long, outer surface strigulose or villulose, limb 3.5–5 mm. in diameter, symmetric or obscurely prolonged on the adaxial side, lobes usually equal or practically so, rounded, 1–1.5 mm. broad and ca. 1 mm. long, throat yellow-villose inside, annulus not differentiated, glabrous; anthers 1–1.2 mm. long, shortly exserted; filaments slightly unequal, 0.5–0.7 mm. long, affixed at unequal heights (at 2.4–2.5 mm., 2.6 mm. and 2.8–3 mm.) above the corolla-base; gynobase ca. 1 mm. broad at base, abruptly narrowing upward, 1–1.5 mm. high, faces excavated; style 1–1.3 mm. long, the sterile tip very short and convex, somewhat emarginate, scarcely surpassing the horizontal stigmas; nutlets usually rosaceous, 1–4 developing, verrucose or tuberculate, sometimes prominently and irregularly so, 1.8–2 mm. long, 1.5 mm. broad, 1.2 mm. thick, areola frequently green, lateral and vertical and tending to be prominent, from a broad base narrowing into an open groove extending upward towards the nutlet-apex.

Western British Somaliland, long. 43°00′ to 45°15′E.

BRITISH SOMALILAND: Upper Sheik, long. 45°15′E. 1896–7, *Mrs. E. Lort Phillips* (BM); Daganeh, 2000 ft., small shrub on rocks, May 30, 1949, *P. R. O. Bally 7266* (K, A); Golis Range, *Drake Brockman 229, 246* (K); Hammar, Golis Range, Feb. 9, 1895, *Edith Cole* (Kew, Type of *H. albo-hispidum*); Adadleh, Habrawal, long. 44°40′E. Feb. 20, 1899, *A. Donaldson Smith* (BM); Adda Gallah, April, *James & Thrupp* (K); Lafarug, April, *James & Thrupp* (K); Deragodle, in glareosis siliceis, Dec. 7, 1892, *D. Domenico Riva 257/13* (Fl); north of Hargeisa, 4800 ft., fl. cream, top of limestone hill, *J. B. Gillett 4026* (K, Fl); Afard, long. 44°8′E. 2000 ft., fl. white, schist slope, Oct. 24, 1932, *Gillett 4448* (K); Dobo Pass, long. 43°15′E., 4000 ft., May 2, 1933, *Gillett 4959* (Fl); betw. Gildessa and Zeila, 1889, *R. Bricchetti 37* (Fl).

From this plant of western British Somaliland the other small-flowered Somalian species are easily separable, *E. arenarium* by its style, *E. vatkei* by its inflorescence, *E. arabicum* by its coarser habit and larger, strongly zygomorphic corollas, and *E. albidum* by its dense, very clean, lustrous white indument. As mentioned in my discussion of *E. albidum*, that species is imperfectly known. Its relationship to *E. verrucosum* must remain in doubt until new collections of it become available for study and comparison.

17. **Echiochilon thesigeri**, sp. nov.

Fruticulus ad 4.5 dm. altus cinerascens; ramis vetustis decumbentibus lignescentibus 2–7 mm. crassis decorticatis; ramulis hornotinis foliosis 5–15 cm. longis 1–1.5 mm. crassis saepe ascendenter ramosis sparse strigosis (pilis 0.5–1 mm. longis rectis valde appressis) internodiis 2–10 mm. longis; foliis 2–12 mm. longis 1–2 mm. latis oblongis vel oblanceolatis sparse strigosis plerumque alternis solum eis fere ad basim ramulorum gestis oppositis, supra concavis, subtus convexis haud costatis, margine crassis sparse hispido-ciliatis; inflorescentia 10–20-flora racemosa unilaterali 2–8 cm. longa ramulos foliosos hornotinos terminante, bracteis oblongis plerumque minus quam 3 mm. longis; calyce ad anthesin 2.5–3 mm. longo, maturitate 0.5–1.5 mm. longe pedicellato, lobis equalibus vel subaequalibus 2–3 mm. longis; corolla 3.5–5.5 mm. longa extus plus minusve villulosis, limbo 4–5 mm. diametro horizontali, lobis ca. 1 mm. longis et 1–1.5 mm. latis rotundis equalibus vel subaequalibus, faucibus intus abundanter flavo-villosis, tubo ca. 0.5 mm. supra basim inconspicue villuloso; antheris breviter exsertis 1–1.4 mm. longis; filamentis aequilongis ca. 0.5 mm. longis omnibus pari altitudine (1.6–3 mm.) supra basim corollae affixis; gynobasi basi 1–1.5 mm. lata deinde sursum abrupte attenuata 1–1.5 mm. alta; stylo 0.9–1.4 mm. longo supra stigmata horizontalia apicem sterilem truncatum perbrevem vel subnullum gerente; nuculis rubicundis ca. 2 mm. longis 1.5 mm. latis et crassis irregulariter et saepe prominenter verrucosis, dorse obtusis imperfecte carinatis; cicatrice laterali verticali viridi ovata supra medium nuculae sursum in sulco producta.

ARABIA: Bahrain Island, Persian Gulf, stony desert south of rifle range south of Safral, March 14, 1950, *R. Good 223* (K); Jabal Hafit, Oman, April 25, 1948, *W. Thesiger* (Type, Brit. Mus.); wadi ascending to jol behind Zamuk, 3400 ft., drainage runnels in sand, intricate shrublet 8–18 in. tall, fl. white and crimson with yellow eye, Feb. 27, 1952, *Popov, Tillin & Gilliland 4212* (BM); on northern jol near Zamuk, 4000 ft. alt., gravelly drainage runnels, intricate rough-hairy shrublet 8–12 inches tall, fl. white becoming blue-purple with yellow hairy throat, Feb. 28, 1952, *Popov, Tillin & Gilliland 4220* (BM); "Red Sea," *Dr. Nimmo* (K).

This plant of eastern and southern Arabia has a habit at times closely simulating that of *E. persicum* of Iran and especially *E. verrucosum* of British Somaliland. From both these species, however, it is readily distinguished by having the stamens all borne at the same distance above the corolla-base and by having a corolla with lobes that are equal or practically so and a limb that is not oblique. In addition to *E. thesigeri* the genus is represented in Arabia by *E. jugatum*, *E. strigosum* and *E. arabicum*, all three very well marked and readily recognizable species.

Among the five collections cited, that from Bahrain Island appears to be a plant from an unusually rigorous situation. Though it has very short stems and very small leaves, it seems to be otherwise characteristic of the species. One of the collections (No. 4220) from near Zamuk [apparently a locality northwest of the Wadi Hadhramaut] is typical except for the fact that some minute stipitate glands are present on the calyx and along the younger stems. The glands, however, are inconspicuous and to be seen must be searched for. They are not conspicuous and should not cause the plant to be confused with the abundantly glanduliferous *E. adenophorum* and *E. collenettei* of British Somaliland.

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A MONOGRAPHIC STUDY OF THE WEST INDIAN SPECIES OF PHYLLANTHUS *

GRADY L. WEBSTER

With five plates

Sect. 11. Phyllanthus

Phyllanthus sect. *Euphyllanthus* sensu Muell. Arg. in DC. Prodr. **15**(2): 374. 1866 (ex p.).

Annual or perennial herbs or subshrubs, with phyllanthoid branching; branchlets simple. Monoecious or dioecious, the flowers in unisexual cymules (the female then solitary) or (in a few species) in bisexual cymules. Male flower: calyx-lobes (4) 5 or 6; disk divided into segments isomerous with the calyx-lobes; stamens 2 or 3 (very rarely 4); filaments free or united into a column, anthers extrorse (except in *P. maestrensis*) and usually dehiscing horizontally or obliquely; pollen grains 3- or 4-colporate, the exine reticulate. Female flower: calyx-lobes 5 or 6, usually larger than the male, persisting in fruit; disk entire or variously lobed or dissected; ovary smooth, obscurely stipitate; styles usually free except at the very base, bifid, the tips of the branches thickened or more often slender. Capsule oblate, elastically dehiscent; columella persistent; seeds sharply trigonous, variously ornamented.

TYPE SPECIES: *Phyllanthus niruri* L.

In its present limited circumscription, sect. *Phyllanthus* comprises about 50 species, including most of the widespread weedy species in the genus. As pointed out previously (Contr. Gray Herb. **176**: 51. 1955) the broad concept of the section held by Mueller and by Pax and Hoffmann (Naturl. Pflanzenf. 2 ed. **19c**: 64. 1931) was unnatural, many unrelated plants being grouped together on the basis of the single criterion of three stamens with more or less horizontally dehiscing anthers. This artificial sect. *Euphyllanthus* in fact included representatives of six of the eight subgenera now recognized in the West Indies! As presently constituted, however, there

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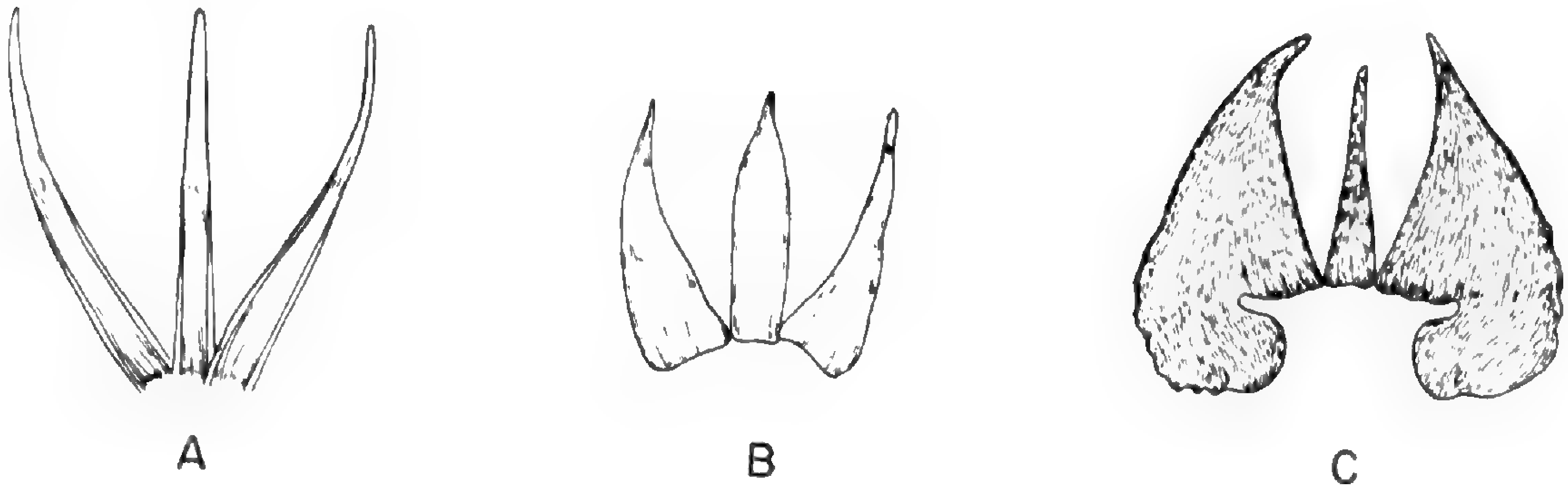
* Continued from volume XXXVIII, p. 198.

can be little doubt that sect. *Phyllanthus* is a phylogenetically natural group, the members of which (with the exception of a few aberrant forms) appear to be the descendants of some common ancestor. It appears probable that this progenitor was an herbaceous species of subg. *Kirganelia* such as *P. tenellus*. This species resembles the West Indian species of sect. *Phyllanthus* in so many ways that it can be positively excluded only on the basis of its five stamens.

Within sect. *Phyllanthus* there are many species which appear extremely similar, at least on casual inspection, so that there has been much confusion in the application of names and circumscription of taxa. The resulting uncertainty has been compounded by the fact that due to the vagaries of human transport, exotic and native weedy species of *Phyllanthus* grow together in many tropical areas. A few of the particularly successful weeds have become so widely dispersed that it is now difficult or impossible to pinpoint their place of origin. However, the majority of species have more restricted ranges, and the three major species groups, or subsections, here recognized have characteristic geographical distributions. Only subsect. *Swartziani*, with representatives in America, Africa, and India, has a nearly cosmopolitan range; subsect. *Niruri* appears to be entirely American (though a few West African species may prove to belong here) and subsect. *Pentaphylli* is essentially restricted to the West Indies. It is striking that there are no indigeous members of sect. *Phyllanthus* in China, Australasia (except for the doubtful *P. lacunarius*), and the Pacific Islands; in these areas their place is occupied by habitally similar representatives of sects. *Urinaria* and *Eriococcus*.



TEXT-FIG. 10. Diagrams of the cataphylls characteristic of the subsections of sect. *Phyllanthus*: A. Subsect. *Niruri* (*P. niruri*). B. Subsect. *Swartziani* (*P. amarus*). C. Subsect. *Pentaphylli* (*P. pentaphyllus*). The cataphylls are shown in dorsal view as they would appear if spread out, with the stipules brought into the plane of the blade.

As indicated in the synoptic key, the three subsections are easily separated by distinctive types of cataphyllary stipules (cf. Text-fig. 10). Although three distinctive types of pollen grains also occur, these are not entirely correlated with the subsectional divisions. Subsection *Niruri*, indeed, has distinctive elongated 4-colporate grains (PLATE VIII, fig. 34); but the grains in subsect. *Swartziana* are precisely like those of most species of subsect. *Pentaphylli* (i.e., similar to PLATE VIII, fig. 37). However, two species of the latter subsection, *P. leptoneurus* and *P. dimorphus*, have coarsely reticulate pollen grains (PLATE VIII, fig. 35), although in other respects they are obviously closely related to adjacent species in subsect. *Pentaphylli.* The causes of these differences in pollen morphology do not appear at all clear.

SYNOPTIC KEY TO THE SUBSECTIONS AND SPECIES

1\. Cataphyllary stipules thin and membranous or scarious (not indurate), not auriculate at the base or only very inconspicuously so.
  2\. Cataphyllary stipules linear-lanceolate; branchlet stipules more or less involute; leaves conspicuously oblique at the base; stamens 3, the filaments free or united below; pollen grains prolate, 4-colporate; seeds verruculose. .... subsect. 11a. **Niruri.**
    3\. Branchlets with c. 15–30 leaves, these 7–15 mm. long; male flowers 3–7 per cymule; calyx-lobes 1.2–1.5 mm. long; filaments 0.6–0.9 mm. long, connate below into a column; seeds 1.4–1.6 mm. long. .... 16. *P. niruri*
    3\. Branchlets with c. 35–45 leaves, these 4–6 mm. long; male flowers 1 per cymule (usually accompanied by a bud); calyx-lobes 0.6–0.8 mm. long; filaments 0.25–0.35 mm. long, free; seeds 0.95–1 mm. long. .... 17. *P. mimicus*
  2\. Cataphyllary stipules broader; branchlet stipules not involute; leaves scarcely if at all oblique at the base; stamens 2 or 3, the filaments free to wholly united; pollen grains ellipsoidal, 3-colporate; seeds striate or ribbed. .... subsect. 11b. **Swartziani.**
    3\. Seeds with 5–7 longitudinal ribs; weedy annual herbs.
      4\. Cymules unisexual; calyx-lobes obtuse.
        5\. Branchlets smooth; stem often angled; leaves usually narrowed to a point at the tip; female disk subentire; styles spreading and appressed. .... 18. *P. debilis*
        5\. Branchlets scabridulous; stem not conspicuously angled; leaves rounded at the tip; female disk divided into irregular segments; styles erect or ascending. .... 19. *P. fraternus*
      4\. Cymules bisexual, consisting of one male and one female flower; calyx-lobes acute .... 20. *P. amarus*
    3\. Seeds with c. 9–12 very delicate scarcely raised longitudinal striae.
      4\. Filaments partially united; pedicel of female flower 1.5–2.5 mm. long; herbs.
        5\. Style-branches peculiarly thickened, similar to the arms of a unusually modified; branchlets mostly with 15–30 leaves; stamens usually 3; female calyx-lobes 1.2 mm. long or more in fruit.
          6\. Filaments completely united; female disk angled or 5-lobed; leaves not narrowed at the tip; seeds 1.1–1.3 mm. long; widespread. .... 21. *P. stipulatus*
          6\. Filaments united only in the lower half; female disk divided

into 3 linear segments; leaves narrowed toward the tip; seeds just under 1 mm. long; Lesser Antilles. .... 22. *P. caribaeus*

5\. Style-branches peculiarly thickened, similar to the arms of a Maltese cross; branchlets mostly with 30–60 leaves; stamens usually 2; female calyx-lobes 0.75–1 mm. long in fruit; Cuba. .... 23. *P. procerus*

4\. Filaments free; pedicel of female flower becoming 3–3.5 mm. long; stem woody; Jamaica. .... 24. *P. fadyenii*

1\. Cataphyllary stipules becoming dark reddish or blackish, indurate, conspicuously auriculate at the base; mostly perennials. .... subsect. 11c. **Pentaphylli.**

2\. Midrib of male calyx-lobes not dorsally carinate.

3\. Plants with a single main stem or, if stems clustered at the base, these subsimple, not repeatedly branching (cf. Plate XXII, B); branchlets with mostly 20–50 leaves (or more); leaves linear to oblong or elliptic, never scabridulous beneath (hispidulous in *P. amnicola*); apical centimeter of stem with c. 3–7 evident branchlets [including any immature branchlets with evident leaf primordia]; stamens 2 or 3.

4\. Staminal column 0.2–0.5 mm. long; leaves various; pollen grains finely reticulate.

5\. Anthers extrorse, dehiscing horizontally or obliquely.

6\. Calyx-lobes 5; stamens 2; dioecious perennial with linear leaves; Cuba. .... 25. *P. micranthus*

6\. Calyx-lobes usually 6 (at least those of male flower); stamens always 3; monoecious or dioecious, leaves broader; Hispaniola.

7\. Branchlets and leaves smooth, never hispidulous; filaments usually united 2/3 their length or more.

8\. Branchlet stipules scarious, becoming reddish but not blackened and indurate; leaves membranous to chartaceous; disk-segments of male flower smooth or slightly glandular-crenulate.

9\. Anthers subsessile or stipitate, dehiscing more or less obliquely; branchlets mostly 5–9 cm. long; leaves mostly 5–8 mm. long; monoecious or dioecious .... 26. *P. fuertesii*

9\. Anthers sessile, compressed together or connate by the connectives, dehiscing horizontally; branchlets mostly 1–5 cm. long; leaves mostly 2.5–4 mm. long; dioecious, with several erect stems from a caudex. .... 27. *P. brachyphyllus*

8\. Branchlet stipules becoming blackened and indurate; leaves coriaceous; disk-segments of male flower conspicuously rugose-papillate; dioecious perennial. .... 28. *P. buchii*

7\. Branchlets and undersurfaces of leaves conspicuously white-hispidulous; filaments united in the lower half; dioecious herb rooting at the nodes. .... 29. *P. amnicola*

5. Anthers introrse, dehiscing more or less vertically; stamens 2; Cuba. . . . . 30. *P. maestrensis*

4. Staminal column (0.5–) 0.7–1.3 mm. long; leaves oblong to linear, with broadly rounded to truncate tips; pollen grains coarsely reticulate; dioecious or subdioecious perennials.

5. Anthers sessile but not completely confluent; staminal column 0.5–0.9 mm. long; styles up to 0.5 mm. long; leaves membranous to chartaceous; Hispaniola. . . . . . . 31. *P. leptoneurus*

5. Stamens completely fused, the anthers confluent in a circumscissile synandrium; staminal column 1.1–1.3 mm. high; styles 1.1–1.7 mm. long; leaves subcoriaceous; Cuba. . . . . 32. *P. dimorphus*

3. Plants without a single main stem, the branches clustered on a caudex, simple or repeatedly branching below (cf. Plate XXII, C); branchlets with mostly 5–25 leaves; leaves mostly elliptic to obovate or suborbicular; apical centimeter of stem usually with only 1–3 evident branchlets; stamens normally 2.

4. Leaves areolate-foveolate above; capsule 3.5 mm. in diameter, the seeds c. 1.4–1.7 mm. long; dioecious; Cuba. . . . . . 33. *P. junceus*

4. Leaves not areolate above; capsule and seeds smaller; usually monoecious.

5. Leaves not scabridulous above; seeds 0.8–1 mm. long, the epidermal cells slightly hygroscopic; widespread . . . . 34. *P. pentaphyllus*

5. Leaves scabridulous on both sides.

6. Suffruticose; female disk cupuliform; seeds 1.–1.1 mm. long, the epidermal cells not appreciably hygroscopic; eastern Cuba. . . . . 35. *P. pulverulentus*

6. Herbaceous; female disk divided into linear segments; seeds 0.6–0.7 mm. long, the epidermal cells usually strongly hygroscopic; western Cuba. . . . . 36. *P. echinospermus*

2. Midrib of calyx-lobes dorsally carinate; psammophilous microphyllous herbs, stamens 2; Isle of Pines.

3. Erect, with the habit of a miniature tree; leaves elliptic to obovate, rounded at the base; male disk-segments subentire; female flower definitely pedicellate (pedicel 0.6–1.4 mm. long) . . . . 37. *P. selbyi*

3. Prostrate herb with habit of *Euphorbia* (*Chamaesyce*) *spp.*; leaves ovate, subcordate or cordate at base; male disk-segments rugose-papillate; female flower subsessile (pedicel only 0.3 mm. long or less). . . . . 38. *P. imbricatus*

Subsect. 11a. **Niruri** Webster, Contr. Gray Herb. 176: 52. 1955.

Annual herbs; cataphyllary stipules linear-lanceolate; branchlet stipules involute; leaves inequilateral at the base; monoecious, cymules unisexual; stamens 3, filaments free or united below, pollen grains 4-colporate, heteroreticulate; disk of female flower patelliform or cupuliform; styles free, the tips capitate; seeds verruculose.

TYPE SPECIES: *Phyllanthus niruri* L.

This entirely American group includes a small number of species, of which by far the most widespread is *P. niruri*. This species is so variable that it can scarcely be delimited from most of the related proposed species, such as *P. chlorophaeus* Baill. of Mexico; further study will be necessary to determine the status of these latter. However, there do appear to be at least two valid species in addition to *P. niruri*: *P. mimicus* of Tobago and *P. rosellus* (Muell. Arg.) Muell. Arg. of Brazil.

The very narrow stipules, oblique leaf base, and distinctive pollen grains clearly distinguish this subsection in the West Indies. However, there are some South American species such as *P. microphyllus* which have pollen grains somewhat transitional between those of the present group and subsect. *Swartziani*. Furthermore, there are a few West African species such as *P. benguelensis* which greatly resemble *P. niruri* and may prove to be related. A re-evaluation of the subsectional limits may thus be necessary when the species from these two areas are studied critically.

16. **Phyllanthus niruri** L. Sp. Pl. 981–982. 1753; ssp. **niruri.** (PLATE XIX, *figs. A–B*).

Niruri barbadense . . . petiolis florum brevissimis Rand, Trans. Roy. Soc. **35**: 295. 1727; Martyn, Hist. Pl. Rar. *pl. 8.* 1728.

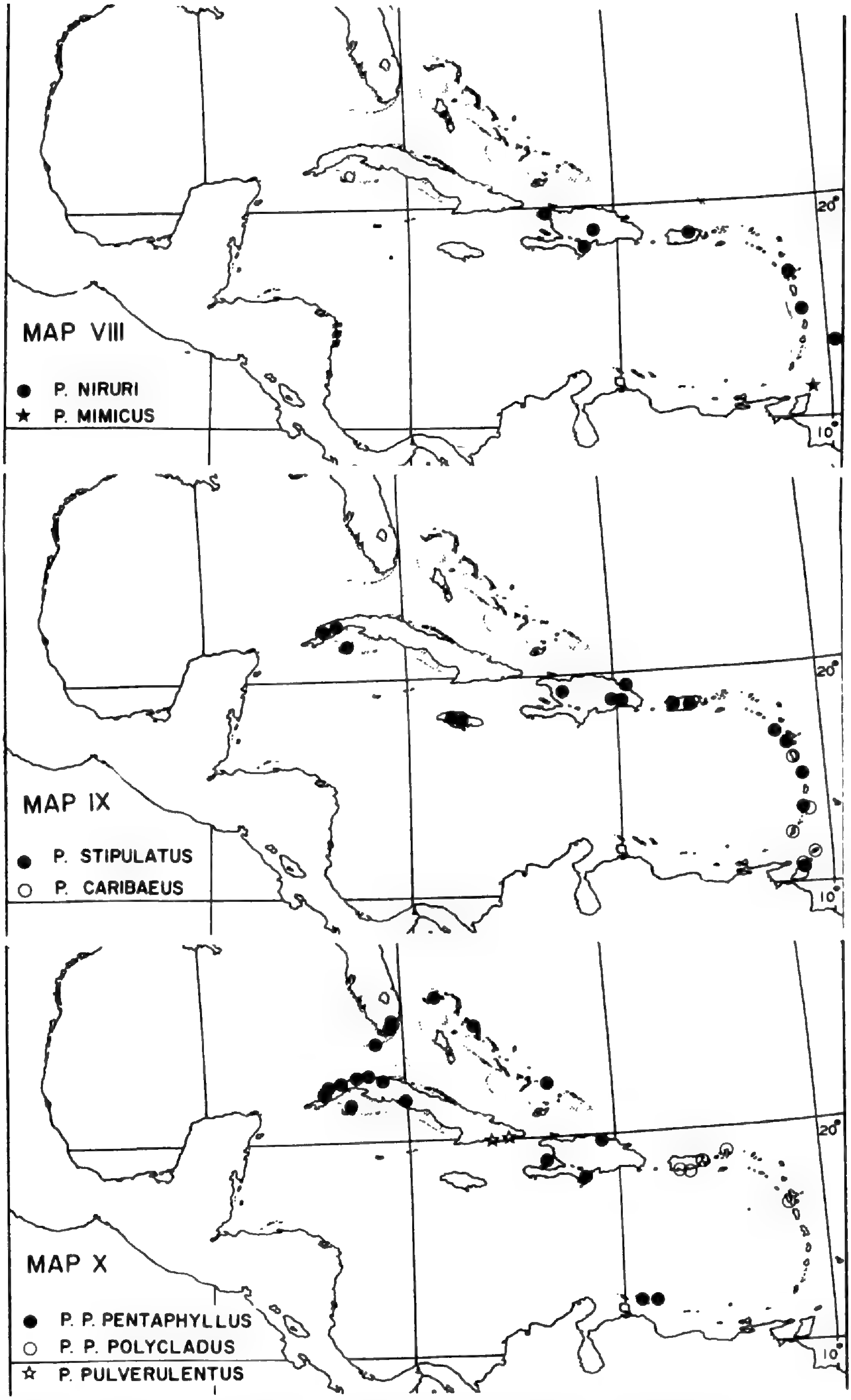
Phyllanthus foliis alternis alternatim pinnatis &c. L. Hort. Cliffort. 439. 1738 (excl. ref. Burm. & Rheede).

Urinaria erecta Medic. Monadelph. 81. 1787.

Phyllanthus lathyroides α *commutatus* Muell. Arg. Linnaea **32**: 41. 1863; DC. Prodr. **15**(2): 403. 1866 (ex p.).

Diasperus niruri (L. "em.") O. Ktze. Rev. Gen. **2**: 600. 1891.

Annual herb; primary stem simple or considerably ramified, 1.5–5 dm. high, 1–2.5 mm. thick, olivaceous, smooth, terete; internodes mostly 1–4 cm. long. Cataphylls: stipules narrowly lanceolate, (1.5–) 1.8–2.5 (–3) mm. long, acuminate, truncate at the base, entire, scarious, olivaceous with reddish tips, turning brownish; blade often fused laterally with the stipules in the lower half. Deciduous branchlets mostly 5–10 cm. long, 0.3–0.5 mm. thick, olivaceous, smooth, more or less terete, with c. 15–30 leaves; first internode (3.5–) 5–10 (–13) mm. long, median internodes 2.5–5 mm. long. Leaves: stipules narrowly linear-lanceolate, unequal, the longer of each pair 2–2.7 mm. long, the shorter 1–1.7 mm. long; both narrow (0.15–0.25 mm. broad) and canaliculate at base due to the involute scarious entire margins; tip filiform-acuminate, often reddish-tinged. Petioles 0.4–0.7 mm. long. Leaf-blades thin, smooth on both sides, asymmetrically ovate or elliptic, mostly 7–15 (–17) mm. long, (3–) 4–8 (–9) mm. broad, acute or subacute at the tip, conspicuously oblique at the base (i.e., acute on one side and rounded on the other); above dark green, the midrib and laterals apparent but not raised; beneath conspicuously pallid, the midrib prominently raised, the laterals (4–7 on a side) fairly



Maps VIII–X. Distribution of some species of sect. *Phyllanthus* in the West Indies (mainland stations of *P. niruri* and *P. stipulatus* not shown).

conspicuous, connecting intramarginally, the tertiary veinlets forming an obscure reticulum; margins smooth or obscurely roughened, sometimes slightly thickened.

Monoecious; branchlets with the (0–) 1–2 (–4) proximal nodes barren, the succeeding (2–) 3–6 (–8) nodes with racemiform cymules of 3–7 successively maturing male flowers, the remaining distal nodes with solitary female flowers.

Male flower: pedicel 1.2–1.8 mm. long. Calyx-lobes 5 (rarely 6), obovate or obcuneate, 1.2–1.5 mm. long, (0.8–) 1–1.5 mm. broad, obtuse or rounded to nearly truncate at the tip, entire, membranous, yellowish-white or sometimes slightly reddish-tinged at the base, dorsally carinate along the midrib; midrib with a few steeply ascending often obscure lateral veinlets. Disk-segments 5, broadly cuneate, 0.25–0.4 mm. across, obscurely to conspicuously glandular-papillate. Stamens 3; filaments c. 0.6–0.9 mm. long, united 2/3 to 3/4 their length into a slender column, the free portions of the filaments very slender; anthers 0.25–0.4 mm. long, 0.3–0.45 mm. broad, anther-sacs nearly parallel, the slits apically convergent, dehiscing obliquely; pollen grains prolate, 4-colporate, 38–48 μ long, 25–34 μ broad.

Female flower: pedicel (2–) 2.5–4 (–4.5) mm. long, olivaceous or stramineous, smooth, below terete, above thicker and angled due to the decurrent midribs of the calyx-lobes. Calyx-lobes 5, broadly elliptic or obovate (1.5–) 1.7–2.3 (–2.7) mm. long, (1.2–) 1.3–1.8 mm. broad, obtuse or rounded at the tip, entire, olivaceous with rather broad whitish scarious margins (sometimes inconspicuously reddish at the base), the dorsally carinate midrib with 4–5 steeply ascending lateral veins on each side. Disk patelliform, obscurely 5-angled, rather massive, the angles slightly upturned. Styles free, more or less ascending and arching, c. 0.5–0.6 mm. long, bifid, the branches spreading and recurved, stigmas capitate.

Capsules oblate, c. 3 mm. in diameter, stramineous, reticulate-veiny. Seeds 1.4–1.5 (–1.6) mm. long, 1.15–1.3 mm. radially and tangentially, fuscous when mature, densely covered with dark raised points; hilum triangular, c. 0.25–0.3 mm. across.

Flowering and fruiting throughout the year.

TYPE: Herb. Hort. Cliffort. (BM, HOLOTYPE). The typification of *P. niruri* and other details of its nomenclatural history have been discussed elsewhere (Jour. Arnold Arb. 37: 4–6, 13. 1956) and need not be repeated here.

DISTRIBUTION: ssp. *niruri* appears to be endemic to the West Indies (MAP VIII); the very similar ssp. *lathyroides* is widespread from Texas south through mainland tropical America into Argentina.

HAITI. NORD-OUEST: coffee plantation, Jean Rabel, *E. C. & G. M. Leonard 13746* (NY, US).

DOMINICAN REPUBLIC. SANTIAGO: Valle del Cibao, Santiago, Hato del

Yaque, irrigation ditches, *Ekman H16022* (A, S, US), *H16515* (S). La Vega: Constanza, El Salto de Constanza, *Jiménez 2971* (US). Barahona: near Barahona, *Fuertes 89 ex p.* (F, GH; mixed with *P. amarus*).

PUERTO RICO. San Juan: Bayamon, *Millspaugh 320* (F, NY); cultivated ground, Catano, *Britton, Britton, & M. S. Brown 6995* (NY); Rio Piedras, *Johnston 215* (NY); clearing, limestone hillside, Pueblo Viejo, *Britton & Boynton 8201* (NY); Santurce, in sand, *Heller & Heller 4* (NY, US).

LESSER ANTILLES. Guadeloupe: dans les champ de manioc, &c., Camp Jacob, Tombe-Novie, *Duss 2921* (F, GH, NY, US); 1839, *Beaupertuis* (P). Martinique: dans les champs de cannes, Vaillant, Carbet, Fort de France, *Duss 47 ex p.* (F [mixed with *P. amarus*], GH, NY [mixed with *P. tenellus*]); *Herb. L. C. Richard* (P). Barbados: 1918, *Freeman 5015* (F); among grass along roads, Forster Hall, *Eggers 7185* (P).

The West Indian population of *P. niruri* is of historical interest, since it (as ssp. *niruri*) represents at once the type of the species and of the genus. The type locality is the island of Barbados, from whence the plant was brought to England and subsequently given to Linnaeus probably by Philip Miller.

Subspecies *niruri* differs from the mainland populations of the species — which for the present may all be grouped under ssp. *lathyroides* — in the characteristically ovate or broadly elliptic leaves and especially in the pinnately veined calyx-lobes of the male flower. However, it must be admitted that these distinctions are very weak. The leaf-shape of the Antillean plants can be matched by various mainland plants, and it is possible that pinnate male calyx-lobes may be observed in specimens from Central or South America, although examination of about thirty mainland specimens has shown only unbranched midribs in the calyx-lobes.

The distribution of ssp. *niruri* in the West Indies is spotty, and it has usually been collected in cultivated fields, clearings, or along ditches. It is very difficult to determine what part of the present range should be considered indigenous, although it may be reasonably presumed that the plant was native at least to the Lesser Antilles before the first colonists arrived.

Although *P. niruri* has been confused in the literature with *P. amarus*, the plant with which it is most easily confounded is probably *P. stipulatus*. Some forms of the latter species are similar in aspect, but it has usually smaller leaves not oblique at the base, different stipules, stamens with the filaments completely united, fruiting pedicels not over 2.5 mm. long, and striate rather than verruculose seeds.

17. **Phyllanthus mimicus** Webster, Contr. Gray Herb. **176**: 52. 1955. (PLATE XIX, *figs. C–D*).

Slender erect annual herb; primary stem simple, 0.7–3.5 dm. high, 0.5–2 mm. thick, stramineous, smooth, terete; internodes mostly 1–2.5 cm. long. Cataphylls: stipules narrowly lanceolate, 1–1.5 mm. long, c. 0.25 mm. broad, attenuate-acuminate, thin and scarious, brownish; blade narrower, c. 1–1.5 mm. long. Deciduous branchlets 3–6 cm. long, 0.15–0.2 mm. thick, olivaceous, minutely scabridulous, obscurely or acutely angled, with c. 35–45 leaves; first internode 3–5 mm. long, median internodes c. 1 mm. long. Leaves: stipules narrowly lanceolate, scarious, more or less involute (as in *P. niruri*), unequal, the longer of each pair c. 1.3–1.8 mm. long, the shorter 0.7–0.8 mm. long, the tip attenuate. Petioles 0.2–0.25 mm. long. Leaf-blades membranous, minutely scabridulous on both sides, mostly oblong, 4–6 mm. long, 1.5–2.5 mm. broad, obtuse-apiculate at the tip, conspicuously oblique at the base; above olivaceous, the midrib raised and minutely roughened; beneath very pale, the midrib raised, the laterals (4 or 5 on a side) ascending, connecting intramarginally, tertiary reticulum obscure; margins thin, plane, smooth or nearly so.

Monoecious, not all branchlets floriferous; proximal 8–15 nodes barren, succeeding 11–14 nodes with male flowers, the distal nodes bearing female flowers; flowers solitary, but the male often accompanied by an abortive bud.

Male flower: pedicel 1.7–2.3 mm. long. Calyx-lobes 5, obovate, 0.6–0.8 mm. long, 0.5–0.65 mm. broad, obtuse, yellowish and scarious, the unbranched midrib slightly dorsally carinate. Disk-segments 5, cuneate, c. 0.2–0.25 mm. across, obscurely glandular-crenulate. Stamens 3; filaments free, slender, c. 0.25–0.35 mm. long; anthers c. 0.2–0.25 mm. broad, anther-sacs divaricate, the slits apically contiguous but not confluent, dehiscing horizontally; pollen grains prolate, 4-colporate, 27–32 μ long, 17–19 μ broad.

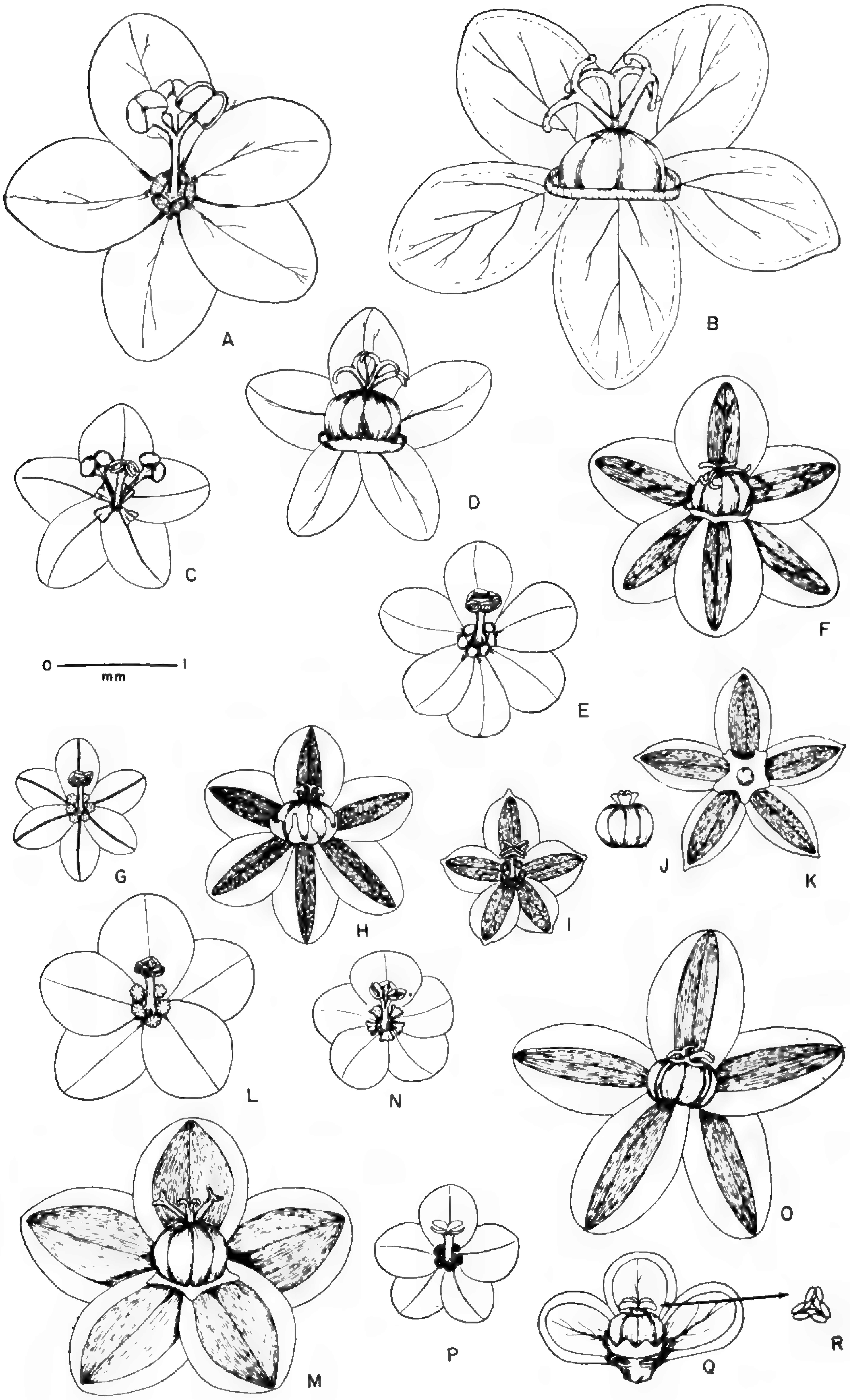
Female flower: pedicel 1.7–2 mm. long, stramineous, minutely scabridulous, terete below, obscurely angled above. Calyx-lobes 5, obovate, (1.3–) 1.5–1.7 mm. long, 0.6–0.9 mm. broad, obtuse, herbaceous with narrow scarious margins, the dorsally carinate midrib sparingly branched. Disk patelliform, roundly 5-angled, not thickened. Styles free, ascending, c. 0.25 mm. long, bifid, the branches recurving, the tips capitate.

Capsule oblate, c. 1.9–2 mm. in diameter, stramineous, obscurely reticulate-veiny. Seeds [all observed immature] c. 0.95–1 mm. long, 0.7 mm. radially and tangentially, with evenly spaced reddish-brown points.

TYPE: Tobago, Big River Bridge, Mason Hall, on a shaded bank, 13 Sept. 1909, *Broadway 3038* (G, HOLOTYPE; F, MO, NY, S, ISOTYPES).

DISTRIBUTION: known only from the type locality (MAP VIII).

PLATE XIX. FLOWERS OF SECT. *Phyllanthus*, SUBSECTS. *Niruri* AND *Swartziani*. FIGS. A-B. *Phyllanthus niruri* L. ssp. *niruri* (*Duss 47* [GH]). FIGS. C-D. *Phyllanthus mimicus* Webster (*Broadway 3038* [G]). FIGS. E-F. *Phyllanthus debilis* Klein ex Willd. (*Boeea 8313* [A]). FIGS. G-H. *Phyllanthus fraternus* Webster (*Collins 225* [GH]). FIGS. I-K. *Phyllanthus amarus* Schum. & Thonn. (*Wilson 7802*) [GH]); female flower with ovary removed to one side. FIGS. L-M. *Phyllanthus stipulatus* (Raf.) Webster (*Howard & Howard 9895* [GH]). FIGS. N-O. *Phyllanthus caribaeus* Urb. (*Hodge 2425* [GH]). FIGS. P-Q. *Phyllanthus procerus* Wright (*Killip 42789* [*US*]).



WEBSTER, WEST INDIAN PHYLLANTHUS

This diminutive plant has received the epithet *mimicus* because of its extraordinary vegetative resemblance to *P. caribaeus*, which also occurs in Tobago. However, in all important respects (viz., narrow stipules, oblique leaf-bases, 4-colporate pollen grains, and verruculose seeds) it certainly agrees with subsect. *Niruri* rather than with the subsection (*Swartziani*) to which *P. caribaeus* belongs. In fact, *P. mimicus* resembles *P. niruri* in so many ways that some observers might prefer to regard it as a subspecies of *P. niruri*. The problem of specific distinctions in subsect. *Niruri* is especially acute because of the great variability of *P. niruri*. The mainland populations of that species have received several specific names (listed in Jour. Arnold Arb. 37: 13. 1956), but most of these certainly cannot be maintained. However, *P. mimicus* differs from all other variants of *P. niruri* heretofore observed in its very small flowers, reduced male inflorescence, and branchlets with 35–45 leaves. Therefore, at least until a thorough survey of variation within *P. niruri* has been made, it appears proper to maintain *P. mimicus* as a distinct species, even though its phylogenetic derivation as a reduced insular counterpart of the wide-ranging *P. niruri* is obvious.

Subsect. 11b. **Swartziani** Webster, Contr. Gray Herb. **176**: 53. 1955.

Annual or perennial herbs; cataphyllary stipules triangular to lanceolate, scarious, not indurate nor auriculate at base; leaves equilateral at base or very nearly so; branchlet stipules not involute; monoecious, cymules unisexual or bisexual; stamens 2 or 3, filaments partially or wholly united; pollen grains ellipsoidal, 3-colporate, finely reticulate; disk of female flower patelliform and angled, or variously lobed or dissected; styles free, the tips slender or somewhat thickened (but not capitate); seeds longitudinally ribbed or striate, or transversely barred.

TYPE SPECIES: *Phyllanthus swartzii* Kostel. [= *P. amarus* Schum. & Thon.]. The choice of subsectional name now appears to have been unfortunate; but at the time it was not realized that *P. swartzii* was a later synonym of *P. amarus*.

This subsection comprises about 20 closely related species which are distributed in America, Africa, and India. There has been much confusion in the interpretation of these plants, many of which are widespread weeds. However, at least in tropical America the species can be easily distinguished by attentive inspection; they are all clear-cut entities, and there is no evidence of hybridization in the West Indies. In Africa and India, where the majority of the species occur, identifications are apt to be much more difficult, and intergradation between different species may occur.

The West Indian representatives of subsect. *Swartziani* fall into three different categories: (1) exotic weeds — *P. fraternus* and *P. debilis*; (2) indigenous weeds — *P. amarus* and *P. stipulatus*; and (3) West Indian endemics — *P. caribaeus*, *P. fadyenii*, and *P. procerus*. The last species is a particularly interesting one, since it forms a connecting link with subsect. *Pentaphylli*; but the phylogeny of subsect. *Swartziani* as a whole cannot be considered here on the basis of the fragmentary representation in the West Indies.

18. **Phyllanthus debilis** Klein ex Willd. Sp. Pl. **4**: 582–583. 1804. (PLATE XIX, *figs. E–F*).

Phyllanthus niruri γ javanicus Muell. Arg. Linnaea **32**: 43. 1863; DC. Prodr. **15**(2): 407. 1866.
Phyllanthus niruri δ debilis ("Willd.") Muell. Arg. ibid.
Phyllanthus debilis "Herb. Ham." ex Hook. f. Fl. Br. Ind. **5**: 299. 1887.

Erect annual herb (sometimes becoming woody at the base) c. 1–7.5 dm. high, the main stem often branching in age, mostly 1–2.5 mm. thick, above usually sharply angled and compressed, becoming subterete below, smooth, olivaceous, with internodes 0.5–5 cm. long. Cataphylls: stipules triangular-lanceolate, (1.2–) 1.4–1.8 (–2) mm. long, 0.6–1 mm. broad, acuminate, entire, truncate or with one side somewhat dilated at the base, olivaceous with an ill-defined scarious margin; blade narrowly lanceolate, acuminate, (1–) 1.4–1.8 mm. long. Deciduous branchlets mostly 4–10 (–12) cm. long, 0.3–0.5 mm. thick, sharply angled and sometimes compressed, quite smooth, olivaceous, with mostly 15–35 leaves; first internode 5–15 mm. long, median internodes 2.5–4.5 mm. long. Leaves: stipules lanceolate, mostly 0.9–1.2 mm. long (proximal ones sometimes longer) and 0.2–0.3 mm. broad, acuminate, entire, olivaceous with yellowish-white scarious margins, carinate along the midrib. Petioles 0.3–0.7 (–1) mm. long. Leaf-blades membranous to chartaceous, smooth on both sides, narrowly elliptic (in West Indian specimens), (6–) 8–20 mm. long, 2.5–5 mm. broad, acute or subacute at the tip, acute at the base; above dark green, all nerves except the midrib obscure; beneath greyish or brownish, the midrib prominent, the chief laterals (c. 4 or 5 on a side) somewhat raised, connecting intramarginally, the tertiary veinlets completely obscure; margins plane, unthickened, smooth.

Monoecious; cymules unisexual. Proximal 2–4 nodes of branchlet with racemiform cymules of c. 3 or 4 male flowers, distal nodes with solitary female flowers; bracteoles yellowish-white, scarious, persistent.

Male flower: pedicel less than 0.5 mm. long. Calyx-lobes 6, biseriate, subequal, obovate to obcuneate, 0.5–0.6 mm. long, 0.45–0.6 mm. broad, broadly rounded to subtruncate or retuse at the tip, entire, membranous, the midrib unbranched. Disk-segments 6, roundish to obcuneate, entire, thin, not glandular, c. 0.15–0.2 mm. across. Stamens 3, the filaments completely connate into a rather slender column 0.25–0.3 mm. high; anthers sessile atop the column, discrete or partially connate by the connectives, deltoid, blunt, c. 0.1–0.15 mm. long, 0.2–0.25 mm. broad; anther-sacs divergent, the slits confluent, dehiscing horizontally; pollen grains finely reticulate, 21–23 μ long, 17–20 μ broad.

Female flower: pedicel becoming 1.1–1.6 mm. long, usually conspicuously angled, dilated above, smooth, olivaceous. Calyx-lobes 6, obovate, (1–) 1.2–1.5 mm. long, (0.5–)0.75–1 mm. broad, rounded at the tip, with very broad whitish scarious margins (the green midstrip less than a third the breadth of the lobe), the midrib unbranched. Disk patelliform, entire or obtusely and shallowly 6-lobed, sometimes crenulate between the lobes. Styles free, spreading, appressed to the ovary (at least at the tips), c. 0.2–0.3 mm. long, bifid about to the middle, the arms divergent, the slender unthickened tips recurved.

Capsule oblate, very rounded in outline, c. 2–2.2 mm. in diameter, reddish-brown, smooth, veins completely obscure. Seeds trigonous, light yellowish-brown, c. 1–1.1 mm. long, 0.75–0.85 mm. radially and tangentially, with c. 6 or 7 straight longitudinal ribs and many fine transverse striae on the back.

TYPE: India, Madras, Tranquebar, in rice-fields, February 1799, *Klein* (B, SYNTYPES; photographs examined). Through the courtesy of the director of the Botanical Institute, Berlin-Dahlem, photographs of three sheets of Klein's original collection (in the Willdenow Herbarium) have been given to the Arnold Arboretum. Although there is considerable variation in leaf size and shape among the type sheets, there is no doubt that a single species is represented and that it is indeed the plant that has been passing as *P. debilis* or *P. niruri* var. *debilis*.

DISTRIBUTION: native probably to southern India and Ceylon; introduced into Indonesia, the Pacific islands, and the West Indies.

LESSER ANTILLES. GUADELOUPE: Ste. Marie, Sous-le-Vent, Goyave, bananeraies recentes, alt. 60 m., 28 July 1936, *Stehlé 1132* (NY); Petit Bourg, 12 Mar. 1936, *Rodriguez 4901* (P).

The description is based on examination of the West Indian and the following additional collections:

INDIA: without locality, Herb. Wight, *Wallich 7895D* (K). BOMBAY: Concan, *Stocks* (GH, mixed with *P. amarus*). CEYLON: Peradeniya, *de Silva 17* (A). INDONESIA. JAVA: *Herb. Hasskarl* (L); Buitenzorg, *Hallier* (L). SUMATRA: Aer Djoman, *Boeea 8313* (A). MICRONESIA. BONINS: Chichi Jima, *Fosberg 31550* (US). MARIANAS: Saipan, *Fosberg 25228* (US). PALAU: *Hosokawa 7494* (US); Koror, *Fosberg 32066B* (US). PONAPE: *Glassman 2556B* (US). HAWAIIAN ISLANDS. OAHU: Honolulu, *Degener 9118, 19286* (GH), *Fosberg 10755* (A).

This species, a newcomer to the Caribbean, cannot be said to have established itself as part of the weedy flora; however, it seems proper to include it in the expectation that it may be introduced into additional islands in the future.

The circumscription of *P. debilis*, which is a rather widely dispersed weed, is attended by difficulties that unfortunately have not been entirely resolved in the present study. Together with *P. fraternus*, *P. rotundifolius*, and a few other related Old World plants, *P. debilis* belongs to a difficult species complex which has still to be critically analyzed. Mueller had such a confused concept of several of these species that it has been most difficult to untangle his synonymy and the work of those who have followed his treatment. He considered the species *P. niruri* to be typified by the plant now known as *P. amarus* (his var. *genuinus*), while *P. debilis* and *P. fraternus* (plus the distantly related *P. pentaphyllus*!) were appended as varieties. Hooker, who had a clearer understanding of these plants, recognized *P. debilis* as distinct; but his description is inaccurate in some details.

The closest relative of *P. debilis* is undoubtedly *P. fraternus*, although the latter usually differs so much in aspect that it has more often been confused with *P. amarus* than with *P. debilis*. The nature of the relationship between *P. debilis* and *P. fraternus* will be discussed below under the latter species.

It seems probable that the *Kirganeli* of Rheede (Hort. Malabar. **10**: 29, *pl. 15*. 1682) and the *Jatha-Aembula* of Hermann (ex Burman, Thes. Zeyl. 230. 1737), which have graced the synonymies of various species, actually represent *P. debilis*. Rheede's figure is characteristic, and when the known distribution of the various Indian species of sect. *Phyllanthus* are taken into account, it appears that he and Hermann are more likely to have had *P. debilis* than any other species.

19. **Phyllanthus fraternus** Webster, Contr. Gray Herb. **176**: 53. 1955. (PLATE XIX, *figs. G–H*).

Phyllanthus scabrellus Webb in Hook. Niger Fl. 175–176. 1849; ex p. (excl. typ.).

Phyllanthus niruri β scabrellus Muell. Arg. Linnaea 32: 43. 1863; DC. Prodr. **15**(2): 406. 1866, as *γ scabrellus*.

Phyllanthus niruri sensu Hook. f. Fl. Br. Ind. **5**: 298. 1887 (ex p.); sensu Hutch. in Fl. Trop. Afr. **6**(1): 731. 1912 (as to description).

Erect annual herb c. 1.5–4 dm. high, the main stem mostly 1–2 mm. thick, subterete, above with narrow sharp angles running longitudinally between the nodes, smooth, stramineous, the internodes c. 1–3 (–4) cm. long. Cataphylls: stipules lanceolate, 0.8–1.3 mm. long, 0.25–0.4 mm. broad, entire, truncate at the base (definitely not auriculate) pale and scarious; blade narrower. Deciduous branchlets (2–) 4–8 (–10) cm. long (0.3–) 0.4–0.5 mm. thick, subterete with a narrow sharp wing on either side, obscurely to densely scabridulous along the wing-edge and sometimes scabridulous between the wings as well, with mostly 10–30 leaves; first internode (8–) 10–18 (–23) mm. long, median internodes (1.5–) 2–3.5 mm. long. Leaves: stipules narrowly lanceolate, 0.7–1.2 mm. long, 0.15–0.3 mm. broad, acuminate, entire, whitish and scarious except for the narrow olivaceous midstrip. Petioles 0.3–0.6 mm. long. Leaf-blades membranous, smooth and glabrous, elliptic-oblong, 6–11 mm. long, 3–5 mm. broad, rounded at the tip, cuneate to obtuse at the base; above dark green, only the plane midrib visible; beneath paler, greyish, the midrib somewhat raised, the laterals (4–7 on a side) conspicuous, ascending, connecting near the margin, the anastomosing tertiary veinlets forming a delicate (sometimes quite obscure) reticulum; margins unthickened, plane, smooth or minutely roughened.

Monoecious; cymules unisexual. Proximal (2–) 3–5 nodes of branchlet with male cymules of 2 or 3 flowers; succeeding nodes with solitary female flowers; transitional node occasionally with a bisexual cymule.

Male flower: pedicel 0.25–0.5 mm. long. Calyx-lobes 6, subequal, elliptic to obovate, c. 0.4–0.6 (–0.7) mm. long, 0.3–0.5 (–0.6) mm. broad, obtuse or rounded at the tip, yellowish and scarious, the midrib unbranched. Disk-segments 6, more or less angled or lobed, obscurely glandular, c. 0.1 mm. broad. Stamens 3, filaments united into a column 0.1–0.25 mm. high; anthers sessile or subsessile atop the column, deltoid, obtuse, c. 0.1 mm. long, 0.15–0.2 mm. broad; anther-sacs divaricate, the slits apically confluent, dehiscing horizontally or nearly so; pollen grains finely reticulate, 19.5–25 μ long, 18–21.5 μ broad.

Female flower: pedicel becoming (1.3–) 1.5–2 mm. long, olivaceous, smooth, angled or subterete. Calyx-lobes 6, often unequal (one or two distinctly smaller than the others), narrowly obovate to linear-spathulate in fruit, (1–) 1.2–1.5 mm. long, 0.35–0.8 mm. broad, rounded to subacute at the tip, with broad scarious margins (the narrow herbaceous midstrip 1/3 the breadth of each calyx-lobe or less), the midrib unbranched. Disk an irregular cup deeply lobed or parted into 6–9 crenulate-lacerate segments. Styles only 0.1–0.15 (–0.2) mm. long, free, erect or ascending, very briefly bifid at the tip, the style-branches blunt, about as thick as long, recurving.

Capsule oblate, c. 2.1 mm. in diameter, stramineous or reddish-brown, smooth, the veins completely obscure. Seeds c. 0.95–1.1 mm. long, 0.7–0.8 mm. radially and tangentially, light yellowish-brown, with c. 6 or 7 straight (only rarely anastomosing) slightly elevated longitudinal ribs and many fine transverse striae on the back.

TYPE: India, Punjab, Tummooghat, Ravee-Chenab Doeb, Oct. 1846, *Thomas Thomson* (K, HOLOTYPE; GH, ISOTYPE). A word of clarification is necessary regarding the typification of this species. Mueller (Linnaea **32**: 43. 1863; DC. Prodr. **15**[2]: 405–406. 1866) referred *P. scabrellus* Webb partly to *P. rotundifolius* Klein ex Willd. and partly to *P. amarus* ("P. niruri") as var. *scabrellus*. It might be concluded that in the latter case he was transferring Webb's name and that the type of Webb's species would belong with the present plant; if such were the case, then the species described above would have to be called *P. scabrellus*. However, it is quite clear from Webb's description and citation of specimens that his proposed species was based mainly on specimens of *P. rotundifolius* (e.g., St. Jago, Cape Verde Islands, *Hooker* [GH, SYNTYPE]) and that he merely cited incidentally the Perrottet specimen which represents *P. fraternus*. Mueller thus in publishing Perrottet's plant as a variety of *P. niruri* adopted Webb's epithet but in such a manner that it evidently must be treated as a new name.

DISTRIBUTION: native probably to West Pakistan and western India; introduced into Africa and the West Indies.

BERMUDA: weed in field, *Collins 225* (GH, NY); Smith's Parish, roadside at church, *Degener 995* (A); Hotel Frascati, *Moore 2973* (GH). CUBA: low pine woods, El Salado [prov. Pinar del Río?], *Wright 1675* ex p. (NY, mixed with *P. procerus*). BARBADOS: *Freeman 215* (NY); *W. Wright* (BR, annotated by Mueller as *P. niruri* var. *genuinus*). TRINIDAD: *Finlay* (TRIN 2461); in Dr. Finlay's garden, *Kuntze 989* (NY).

The description is based on examination of the type collection, the West Indian specimens cited above, and the following:

INDIA: "East India", *Roxburgh* [Hb. Forsyth] (K). BENGAL: *Griffith* (GH). KUMAON: Bagesar, *Strachey & Winterbottom 2* (GH).

A prolonged study of the available specimens of the complex which Mueller included in his "P. niruri" has made it clear that I acted too hastily in reducing *P. fraternus* to the status of a synonym of *P. asperulatus* Hutch. This disposition (Jour. Arnold Arb. **37**: 8. 1956) was made after comparison with the type (*Schlechter 11866*, Komati Poort, Transvaal [K]); but later more detailed study of a duplicate sheet in the Gray Herbarium indicates that *P. fraternus* and *P. asperulatus* are by no means identical and had best be kept separate for the time being. The plant collected by Schlechter differs from *P. fraternus* in its slightly longer fruiting pedicels and especially in its entire female disk and spreading styles. In the latter two characters, indeed, *P. asperulatus* agrees much better with *P. debilis*, although its leaf shape and scabridulous branchlets suggest *P. fraternus*. From both *P. debilis* and *P. fraternus*, *P. asperulatus* differs in the broader green midstrip of its calyx-lobes; but this is admittedly not a very convincing distinction. Unfortunately, no seeds of *P. asperulatus* have been seen; these might possibly furnish additional distinguishing characters. For the present, one can only conclude that *P. asperulatus* represents an entity closely related to both *P. debilis* and *P. fraternus*, but that its exact affinity cannot be determined at this time.

In the original publication of *P. fraternus* it was remarked that the species was rather closely related to *P. amarus*. Although that statement is correct as far as it goes, it should be made clear that the closest relative of *P. fraternus* is *P. debilis*. Typical specimens of the two differ so strongly in aspect (due to the more angled stems and narrower leaves of *P. debilis*) that on casual inspection the two species may appear to be very distinct. However, *P. debilis* proves to be so variable with respect to both angularity of stem and leaf shape that vegetative distinctions alone are insufficient to distinguish the two species. The very similar male flowers are so small that it is impossible to tell if any significant size differences exist; and the seeds appear almost identical. The only sure mark of distinction, therefore, lies in the female flowers; and here, too, the size of the floral parts is so small that measurement with a conventional binocular microscope is too inexact to reveal significant differences. Fortunately, certain qualitative characters are readily visible under low magnification: the disk of the female flower of *P. fraternus* is always deeply dissected into irregular segments, and the short styles are erect or at least ascending at a 45° angle, while the style-branches are very short and blunt. In contrast, the disk of the female flower of *P. debilis* is a shallow cup with a continuous rim which is merely angled or at most shallowly lobed; and the styles are appressed to the ovary (at least at the tips) and much more deeply parted. The erect vs. appressed character of the styles of the two species may be observed even in young buds, so that here it is not a feature which becomes highly modified during ontogeny (as is the case in some other species).

Although these characters of the female flower appear to be constant, so that they will serve dependably to separate the two species, it must be confessed that in the majority of features the two are extremely similar. It is possible that a future study, based on the examination of many more specimens from India than have been available here, may demonstrate that the two taxa should be considered subspecies of a single variable species (which might also include such forms as *P. asperulatus*). Supporting this possibility is the fact that specimens more or less intermediate between *P. fraternus* and *P. debilis* have been observed. One of these is the Griffith collection from "Bengal Presidency" cited above, which has vegetative features much as in *P. debilis* but which in floral characters agrees with *P. fraternus*. On the basis of the specimens cited and others examined at Kew (not referred to in the writing of the description), it appears that *P. fraternus* occupies a range chiefly in West Pakistan (Indus River valley) and northwestern India (Punjab and United Provinces), while *P. debilis* is mainly distributed from Bombay and Madras south to Ceylon, and also in Sikkim and Bhutan. Only in Bengal is it clear that the two come together, and it is here that the intermediate specimen occurs. This gives the impression of two allopatric subspecies of a single species which interbreed where brought together; but at present the documentation for this possibility is so slight that it appears most practical to retain *P. debilis* and *P. fraternus*, at least provisionally, as distinct species.

Phyllanthus fraternus has also been introduced into Africa, on the basis of at least one specimen examined (Senegal, *Perrottet 755* [G]); and Hutchinson's description of "P. niruri" appears to be based mainly on the present species, although it has not been possible to check any of the other specimens cited. In the later treatment by Hutchinson & Dalziel (Fl. W. Trop. Afr. 1: 290–291. 1928) *P. fraternus* still appears as "P. niruri." In most of the tropics, however, *P. fraternus* is very much less common than *P. amarus* and so far has not been reported from South America, eastern Asia, or the Pacific Islands.

20. **Phyllanthus amarus** Schum. & Thonn. Kongl. Danske Vidensk. Selsk. Skr. **4**: 195–196. 1829. (PLATE XIX, *figs. I–K*).

Fruticulus capsularis, hexapetalis &c. Pluk. Phytogr. 3: *pl. 183, fig. 5.* 1692.
Phyllanthus urinaria sensu L. Sp. Pl. 982. 1753; ex p. (excl. typ.).
Phyllanthus niruri sensu Sw. Obs. Bot. 354–355. 1791 (ex p.).
Phyllanthus swarzii Kostel. Allgem. Med. Pharm. Fl. 1771. 1836.
Phyllanthus niruri β genuinus Muell. Arg. in DC. Prodr. **15**(2): 406. 1866. Non *P. niruri* L.
Phyllanthus nanus Hook. f. Fl. Br. Ind. **5**: 298. 1887.

Erect annual herb (sometimes slightly woody at the base) 1–5 dm. high, the main stem simple or branched, smooth, terete, stramineous or brownish, c. 1.5–2 mm. thick; internodes mostly 1–3 cm. long. Cataphylls: stipules broadly deltoid, 1.3–2.1 mm. long, 0.6–1 mm. broad, acuminate, entire, scarious, brownish; blade subulate, acuminate, c. 1–1.5 mm. long. Deciduous branchlets 4–12 cm. long, c. 0.4–0.5 mm. thick, subterete (never winged or sharply angled), smooth or sometimes slightly scabridulous in the first internode, with c. 15–30 leaves; first internode 5–14 mm. long, median internodes c. 2–3 mm. long. Leaves: stipules ovate-lanceolate or lanceolate, 0.8–1.3 mm. long, 0.2–0.4 mm. broad, acuminate (often attenuately so), scarious except for the narrow yellowish-green midstrip, entire. Petioles 0.3–0.5 mm. long. Leaf-blades membranous or somewhat thickened, usually elliptic-oblong (sometimes somewhat obovate), mostly 5–11 mm. long and 3–6 mm. broad, obtuse or rounded and often apiculate at the tip, obtuse or rounded and sometimes slightly inequilateral at the base; above bright green, the midrib raised, the laterals invisible; beneath greyish or glaucous, the midrib and laterals (c. 4 or 5 on a side) raised and conspicuous, the tertiary veinlets forming a delicate reticulum or sometimes obscure; margins plane, not especially thickened, smooth or obscurely and minutely roughened.

Monoecious; proximal (1–) 2 axils with unisexual cymules of (1–) 2 male flowers, all succeeding axils with bisexual cymules, each consisting of one male and one female flower.

Male flower: pedicel 0.6–1.3 mm. long. Calyx-lobes 5 (very rarely 6), subequal, ovate or elliptic, 0.3–0.6 mm. long, 0.2–0.55 mm. broad, abruptly acute, herbaceous with broad scarious margins, the midrib unbranched. Disk-segments 5, orbicular, c. 0.1 mm. in diameter, entire, not glandular. Stamens 3 (rarely 2); filaments completely connate into a column 0.2–0.3 mm. high; anthers sessile atop the column, one often reduced to a single anther-sac (or sometimes only 2 functional anthers present), 0.2–0.3 mm. broad; anther-sacs divergent, the silts completely confluent, dehiscing obliquely to less commonly horizontally; pollen grains finely reticulate, 19–23 μ long, 16–21 μ broad.

Female flower: pedicel c. 0.6–0.75 mm. in anthesis, becoming (1–) 1.2–1.7 (–2) mm. long, terete or somewhat angled, smooth, olivaceous. Calyx-lobes 5 (very rarely 6), obovate-oblong, becoming (0.75–) 0.9–1.1

mm. long and (0.25–) 0.4–0.6 mm. broad, acute, herbaceous with rather broad yellowish-white scarious margins (the green midstrip c. 1/3 the breadth of the calyx-lobe), the midrib unbranched. Disk flat, deeply 5-lobed, sometimes with 1 or more small extra lobes, otherwise entire, not glandular. Styles free, erect or ascending (later becoming more or less spreading), c. 0.1–0.15 mm. long, very shallowly bifid, the lobes blunt. Capsule oblate, obtusely trigonous, (1.8–) 1.9–2.1 mm. in diameter, smooth, stramineous, the veins almost or completely invisible. Seeds sharply trigonous, light brown, 0.9–1 mm. long, 0.7–0.8 mm. radially and tangentially, with 5 or 6 straight parallel longitudinal ribs on the back (these rarely or never anastomosing), minutely transversely striate with hygroscopic cells which project as hyaline setae with a pronounced notching of the lumen.

Collected flowering and fruiting throughout the year.

TYPE: Africa, Guinea, *Schumacher & Thonning* (C, HOLOTYPE, not seen; K, type fragment and sketches).

DISTRIBUTION: native to America, now a circumtropical weed. It being impracticable to cite all the specimens examined of this ubiquitous species (which probably occurs on all the islands of the West Indies), only the following representative collections are listed.

BERMUDA: *Brown & Britton 369* (F, GH, NY, US). BAHAMAS: Castle Island, *Wilson 7802* (F, GH, MO, NY). CUBA: Santiago de las Vegas, *Wilson 1075* (F, GH, L, MO, NY, P, US). JAMAICA: Hope Gardens, *Harris 12136* (C, F, GH, JAM, NY, P, US). HAITI: Gros Morne, *Leonard 9803* (US). DOMINICAN REPUBLIC: Paraíso, *Fuertes 1004* (F, GH, NY, P, US). PUERTO RICO: Santurce, *Heller 6406* (F, GH, NY, P, US). ST. THOMAS: *Wydler 76bis* (F, NY). ST. CROIX: *Ricksecker 132* (GH, NY, US). ST. MARTIN: *Rijgersmaa* (S). ST. BARTHELEMY: *von Goes* (S). GUADELOUPE: *Duss 2447* (NY). DOMINICA: *W. & B. Hodge 3038* (GH). MARTINIQUE: *Sieber Herb. Mart. Suppl. 3* (F). ST. VINCENT: *Morton 5156* (US). GRENADINES: Carriacou, *Howard 10871* (GH). GRENADA: *Broadway 4437* (BR). TOBAGO: *Broadway 3064* (F, GH, L, P). TRINIDAD: *Baker* (TRIN 14789).

Although it is doubtless the commonest species in the genus, *P. amarus* has been poorly understood up to the present. Linnaeus initiated much of the confusion by listing Plukenet's reference to *P. amarus* in the synonymy of *P. niruri*, although he filed his only specimen of the former with *P. urinaria* (in the Linnaean Herbarium). Swartz (Obs. Bot. 355. 1791) unfortunately completed the confusion by confounding *P. amarus* and two other species (neither of them Linnaeus's plant!) under "P. niruri" and observing that the Linnaean species appeared to have been introduced into Jamaica from the East Indies. Baillon (Adansonia **2**: 18. 1861) definitely regarded *P. niruri* as an "East Indian" species; but his concept, to judge from the specimens he cited, was based on a mixture of *P. amarus* and *P. stipulatus*. Mueller stabilized the situation by equating *P. amarus* with the typical variety (*genuinus*) of his polytypic *P. niruri*, and as a result the specimens of *P. amarus* from America and Asia have been 100 percent misidentified. Further details of the nomenclatural history have been reviewed previously (Jour. Arnold Arb. 37: 6–8. 1956) and need not be repeated here.

Although superficially *P. amarus* resembles many other species in sect. *Phyllanthus*, it is taxonomically rather isolated and can always be identified even from fragmentary herbarium specimens. Its best distinguishing feature is the inflorescence of bisexual rather than unisexual cymules; but in addition, the pentamerous calyx with acute lobes, the very short erect styles, and the usually 5-lobed female disk together make it easy (at least with the use of a lens) to distinguish *P. amarus* from such apparently similar plants as *P. stipulatus* or *P. fraternus*. The seeds of *P. amarus*, however, are very similar to those of *P. fraternus*, which in a number of ways appears to be rather closely related to the present species.

The closest relative of *P. amarus*, however, is undoubtedly *P. abnormis* Baill. of the southern United States, which is the only other species in the subsection with bisexual cymules. The two resemble one another in so many respects that they are obviously intimately related, although *P. abnormis* is unquestionably distinct by virtue of its larger capsule, perennial habit, and 4-merous male calyx. This close affinity with *P. abnormis* is incidentally perhaps the best evidence that *P. amarus* is a natively American species, which probably originated somewhere in the Caribbean area before it began its highly successful peregrinations in the footsteps of man.

21. **Phyllanthus stipulatus** (Raf.) Webster, Contr. Gray Herb. 176: 53. 1955. (PLATE XIX, *figs*, *L–M*).

Phyllanthus niruri sensu Sw. Obs. Bot. 354–355. 1791 (ex p.).
Moeroris stipulata Raf. Sylva Tellur. 91–92. 1838.
Phyllanthus diffusus Klotzsch, Bot. Voy. Herald 105. 1853.
Phyllanthus hoffmannseggii Muell. Arg. Linnaea **32**: 45. 1863.
Phyllanthus diffusus α *genuinus* Muell. Arg. in DC. Prodr. **15**(2): 409–410. 1866.
Phyllanthus aquaticus Wright, Anal. Acad. Ci. Habana **7**: 110. 1870.
Diasperus diffusus (Kl. "em.") O. Ktze. Rev. Gen. **2**: 599. 1891.

Erect annual herb, usually with a single sparsely to copiously branching main stem 2–5 (–10) dm. high and 1–2 (–4) mm. thick, sometimes spongy or bladdery at base (when plant grows in water), above light brown, smooth, terete; internodes (0.5–) 1.5–5 (–6) cm. long. Cataphylls: stipules triangular, (0.6–) 0.7–1 mm. long, (0.3–) 0.4–0.6 mm. broad, acuminate, not auriculate at base (or at most obscurely so), entire, light reddish-brown becoming darker, but remaining thin and scarious; blade linear-lanceolate, acuminate, 0.5–0.9 mm. long, 0.1–0.3 mm. broad. Deciduous branchlets (1–) 2–6 (–9) cm. long, light brown, often reddish-tinged, smooth or scabridulous, more or less terete, with (12–) 15–30 (–35) leaves; first internode 2.5–13 mm. long, internodes between male flowers 1–2.7 mm. long, between female flowers 1.3–3 mm. long. Leaves: stipules lanceolate, (0.5–) 0.7–1 mm. long, (0.1–) 0.2–0.3 mm. broad, acuminate-attenuate, entire, reddish-brown, scarious. Petioles 0.4–0.6 mm. long. Leaf-blades membranous to chartaceous, smooth or minutely scabridulous on one or both sides, mostly oblong-elliptic but sometimes ovate or suborbicular, (2.5–) 3–10 (–13) mm. long, 2–4 (–6) mm. broad, obtuse or rounded to nearly truncate at the tip, obtuse or rounded at the base, not oblique or scarcely so; above bright green, midrib raised in lower half, running obscurely to the tip, the laterals obscure; beneath pale, the midrib raised, the laterals (4–6 on a side) rather conspicuous, the reticulum of tertiary veinlets evident to obscure; margins smooth, not especially thickened, often reddish-tinged.

Monoecious; proximal (0–) 2–8 axils barren; succeeding (2–) 3–7 (–9) axils with monochasial cymules of 3–5 (–10) male flowers; distal axils with solitary female flowers.

Male flower: pedicel 0.4–0.7 mm. long. Calyx-lobes 5 (rarely 4 or 6), obovate or broadly elliptic to orbicular, (0.5–) 0.6–0.9 mm. long and about as broad, rounded at the tip, entire, pale yellowish, scarious except for the unbranched midrib. Disk-segments 5 (rarely 6), elliptic to orbicular, entire or crenulate-lobate, sometimes conspicuously glandular, c. 0.1–0.2 mm. across. Stamens 3 (rarely 2); filaments completely connate into a column c. 0.25–0.35 mm. high; anthers sessile atop the column, ascending, c. 0.2–0.25 mm. broad; anther-sacs divergent, the slits apically confluent, dehiscing more or less horizontally; pollen grains finely reticulate, 20–24 μ long, 17–21 μ broad.

Female flower: pedicel becoming 1.5–2.5 mm. long, olivaceous, minutely scabridulous or nearly smooth, terete below, somewhat angular above. Calyx-lobes 5, obovate, in flower c. 0.8–1.2 mm. long, in fruit becoming (1.2–) 1.4–1.8 (–2) mm. long and 0.8–1.3 (–1.5) mm. broad, obtuse or rounded at the tip, olivaceous with broad whitish scarious margins, the more or less dorsally carinate midrib unbranched. Disk patelliform and obscurely 5-angled or variously lobed, sometimes markedly asymmetric. Styles separate, ascending or spreading, 0.2–0.3 mm. long, bifid, the branches recurved, subcapitate at the tips.

Capsule c. 2.4–2.5 mm. in diameter, obscurely rugulose above, stramineous, the veins completely obscure. Seeds sharply trigonous, 1.1–1.3 mm. long, 0.8–0.9 mm. radially and tangentially, light brown, with c. 10–12 subpaired very delicate longitudinal striae (these often completely obscure), transversely banded with clavate hygroscopic epidermal cells.

Collected throughout the year.

TYPE: Jamaica, *Swartz* (S, HOLOTYPE). The typification of this species, which formed a portion of Swartz's concept of *P. niruri*, has been discussed in detail elsewhere (Jour. Arnold Arb. 37: 9. 1956).

DISTRIBUTION: widespread in tropical America, usually in moist habitats and sometimes growing in shallow water (MAP IX).

CUBA. PINAR DEL RÍO: Pinar del Río City, road to Matea Sanchez, *Ekman 17855* (NY, S); Santa Cruz de los Pinos, in savannas, *Ekman 17696* (S); "a la orilla de lagunas cerca de Pinar del Río" [ex Sauvalle], *Wright 3683* (F, GH, NY, P, S, US); type collection of *P. aquaticus* Wright). ISLA DE PINOS: Santa Barbara, Westport, *Ekman 12070* (S); road to San Francisco de las Piedras, *Killip 45238* (GH); Salta Mamey, *Killip 45276* (GH); San Pedro and vicinity, *Britton & Wilson 15437* (F, MO, NY, US).

JAMAICA: without exact locality, *Swartz* (S, HOLOTYPE). ST. ELIZABETH: Cornwall, shallow water in pond, *Harris 12555* (GH, JAM, MO, NY, US). CLARENDON: Hollis's Savanna, 2,400 ft. alt., *Harris 12224* (F, NY, P). ST. CATHERINE: boggy pond, 2 miles southwest of Ewarton, *Proctor 6177* (A).

HAITI. ARTIBONITE: St.-Michel de l'Atalaye, savannas toward Maissade, *Ekman H9406* (S).

DOMINICAN REPUBLIC. SAMANÁ: Peninsula Samaná, Samaná, road to Río San Juan, *Ekman H14836* (S); Peninsula Samaná, Sanchez, along the railroad in the Gran Estero, *Ekman H14721* (S). LA VEGA: Loma del Oro, cerca de Hatillo, alt. 240 m., *Jiménez 2697* (US). TRUJILLO: Villa Altagracia, *Ekman H11220* (A, S); savanna land between Bayaguana and Guerra, *R. A. & E. S. Howard 9895* (GH). SANTO DOMINGO: Llano Costero, Cuenca, *Ekman H10093* (S).

PUERTO RICO: without specific locality, *Ridley* (G), *Herb. Ventenat* (G). AGUADILLA: near Lares, *Underwood & Griggs* (NY). GUAYAMA: mountain between Guayama and Cayey, alt. 700–900 m., *Britton, Britton, & Brown 6359* (NY). MAYAGUEZ: Cabo Rojo, *Sintenis 775* ex p. (GH); Mayaguez, *Stevens 2516* (NY). SAN JUAN: Luquillo, Bayamon, *Otero 523* (A, MO); University Farm, Río Piedras, *Dale* (MICH); near Bayamon, *Underwood & Griggs 874* (NY).

LESSER ANTILLES. MONTSERRAT: near the lake of the mountains, alt. c. 1200 ft., *Shafer 179* (NY). GUADELOUPE: Dugommier (Gourbeyre), *Stehlé 1028* (NY); Basse-Terre, *Duss 214* (P); Plonel, *Rodriguez 3896* (P). MARTINIQUE: Saint-Pierre, Parnasse, Macouba, Marigot, *Duss 46* (NY); quartier du Lamentin, *Plée* (P). ST. VINCENT: 1826, *Parker* (P). TRINIDAD: without locality, *Finlay* (TRIN 2462); Piarco Savanna, *Baker* (TRIN 14855), *Warming 829* (C), *H. Wright P-10* (TRIN).

Phyllanthus stipulatus is a plant of predominantly moist habitats, and it often grows in shallow water in swamps, where it may develop aerenchyma prominently at the base of the stem. Its relatively narrow habitat preference explains the spottiness of its distribution as compared to the more nearly ubiquitous *P. amarus* of this same subsection. It has often been confused with *P. niruri* and *P. amarus*; but the first may be easily distinguished by its inequilateral leaves, narrower stipules, and verruculose seeds, while the latter is always recognizable by its bisexual cymules and narrower acute calyx-lobes. The species in the West Indies most closely related to *P. stipulatus* is undoubtedly *P. caribaeus*, which, however, differs in its partially united filaments and peculiar female disk.

Phyllanthus microphyllus H.B.K., of South America, is also similar but differs among other respects in being dioecious.

It is interesting that one of the species most similar to *P. stipulatus* is *P. nigericus* Brenan, recently (Kew Bull. **1950**: 215) described from tropical West Africa. This species, to judge from the description, is exceedingly similar to *P. stipulatus* in almost all morphological details except for its 9-lobed female disk and longer fruiting calyx-lobes. Its habitat preference, as cited for the type collection, is also like that of *P. stipulatus*. This close relationship between an American and African species, which is paralleled elsewhere in sect. *Phyllanthus*, presents an interesting and as yet unelucidated phytogeographic problem.

In contrast to such wide-ranging American species as *P. caroliniensis* and *P. niruri*, *P. stipulatus* exhibits little, if any, geographic variation. The variations which do occur, such as the production of 2 stamens instead of 3 or nearly orbicular leaves instead of elliptical ones, appear to have a purely random distribution throughout the range of the species. Mueller (DC. Prodr. **15**[2]: 410. 1866) distinguished a narrow-leaved var. *oblongifolius*, from South America, but this appears to be specifically distinct and identical with the plant he later (Fl. Bras. **11**[2]: 54. 1873) described as *P. minutulus*. It seems unlikely that any subspecific entities will ever be distinguished within *P. stipulatus*.

22. **Phyllanthus caribaeus** Urb. Symb. Ant. 5: 382–383. 1908. (PLATE XIX, *figs. N–O*).

Slender erect annual herb; primary stem simple, 1–3.5 dm. high, 0.5–2 mm. thick, stramineous or pale brown, smooth, terete; internodes mostly 2–4 cm. long. Cataphylls: stipules lanceolate, mostly 0.6–0.9 mm. long and 0.3–0.35 mm. broad, acuminate, scarious, entire, not auriculate at base, reddish-brown; blade linear-lanceolate, 0.5–0.8 mm. long. Deciduous branchlets (2–) 3–7 cm. long, 0.15–0.25 (–0.3) mm. thick, light brown, smooth or minutely scabridulous, terete or obtusely angled, with mostly 15–30 leaves; first internode 5–12 (–15) mm. long, median internodes 1–2 (–2.5) mm. long. Leaves: stipules lanceolate, (0.5–) 0.7–0.8 (–1) mm. long, c. 0.2–0.25 mm. broad, attenuate-acuminate, entire, reddish-brown with very narrow whitish edges, scarious. Petioles 0.3–0.4 mm. long. Leaf-blades membranous, minutely scabridulous on both sides, mostly ovate-oblong but sometimes elliptic (usually narrowed from below the middle to the tip), 4–8 mm. long, 2–3.3 mm. broad, obtuse at the tip, obtuse or truncate-rounded at the base; above bright green, the nerves rather obscure; beneath paler, the midrib prominent, the laterals (c. 4 or 5 on a side) quite evident, the tertiary veinlets forming a delicate reticulum; margins smooth or minutely roughened, scarcely if at all thickened, plane, sometimes reddish-tinged.

Monoecious; proximal (2–) 3–7 (–9) nodes barren, succeeding 4–6 (–8) nodes with bracteolate cymules of up to 4 or 5 successively maturing male flowers, distal nodes with solitary female flowers.

Male flower: pedicel c. 0.3–0.8 mm. long. Calyx-lobes 5, suborbicular or broader than long, 0.4–0.5 mm. long, 0.4–0.6 mm. broad, obtusely rounded to nearly truncate at the tip, entire, membranous, yellowish-white, the midrib unbranched. Disk-segments 5, cuneate or nearly round, 0.15–0.2 mm. across, glandular-crenate. Stamens 3, filaments c. 0.2–0.25 mm. long, united in the lower half into a slender column; anthers c. 0.1–0.15 mm. long, 0.15–0.2 mm. broad; anther-sacs divaricate, the slits apically confluent, dehiscing horizontally or nearly so; pollen grains finely reticulate, 20–22 μ long, 17–20 μ broad.

Female flower: pedicel becoming 1.5–2 mm. long, stramineous, minutely scabridulous or nearly smooth, terete below, angular and broader above. Calyx-lobes 5, oblong to obovate, somewhat unequal, c. 1–1.2 mm. long at anthesis, becoming 1.2–1.4 (–1.6) mm. long and 0.6–0.9 mm. broad in fruit, obtuse at the tip, entire, olivaceous in the middle with very broad whitish scarious margins, the midrib not evidently branched. Disk dissected into 3 erect narrowly linear somewhat unequal segments (the largest one often bifid or rarely double) c. 0.3–0.5 mm. long, these later spreading. Styles free, spreading or ascending, c. 0.25 mm. long, bifid, the branches spreading, the tips slightly thickened.

Capsule c. 2 mm. in diameter, stramineous, obscurely rugulose above, the veins completely obscure. Seeds yellowish-brown, 0.9–0.95 mm. long, 0.7–0.75 mm. radially and tangentially, with c. 10 very delicate longitudinal striae and many fine transverse bars.

Collected in flower and fruit September through March.

TYPE: Tobago, *Eggers 5733* (F, LECTOTYPE; NY, ISOTYPE). This Eggers collection is hereby designated as the lectotype, since Urban failed to make any distinction among the six collections he cited.

DISTRIBUTION: apparently endemic to the Lesser Antilles and Trinidad, but possibly to be discovered in South America (MAP IX).

LESSER ANTILLES. DOMINICA: Lisdara, pastureland weed, *Hodge 2425* (GH). ST. VINCENT: open places, fields, &c., *H. H. & G. W. Smith 515* ex p. (NY, mixed with *P. amarus*). GRENADA: banks of the main road, Animas, *Broadway* (F; NY, mixed with *P. urinaria*); cultivated ground, Grenville, *Hunnewell 19477* (GH). TOBAGO: Cradley, *Eggers 5733* (F, LECTOTYPE; NY, ISOTYPE); northside road, King's Bay to Charlotteville, *Freeman & Williams* (TRIN 11387).

TRINIDAD: without specific locality, *Wullschlaegel 1073* ex p. (W, mixed with *P. stipulatus*); Aripo Savanna, *Broadway 6489* (M, T, NY); Cascade, St. Ann's, on banks in shade, *Broadway 5124* (F, G, MO, NY); Long Stretch, *Broadway 6545* (MO, S); Maracas, road to the bay, south, *Broadway 6756* (F, MO, S); Morne Bleu, Arima, *Freeman* (TRIN 9566).

This species is closely related to *P. stipulatus* and at first glance may appear to be merely a slender form of that species. The leaves, however, tend to be more pointed, tapering the entire length from base to apex, whereas they are usually elliptic or oblong in *P. stipulatus*. Furthermore, *P. caribaeus* is well distinguished by its only partially connate filaments, peculiar female disk, and smaller seeds. Consequently, there can be little doubt that *P. caribaeus* merits specific rank despite its obviously very near relationship to *P. stipulatus.* It would be of considerable interest to study the two species in the field in St. Vincent or Trinidad, where they occur sympatrically, to determine what differences — if any — they show in habitat preference.

23. **Phyllanthus procerus** Wright, Anal. Acad. Ci. Habana 7: 149. 1870. (PLATE XIX, *figs, P–R*).

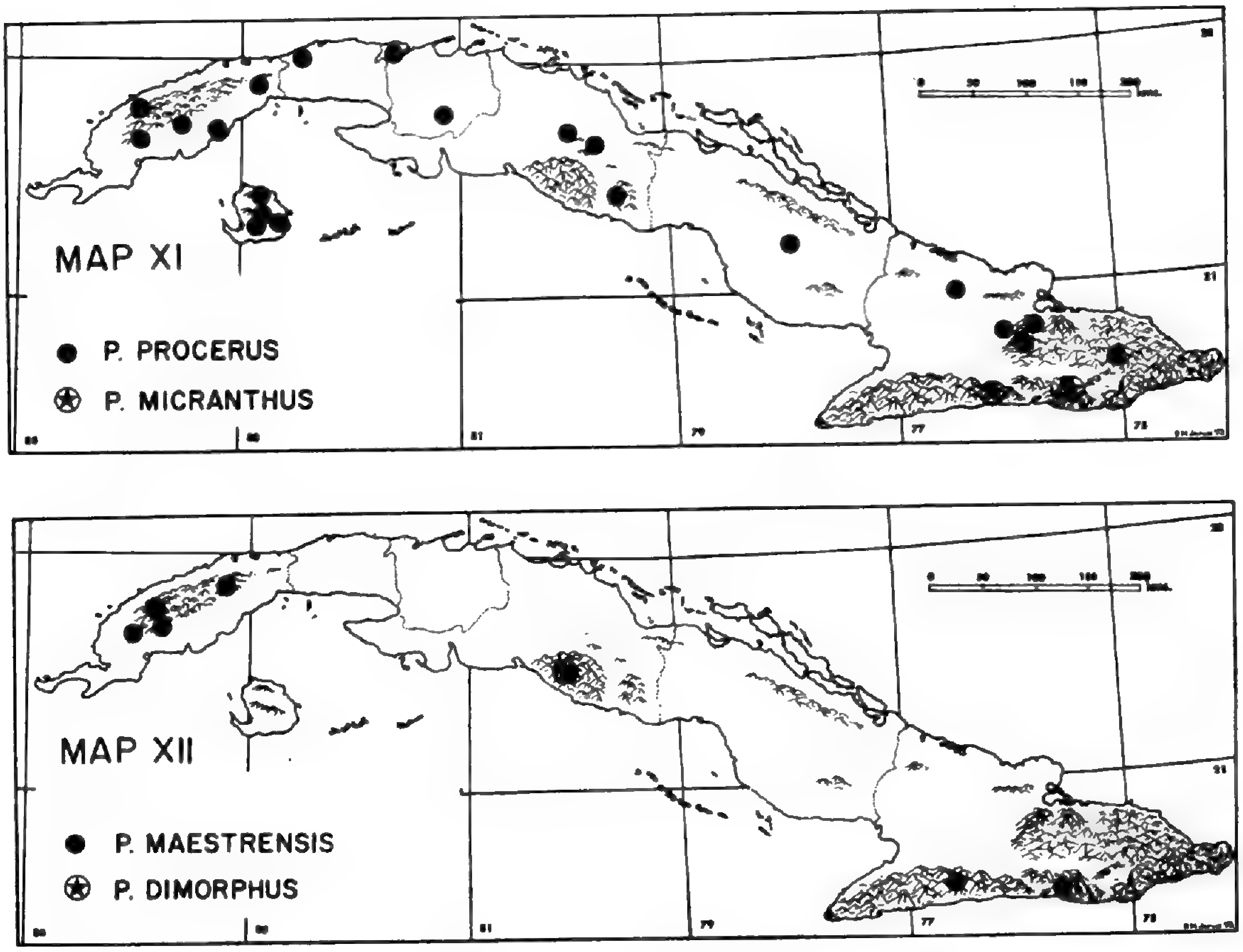
Slender to robust annual herb, usually with a single subsimple primary stem 1–7.5 dm. high, 0.5–1.5 mm. thick, light brown, smooth, terete, slightly channeled; internodes 1–9 cm. long (usually at least one or more as much as 2.5 cm. long). Cataphylls: stipules ovate-triangular, 0.6–1.5 mm. long, 0.4–0.8 mm. broad, acuminate, truncate or with a small usually poorly developed auricle at base, entire or obscurely toothed, pale pinkish-brown becoming reddish or dark brown, remaining scarious (never blackish and indurate); blade linear-lanceolate, acuminate, 0.5–1 mm. long. Deciduous branchlets (3–) 5–15 (–20) cm. long, 0.3–0.45 mm. thick, olivaceous, smooth, terete or obscurely angled, with (20–) 30–60 leaves; first internode (2–) 3.5–11 mm. long, median internodes 1–3 mm. long. Leaves: stipules narrowly ovate-lanceolate, 0.5–1 mm. long, 0.15–0.3 mm. broad, acuminate, entire, brownish or pinkish with narrow whitish or yellowish margins. Petioles 0.2–0.4 mm. long. Leaf-blades membranous, linear to narrowly elliptic or ovate-oblong, (3–) 4–7 mm. long, 1–1.8 mm. broad, obtuse or rounded and more or less apiculate at the tip, obtuse at the base; above olivaceous, smooth, the midrib plane, the laterals completely obscure; beneath paler, smooth, the midrib proximally raised, the laterals (4 or 5 on a side) inconspicuous or obsolete; margins slightly thickened, smooth or obscurely roughened, sometimes slightly reddish-tinged.

Monoecious; proximal (0–) 4–18 (–30) nodes barren; succeeding (3–) 10–25 (–36) with racemiform cymules of 3–8 male flowers, the cymule axis c. 0.5 mm. (rarely to 0.75 mm.) long; distal nodes with solitary female flowers.

Male flower: pedicel 0.3–0.8 mm. long. Calyx-lobes 5, subequal, suborbicular to broadly obovate or obcordate, often broader than long, c. 0.5–0.7 mm. long and broad, rounded or emarginate at the tip, yellowish-white, the median area poorly demarcated from the broad scarious subhyaline margins, the midrib unbranched. Disk-segments 5, cuneate to orbicular, 0.15–0.2 mm. across, smooth, entire, not evidently glandular. Stamens usually 2, occasionally 3 but then the third anther usually reduced; filaments completely united into a column 0.2–0.25 mm. high; anthers sessile atop the column, more or less fused back-to-back by the connectives, c. 0.15–0.2 mm. long, 0.3–0.4 mm. broad; anther-sacs divergent, dehiscing horizontally, the slits apically confluent (and the slits of both anthers sometimes becoming confluent); pollen grains finely reticulate, 28–32 μ long, 25–27 μ broad.

Female flower: pedicel becoming 1.2–1.8 (–2) long, olivaceous, smooth, subterete, gradually dilated from the base upwards. Calyx-lobes 5, ovate to suborbicular at anthesis, in fruit becoming elliptic or obovate and 0.75–1 mm. long, 0.7–1 mm. broad, obtuse or rounded at the tip (sometimes acute in fruit), olivaceous with usually broad whitish scarious margins, the midrib unbranched. Disk obtusely (or less commonly, acutely) shallowly or deeply 5-lobed, smooth, rather thin. Styles free, horizontal or somewhat ascending, c. 0.15 mm. long, bifid c. ½ their length, the branches bent at a right angle and unequally thickened so that each style resembles the arm of a Maltese cross.

Capsule oblate, 2.3–2.5 mm. in diameter, light yellowish-brown, obscurely rugulose at the top, the veins not visible. Seeds (1.1–) 1.2–1.3 (–1.35) mm. long, 0.9–1.05 mm. radially, 0.8–1.05 mm. tangentially, fuscous (when mature), with c. 11–13 very tenuous subpaired longitudinal striae and many transverse striae (of not or scarcely hygroscopic cells) on the back, the intersections of longitudinal and transverse striae often darkened to give a banded effect.



Maps XI and XII. Distribution of some species of sect. *Phyllanthus* in Cuba.

Collected in flower and fruit throughout the year.

Type: Cuba, Pinar del Río, *Wright 3684* ex p. (GH, lectotype; NY, P, S, US, ISOTYPES). This collection consists of a mixture of *P. procerus* and *P. maestrensis*. However, since Wright's description of the flowers clearly does not apply to the latter element, which has introrse anthers, the name *P. procerus* must be associated with the other plant, which has been described above.

DISTRIBUTION: endemic to Cuba, usually occurring in savannas (MAP XI).

CUBA. PINAR DEL RÍO: Baños San Vicente, *Britton et al. 7483* (NY); among tall grasses in thickets surrounded by pine woods, Pinar del Río, *Wright 3684* (GH, LECTOTYPE; NY, P, S, US, ISOTYPES; data ex S); *Colpothrinax* savanna, Herradura, *Britton et al. 6465* (NY); Herradura to Paso Real, savanna, *Shafer 11747* (NY); San Gabriel to Pinal de la Catalina, sandy pineland, *Shafer 11852* (MO, NY); between Candelaria and Artemisa, *Wilson 1733* (NY); San Isidro, along arroyo, *Britton et al. 13961* (NY). ISLA DE PINOS: sabanas between Santa Barbara and Mina de Oro, *Killip 42789* (US); sabanas, Nueva Gerona, *Curtiss* (NY), *Killip 42547* (US); Nueva Gerona, Loma Vista, *Ekman 12372* (S); ditch along road, San Francisco de las Piedras, *Killip 42789* (US); fields, Finca Mamey, headwaters of Río Casas, *Killip 44705* (US); woods at base of Sierra de Caballos, near Presidio, *Killip 44534* (US); San Pedro, river woods, *Britton et al. 14457* (NY); sabanas near southeast corner of Cerro Daguilla, *Killip 43952* (US); field near pond, San Juan, *Killip 45332* (GH). HABANA: Punta Brava, *Baker & O'Donovan 3999* (NY). MATANZAS: Tetas de Camarioca, serpentine barren, *Britton et al. 14059* (NY, US); Jaguey Grande, pastures, *Ekman 16967* (S). LAS VILLAS: serpentine barrens near Santa Clara, *Britton et al. 6114* (F, NY), *Webster 4173* (GH, MICH); Lomas de Banao, *Luna 90* (NY); Placetas del Sur, palm barren, *Leon & Roca 8163* (NY); wet savannas, La Sierpe, south of Sancti Spiritus, *Alain 1562* (MICH). CAMAGUEY: savannas near Camaguey, *Britton et al. 13127* (NY). ORIENTE: roadside 8 km. west of Holguin, *Jervis 1961* (MICH); savanna, Hato del Medio, 23 Aug. 1860, *Wright 1936* (GH); Sierra de Nipe, Pinar de Mayarí, *Carabia 3807* (NY); in charrascales prope Río Pilote, *Ekman 2164* (S); open grass-covered places in pinelands near Río Piedra, *Ekman 1835* (S); open pines near Bandera trail, *Shafer 3245* (NY); San Andrés [near Monte Verde], margin of rivulets, *Wright* (W, probably *Wright 1675*); banks of Pinal Creek, Monte Verde, *Wright 1675* ex p. (GH); without definite locality, *Wright "420"* (GOET), *Wright* (S; these two collections representing either *Wright 1936* or *1675*).

This common species of savannas throughout Cuba is doubtlessly closely related to *P. micranthus*, to which it has been referred by Urban (Repert. Sp. Nov. 13: 452. 1914) and Alain (Fl. Cuba 3: 58. 1953). However, it appears to be sufficiently distinct by virtue of its peculiar stylar configuration and its smaller and broader male calyx-lobes. The anthers are definitely connate at their bases in *P. procerus*, and occasionally the slits of the two anthers become confluent so that the androecium approaches the synandrial condition of *P. dimorphus*; in *P. micranthus*, on the other hand, the anthers are discrete.

Also related to *P. procerus* is *P. maestrensis*, which unlike *P. micranthus* has a sympatric distribution in Pinar del Río; it has already been noted that Wright himself apparently gathered the two species together when he made the type collection of *P. procerus*. *Phyllanthus maestrensis* differs from *P. procerus* in its larger male flowers with introrse stamens, larger leaves, and indurate cataphyllary stipules.

24. **Phyllanthus fadyenii** Urb. Symb. Ant. **6**: 13. 1909; Fawc. & Rend. Fl. Jam. **4**:255. 1920. (PLATE XXII, *fig. A*).

Phyllanthus orbicularis sensu Griseb. Fl. Br. W. Ind. 34. 1859; non *P. orbicularis* H. B. K.

Apparently a subshrub or woody herb, glabrous; branches terete, 1–3 mm. thick, furrowed, smooth, or the bark somewhat cracking, greyish or dark brown. Cataphylls: stipules lanceolate, 1.5–1.8 mm. long, 0.6–0.7 mm. broad, acuminate, entire, not auriculate at the base, dark reddish-brown, becoming more or less persistent; blade linear-lanceolate, 1–1.5 mm. long, less than 0.3 mm. broad, acuminate. Deciduous branchlets (0.5–) 1–1.5 cm. long, 0.25–0.3 mm. thick, terete, smooth, reddish-brown, with (7–) 10–15 nodes; first internode c. 1.5–2.5 mm. long, median internodes 0.5–1.2 mm. long. Leaves: stipules linear-lanceolate, those of each pair slightly unequal, 1.1–1.3 mm. long, 0.2–0.3 mm. broad, acuminate (or sometimes bluntish), reddish-brown, firm, persistent. Petiole 0.2–0.3 (–0.4) mm. long. Leaf-blades firm but hardly coriaceous, broadly oblong or ovate, 4–5.5 mm. long, 2.5–4 mm. broad, rounded or obtuse at the tip, emarginate-cordate at the base; above olivaceous, the midrib plane, the laterals obsolete or invisible; beneath brownish, the midrib scarcely raised, the laterals (c. 4 or 5 on a side) conspicuous, straight, only slightly anastomosing; margins somewhat thickened, deeply reddish-tinged, plane.

Monoecious; flowers apparently solitary or paired, the male and female flowers at separate axils.

Male flower: pedicel less than 1 mm. long. Calyx-lobes 5, subequal, broadly obovate or suborbicular, 0.7–0.8 [–1.2, ex Urban] mm. long, 0.6–0.9 mm. broad, the midrib unbranched. Disk-segments 5, reniform, smooth, entire, c. 0.2 mm. broad. Stamens 3; filaments free, becoming 0.5 mm. long (Urban); anthers erect, 0.3–0.4 mm. long, 0.4–0.5 mm. broad; anther-sacs divergent, opening longitudinally.

Female flower: pedicel 3–3.5 mm. long. Calyx-lobes 5, subequal, suborbicular or broadly elliptic in fruit, 1.7–2 mm. long, 1.4–1.7 mm. broad, rounded at the tip, entire, herbaceous with narrow and inconspicuous pale scarious margins, the midrib unbranched. Disk shallowly cupuliform, thin, the rim undulate. Ovary smooth, subglobose; styles coherent at the base, spreading, 0.2 mm. long, bifid, the branches reflexed with thickened subcapitate tips.

Capsule and seeds not seen; persistent columella 0.7 mm. long.

TYPE: Jamaica, *McFadyen* (K, HOLOTYPE).

DISTRIBUTION: known only from the type collection.

Although this plant is still incompletely known, there is little doubt that it belongs in sect. *Phyllanthus*; as Urban pointed out, it has nothing more in common with *P. orbicularis* (sect. *Orbicularia*) than a superficially similar aspect. However, the place of *P. faydenii* within subsect. *Swartziani* is very doubtful, for its woody stems and free stamens do not accord with the subsectional character. When pollen grains and seeds of *P. fadyenii* become available, it may be possible to assign it to a more definite position. For the present, it is kept in subsect. *Swartziani* because of its non-auriculate stipules, but it should be noted that in aspect it resembles such species of subsect. *Pentaphylli* as *P. selbyi* and may ultimately prove to belong to that subsection.

Subsect. 11c. **Pentaphylli** Webster, Contr. Gray Herb. **176**: 54. 1955.

Annual or perennial herbs, sometimes woody at the base; cataphyllary stipules conspicuously auriculate at the base, usually blackened and indurate; leaves equilateral at base; branchlet stipules not involute; monoecious or dioecious, cymules unisexual; calyx-lobes 5 or 6; stamens 2 or 3, filaments partially to wholly united, pollen grains 3-colporate, finely or coarsely reticulate; female disk patelliform or variously lobed or divided; styles free, deeply to shallowly bifid, the tips not capitate; seeds finely longitudinally striate or banded and transversely striate or barred.

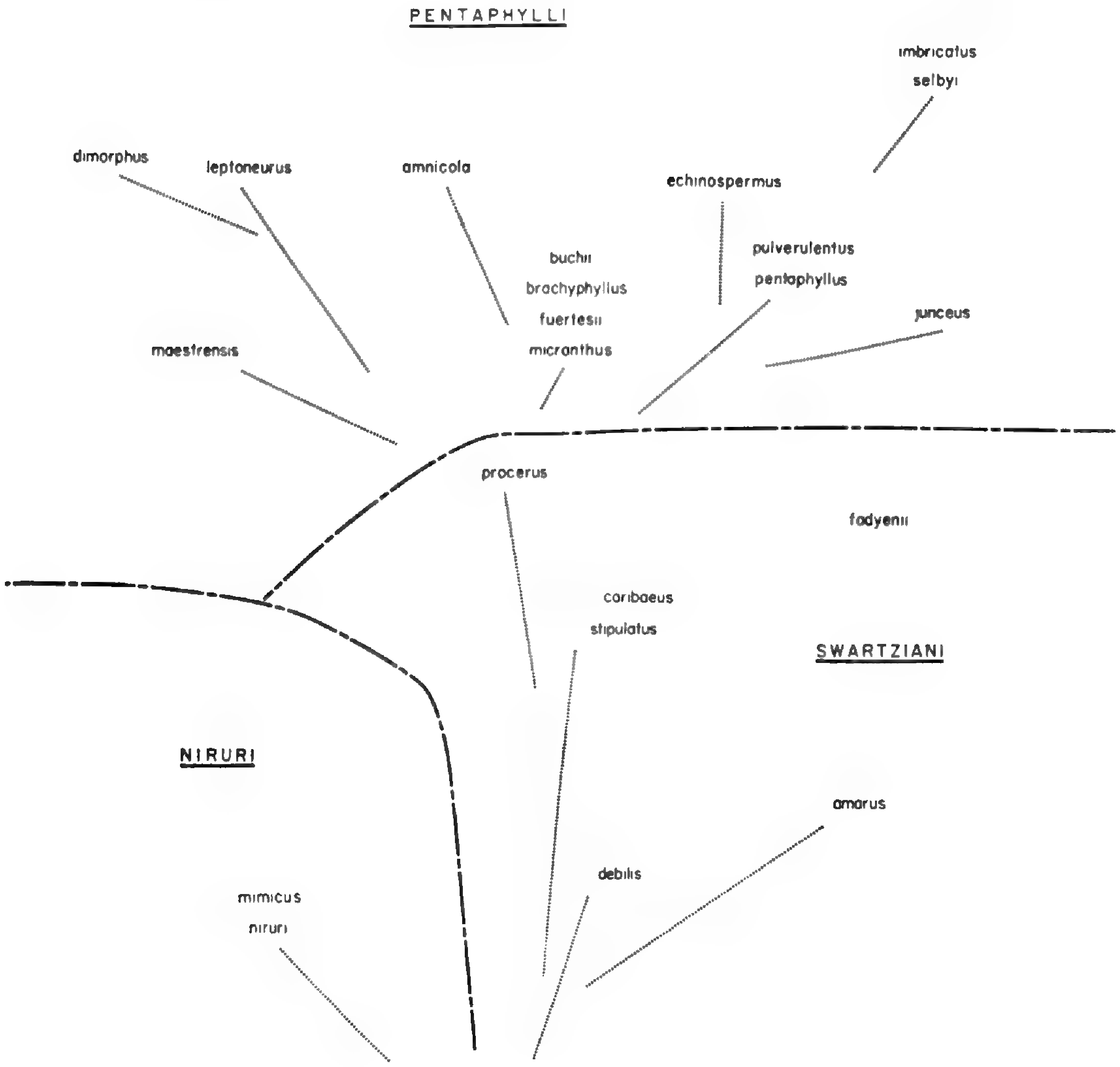
TYPE SPECIES: *Phyllanthus pentaphyllus* Wright.

Subsect. *Pentaphylli*, which appears to be essentially endemic to the West Indies, shares with sect. *Orbicularia* the distinction of having the largest number of endemic West Indian species and subspecies. As might be expected, its component species show adaptive radiation to a considerable variety of habitats, such as white sands along lagoons (*P. echinospermus*), savannas (*P. junceus*), coral platforms near the sea-coast (*P. pentaphyllus*), grassy hillsides (*P. dimorphus*), and stream-beds (*P. maestrensis*).

The variation in the male flowers — particularly with regard to the androecium — within this subsection is remarkably large; and on the basis of purely formal morphology, such species as *P. dimorphus* (with a synandrium like that of sect. *Cyclanthera*) and *P. maestrensis* (with unique introrse anthers) could be placed in special monotypic subsections. However, both of these species are manifestly rather closely related to species with conventional androecia.

The Cuban species of subsect. *Pentaphylli* are on the whole well-defined and not difficult to classify, but the situation is very different with regard to the species in Hispaniola. Here the species complex comprising *P. brachyphyllus*, *P. buchii*, and *P. fuertesii* has proved to be completely intractable to systematic analysis; these species cannot be satisfactorily demarcated from one another nor from *P. micranthus* of eastern Cuba. The numbers of stamens and calyx-lobes, which elsewhere are useful taxonomic characters, are here so variable that it is impossible to devise a really satisfactory key, even for the relatively few available specimens. Studies of leaf anatomy (including measurement of stomatal size) based on leaves cleared and stained in safranin or haematoxylin have yielded no conclusive results.

Examination of pollen grains has shown an unexpected distinction between *P. dimorphus* and *P. leptoneurus*, which have coarsely reticulate grains unique in sect. *Phyllanthus*, and the remaining species of the subsection, which have the finely reticulate grains of subsect. *Swartziani.* But within the *P. micranthus* complex, pollen studies have not been particularly rewarding. At first it was hoped that the presumed hybrid or intermediate nature of certain specimens could be confirmed by determination of the percentage of good pollen; but the results have been both puzzling and disappointing, for some presumptive hybrids proved to have apparently good



TEXT-FIG. 11. Diagrams of putative relationships within the indigenous West Indian species of sect. *Phyllanthus*. The three subsections are separated by black lines, while the apparent lineages of affinity are indicated by broken lines. The degree of relationship is roughly indicated by the distance between the different entities.

pollen, while some specimens which appeared to represent "pure" species yielded a large percentage of defective pollen. Thus, although there remains in many cases, a strong presumption of the hybrid nature of some collections, no decisive confirmation is forthcoming from examination of the pollen. The present treatment of the species of the *P. micranthus* complex is admittedly the least satisfactory portion of this entire study; but the problem appears to be insoluble on the basis of the herbarium material at hand and can probably be resolved only by laborious field study, including cytological analysis of the populations from which mongrel or dubious specimens have been collected.

In fortunate contrast to the obscure situation in the Hispaniolan species, the general phylogenetic relationships of subsect. *Pentaphylli* are rather more clear. It is quite evident that the subsection represents a local Antillean development from some ancestral form in subsect. *Swartziani*; and in fact *P. procerus*, certainly, and *P. fadyenii*, probably, may be considered directly related to the members of subsect. *Pentaphylli. Phyllanthus procerus*, indeed, resembles *P. micranthus* so closely that it has usually been combined with that species; but it clearly belongs in subsect. *Swartziani* because of its non-indurate, scarcely (if at all) auriculate cataphyllary stipules. It would thus appear that in passing from *P. procerus* to *P. micranthus* we have traced the origin of subsect. *Pentaphylli*, but — as is so often the case — the matter is not quite so simple as that. *Phyllanthus procerus* is highly specialized in a number of respects, particularly in its reduced androecium of two stamens and its peculiarly modified styles; it is therefore necessary to postulate some less highly modified species as the ancestor of subsect. *Pentaphylli. Phyllanthus fadyenii*, with its androecium of three free stamens and less highly specialized styles, may prove to be closer to the prototype, but its affinity must remain doubtful until its seeds and pollen grains can be studied.

The graphical arrangement of presumed species relationships (Text-fig. 11) is intended only to point out lines of affiliation but not to convey the impression that some species are any more "highly evolved" than others. Thus *P. procerus*, although placed at the base of the lines leading to the species of subsect. *Pentaphylli*, is not to be regarded as the ancestor of that subsection, but rather as the closest living relative of that ancestral form.

25. **Phyllanthus micranthus** A. Rich. Hist. Nat. Cuba 11: 216. 1850; Muell. Arg. in DC. Prodr. **15**(2):412. 1866. (PLATE XX, *fig. A*).

Diasperus micranthus (A. Rich.) O. Ktze. Rev. Gen. **2**: 600. 1891.

Perennial herb, suffruticose at the base, with few to several erect sparsely branched wand-like stems c. 3–6 dm. high; stems terete, smooth, silvery or brownish; internodes mostly 3–7 (–11) cm. long, 1–1.5 mm. thick. Cataphylls: stipules triangular-ovate, (0.6–) 1–1.4 mm. long, 0.5–0.7 mm. broad, acuminate, entire or basally dentate, conspicuously auriculate, reddish and scarious becoming darker and rigid or reddish-black and indurate from the first; blade linear-lanceolate, 0.5–0.9 mm. long. Deciduous branchlets (3.5–) 5–13 (–35) cm. long, 0.15–0.3 mm. thick, subterete or obtusely angled, smooth, brownish, with 25–50 (–75) leaves; first internode 4–7 mm. long, median internodes 2.5–4.5 mm. long. Leaves: stipules subpersistent, narrowly lanceolate, 0.6–0.9 mm. long, 0.2–0.3 mm. broad, acuminate, somewhat dilated basally, olivaceous becoming reddish, entire. Petioles 0.3–0.5 mm. long. Leaf-blades membranous, linear-oblong, 4–7 mm. long, 1.2–1.7 mm. broad, acute to obtuse-apiculate at the tip, acute to obtuse at the base; above dark green, the midrib somewhat raised above and below, the laterals obsolete on both sides, pale beneath; margins unthickened, plane, more or less smooth.

Dioecious; first (0–) 2–4 (–8) nodes of male branches barren, succeeding nodes with racemiform cymules of 3-5 male flowers; female flowers solitary.

Male flower: pedicel 0.6–1.1 mm. long. Calyx-lobes 5, obovate or spathulate, 1–1.2 mm. long, 0.7–1 mm. broad, broadly rounded to emarginate at the tip, entire, with broad scarious margins, the midrib unbranched. Disk-segments 5, elliptic or orbicular, 0.2–0.3 mm. across, entire, flattened, not glandular. Stamens 2 or sometimes (usually in the first flower of a cymule) 3; filaments connate their entire length into a column c. 0.5 mm. long, c. 0.15–0.2 mm. broad; anthers subsessile, discrete, 0.2–0.25 mm. long, 0.25–0.35 mm. broad; anther-sacs divergent, the slits apically confluent, dehiscing more or less horizontally; the pollen grains finely reticulate, 20–22 μ long, 17–18 μ broad.

Female flower: Calyx-lobes 5, oblong-obovate, c. 1.5–1.8 mm. long, rounded at the tip, entire, with rather narrow whitish scarious margins. Disk shallowly 5-lobed, the lobes thin and flat. Styles free, ascending, c. 0.5 mm. long, bifid c. ½ their length, the branches spreading, subcapitate at the tips.

Fruit and seeds unknown.

TYPE: Cuba, *Linden 2074.*

DISTRIBUTION: endemic to eastern Cuba (MAP XI).

CUBA. ORIENTE: St. Yago de Cuba, Pinal de Nimanima, alt. 400 ft., August 1844, *Linden 2074* (G, LECTOTYPE; BR, G, P, ISOTYPES; A, type fragment); pinelands, vicinity of El Cuero, alt. 400 m., 18–19 Mar. 1912, *Britton & Cowell 12781* (NY).

This species, still imperfectly known, requires further study before its circumscription can be exactly defined. Not only are the capsules and seeds unknown, but female flowers have been observed only on the sheet of Linden's collection in the Prodromus Herbarium, and the notes taken on that specimen are incomplete in some details. It is not surprising that *P. micranthus* has been confused with other species, mainly with *P. procerus*; it does appear to be rather closely related to that species but clearly differs in its perennial growth, dioecious inflorescence, larger spathulate male calyx-lobes, and discrete anthers. Furthermore, *P. procerus* does not have indurate auriculate cataphyllary stipules and thus must be excluded from subsect. *Pentaphylli*. However, *P. micranthus* is also closely related to two Hispaniolan species, *P. fuertesii* and *P. brachyphyllus*. These differ in having usually 6-merous calyces and 3 stamens, as well as broader leaves. Previously (Contr. Gray Herb. **176**: 55. 1955) it was suggested that *P. fuertesii* represented only a subspecies of *P. micranthus*. There still is no question of its very close relationship, but until the Hispaniolan species are better understood it seems preferable not to combine them with *P. micranthus*.

26. **Phyllanthus fuertesii** Urb. Repert. Sp. Nov. **13**: 451–452. 1914. (PLATE XX, *figs. B–C*).

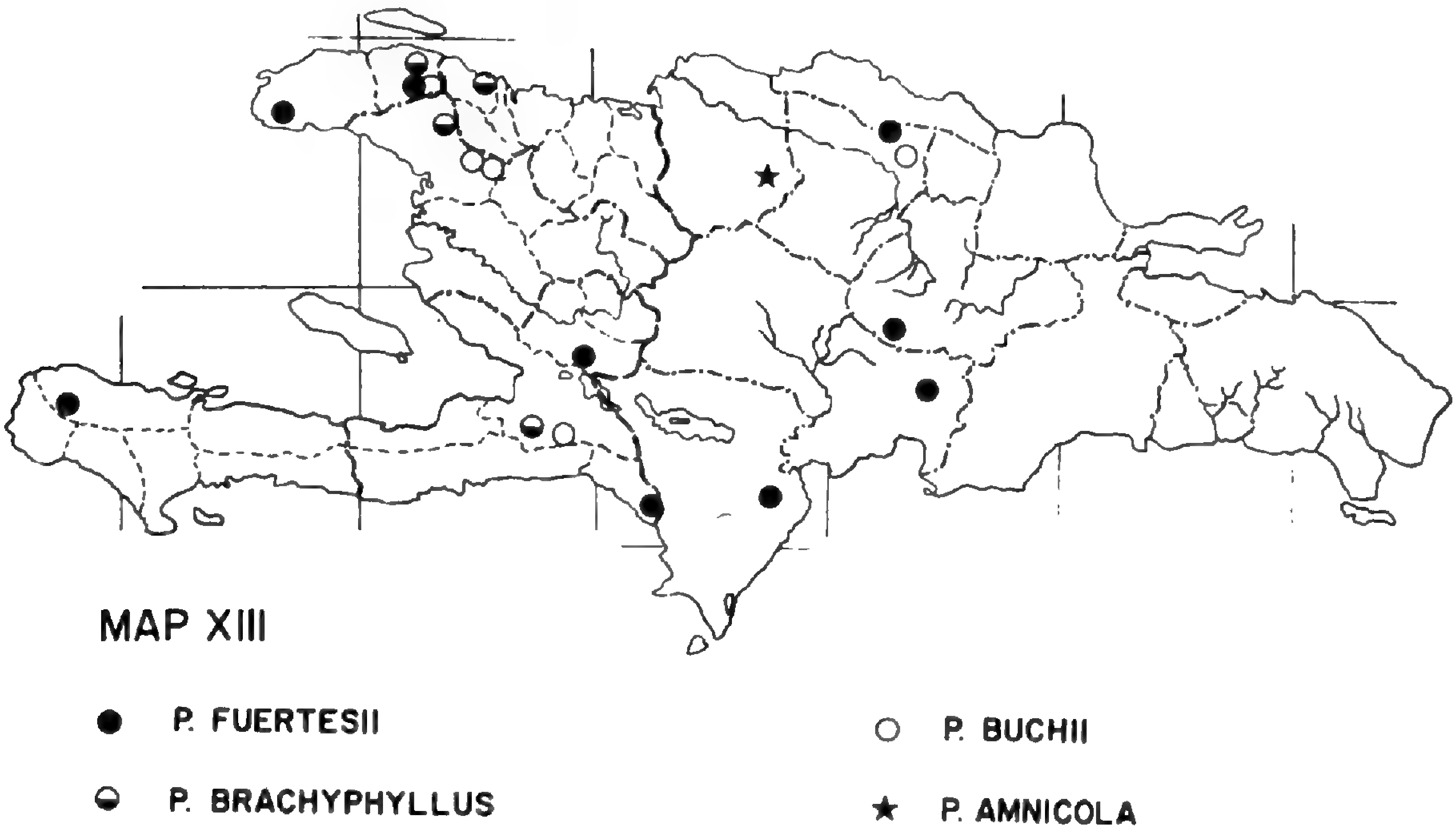
Phyllanthus micranthus ssp. *fuertesii* (Urb.) Webster, Contr. Gray Herb. **176**: 55. 1955.

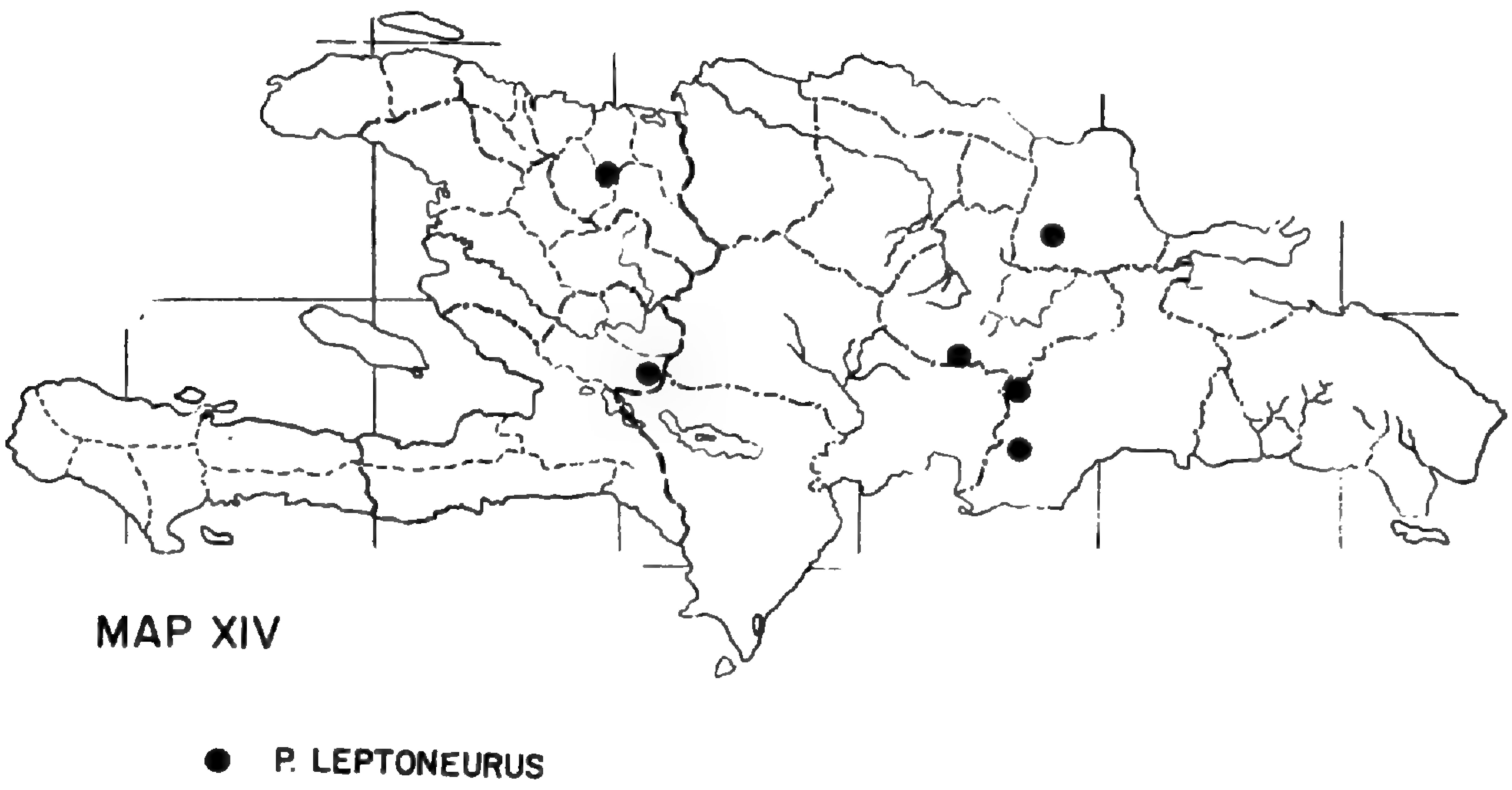
Sparsely branching annual or perennial herb or subshrub, c. 3–8 dm. high; main stems terete, smooth or with a few scattered raised striae, brown or grayish, 1–3 mm. thick, with internodes mostly 2–5 cm. long beneath, decreasing to 0.5–2 cm. long above. Cataphylls: stipules triangular-ovate, 1.2–1.8 mm. long, 0.6–0.9 mm. broad, acuminate, dentate, conspicuously auriculate, at first reddish and scarious becoming dark and rigid, or reddish-black and indurate from the first; blade linear-lanceolate, 0.9–1.1 mm. long. Deciduous branchlets (4–) 5–9 (–11) cm. long, 0.2–0.4 mm. thick, subterete or obtusely angled, smooth or the first internode roughened with raised striae, greenish or brownish, with mostly 20–40 (–45) leaves; first internode 3–6 mm. long, median internodes 2–4 mm. long. Leaves: stipules narrowly lanceolate, 0.6–1 mm. long, 0.2–0.25 mm. broad, acuminate, olivaceous becoming more or less reddish with age, scarious but not indurate. Leaf-blades membranous to chartaceous, smooth on both sides, narrowly oblong or oblong-lanceolate, (4–) 5–8 (–9) mm. long, 1.8–3 mm. broad, acute or obtuse-apiculate at the tip, obtuse to rounded at the base; above dark green, the midrib not prominent, the laterals obscure; beneath pale, the midrib raised, the laterals forming a rather obscure reticulum; margins slightly thickened, sometimes reddish-tinged, plane, smooth or minutely roughened.

Monoecious or subdioecious, or sometimes dioecious; floriferous branchlets typically with the (0–) 2–10 (–15) proximal nodes barren, the succeeding (5–) 7–15 (–25) nodes with racemiform cymules of 3 or 4 male flowers, the bracteoles yellowish-scarious; female flowers solitary in the distal axils.

Male flower: pedicel 0.5–1 mm. long. Calyx-lobes 6 (rarely 5), subequal, broadly elliptic to obovate or sometimes spathulate, 0.8–1.1 mm. long, c. 0.6–0.8 mm. broad, rounded or obtuse at the tip, entire, yellowish and scarious, the midrib unbranched. Disk-segments 6 (5), thin and flattened, roundish, c. 0.1–0.2 mm. across, entire or somewhat glandular and then crenulate in outline, but never massive and rugose. Stamens 3;

filaments united most of their length into a rather slender column (0.2–) 0.3–0.4 mm. high and c. 0.1–0.15 mm. thick; anthers shortly stipitate or subsessile atop the column, 0.15–0.2 mm. long, 0.2–0.25 mm. broad; anther-sacs divergent, the slits apically confluent, dehiscing obliquely; pollen grains finely reticulate, 20–25 μ long, 17–20 μ broad.


MAP XIII


MAP XIV

Maps XIII and XIV. Distribution of some species of subsect. *Pentaphylli* in Hispaniola.

Female flower: pedicel becoming 1.5–2.5 mm. long, terete and slender below, obtusely angled above, olivaceous. Calyx-lobes 6 (rarely 5), subequal, mostly obovate, becoming (0.9–) 1.1–1.5 mm. long, 0.7–1 mm. broad, rounded at the tip, entire, with broad yellowish or whitish scarious margins, the midrib obscurely branched. Disk 6–(5–)lobed, the lobes thin, flat, triangular or lanceolate. Ovary often becoming rugulose after anthesis; styles ascending or spreading, 0.25–0.4 mm. long, bifid ¼ to ½ their length, the arms spreading, the tips slender, recurved.

Capsule oblate, 2.2–2.4 mm. in diameter, shallowly sulcate, obscurely rugulose, yellowish-brown, not veiny. Columella 0.6–0.75 mm. long. Seeds trigonous, 1.1–1.2 (–1.3) mm. long, 0.8–0.9 mm. radially and tangentially, yellowish-brown, with c. 10–12 very delicate longitudinal striae, obscurely transversely barred.

TYPE: Dominican Republic, Barahona, *Fuertes 561.*

DISTRIBUTION: Hispaniola (MAP XIII).

HAITI. NORD-OUEST: Presquîle du Nord-Ouest, La Bombarde, *Ekman H4511* (A, US); rocky slope, vicinity of Bombardopolis, alt. 610 m., *E. C. & G. M. Leonard 13407, 13435, 13468* (US); vicinity of Bassin Bleu, Trail Moustique, *E. C. & G. M. Leonard 14996, 15004* (US). OUEST: Massif des Matheux, Grand-Bois, road Thomazeau to Cornillon, limestone slopes, alt. 800–900 m., *Ekman H5679* (S); Massif de la Selle, Port-au-Prince, Group Crête-à-Piquants, Morne Aux-Fourques, limestone, c. 1000 m., *Ekman H5922* (S); Massif de la Selle, Morne Commissaires, Auses-à-Pitres Banane, at Río Pedernales, alt. 200 m., *Ekman H6917* (S). SUD: Massif de la Hotte, western group, Jerémie, between La Source Chaude and Source-Cahouane, edge of river, alt. c. 150 m., *Ekman H10223* (S, US).

DOMINICAN REPUBLIC. SANTIAGO: Cordillera Septentrional, top of Loma Diego de Ocampo, c. 1250 m., *Ekman H16324* (S). LA VEGA: Constanza, El Salto de Constanza, alt. 1200 m., *Jiménez 2961* (US). BARAHONA: Barahona, in collibus apricis, alt. 275 m., *Fuertes 561* (GH, LECTOTYPE; C, F, G, S, ISOTYPES). AZUA: Maniel de Ocoa [San José de Ocoa], alt. 300 m., *Türckheim 3688* (BR).

This perplexing species is as variable as it is common and widespread in Hispaniola. Urban originally compared it with *P. leptoneurus* and *P. micranthus* (the latter confounded with *P. procerus*), both of which indeed resemble some forms of the present species. He distinguished *P. micranthus* by means of its 5-merous calyx and two sessile anthers; and the Fuertes collection further differs from *P. micranthus* in its broader leaves and monoecious inflorescence. However, examination of the several other collections of *P. fuertesii* show that it is, in fact, quite variable with regard to its supposedly diagnostic characters. The number of calyx-lobes is at least occasionally 5 in the following collections: *Leonard & Leonard 14996, Ekman H6917,* and *Ekman H10223.* The inflorescence is dioecious or transitional to that condition in *Leonard & Leonard 14996, Ekman H6917,* and *Ekman H5922.* The Ekman collection from the Massif de la Hotte has the habit of *P. amnicola,* but is monoecious and otherwise appears typical for *P. fuertesii.* The collection from Azua, *Türckheim 3688,* has exceptionally large male flowers with spathulate calyx-lobes up to 1.3 mm. long, and so closely resembles *P. leptoneurus* that it was originally annotated as that species; but it has the finely reticulate pollen grains typical for *P. fuertesii.* These and other divergences from the mean make it difficult to characterize *P. fuertesii*, but at least in the typical form it may be separated from all the closely related species: from *P. micranthus* by the 3 stamens with obliquely dehiscing anthers, from *P. buchii* by its non-indurate stipules and subentire disk-segments; from *P. brachyphyllus* by its obliquely dehiscing anthers; and from *P. leptoneurus* by its pollen grains. Unfortunately the dioecious nature of all these related species makes identifications very difficult when only female individuals are at hand.

The occurrence of specimens which appear to be intermediate in one or more respects between this and the other species suggests that hybridization may well be a contributing factor to the systematic difficulties. *Ekman H5679*, which appears to be somewhat intermediate between *P. fuertesii* and *P. buchii*, has only 25% good pollen as one might expect if it represented a hybrid, but on the other hand it has produced good seed. However, *Ekman H5922*, which appears intermediate to about the same degree has nearly 100% good pollen. The admittedly crude evidence available from herbarium specimens is thus of no real assistance in determining if there is really any sterility effect consequent on hybridization, nor does it even demonstrate that crossing has actually occurred; but there does not appear to be any more reasonable hypothesis which accounts for the evident intergradation between species.

27. **Phyllanthus brachyphyllus** Urb. Repert. Sp. Nov. 13: 452–453. 1914.

Subshrub c. 0.5 m. high or less, the straight stiffly erect main stems clustered on a short caudex; stems terete, brownish or greyish, smooth, furrowed or roughened by discontinuous longitudinally raised striae, 1–1.5 mm. thick; internodes mostly 3–5 cm. long below, decreasing to 0.5–2 cm. long above. Cataphylls: stipules triangular-lanceolate, 1–1.5 mm. long, 0.5–1 mm. broad, acuminate, conspicuously auriculate at the base, subentire, becoming reddish-black and indurate; blade linear-lanceolate, 0.5–1 mm. long. Deciduous branchlets 1–4 (–6) cm. long, 0.2–0.4 mm. thick, subterete or obtusely angled, olivaceous, smooth or sometimes roughened in the first internode, with c. 15–35 (–45) leaves; first internode 1.5–3 mm. long, median internodes 0.5–1.8 mm. long. Leaves: stipules persistent or subpersistent, firm, triangular-lanceolate, (0.5–) 0.7–1 mm. long, 0.2–0.35 mm. broad. Petioles 0.2–0.4 mm. long. Leaf-blades firm, ovate or elliptic to narrowly oblong-lanceolate, (2–) 2.5–4 (–5) mm. long, (0.7–) 1-1.7 mm. broad, usually abruptly apiculate at the tip, obtuse to emarginate at the base; above olivaceous, the midrib not raised, the laterals obsolete; beneath slightly paler, the midrib plane or slightly raised, the laterals obsolete or 1–3 pairs evident but a reticulum of veinlets never visible; margins slightly thickened, plane, smooth, more or less reddish-tinged.

Dioecious. Male branchlets with the 2–7 (–14) proximal nodes barren, the succeeding nodes with racemiform cymules of 3–5 male flowers; bracteoles reddish-brown, scarious but not indurate, subpersistent. Female branchlets with c. 10–25 proximal nodes barren, the succeeding nodes with solitary female flowers.

Male flower: pedicel up to 0.5 mm. long. Calyx-lobes 6, subequal, broadly elliptic to obovate, 0.9–1.2 mm. long, 0.6–0.8 mm. broad, obtuse or rounded at the tip, entire, yellowish-scarious, the midrib unbranched. Disk-segments 6, irregularly roundish or rectangular, glandular-lobed but scarcely rugose, c. 0.1–0.15 mm. across. Stamens 3; filaments completely united into a rather stout column c. 0.4–0.5 mm. high and 0.15–0.2 mm. thick; anthers sessile atop the column, connectives compressed back-to-back, discrete or fused, c. 0.15–0.2 mm. long, 0.3 mm. broad; anther-sacs with confluent slits, dehiscing strictly horizontally; pollen grains finely reticulate, 20–25 μ long, 16–21 μ broad.

Female flower: pedicel 0.8–1.7 mm. long, olivaceous, rather stout, gradually dilated upwards, obtusely angled. Calyx-lobes 6, subequal, elliptic to obovate, 1–1.5 mm. long, 0.8–1.3 mm. broad, entire, olivaceous with broad yellowish-white scarious margins, the midrib unbranched. Disk 6-angled or obtusely 6-lobed, thin, plane. Styles more or less ascending, slender, c. 0.4–0.45 mm. long, parted ¼ to ⅓ their length, the branches only slightly divergent, the unthickened tips more or less recurved.

Capsule slightly over 2 mm. broad, yellowish-brown, obscurely rugulose at the top, not veiny. Seeds c. 1.2 mm. long, 1 mm. radially and tangentially, yellowish-brown, finely transversely barred (the longitudinal striae obscure or quite invisible).

TYPE: Haiti, *Nash & Taylor 1718.*

DISTRIBUTION: mountainous areas, Haiti (MAP XIII).

HAITI. NORD-OUEST: Massif du Nord, Port-de-Paix, Haut-Piton, open place on the eastern slope of the top, c. 1200 m. alt., 9 Aug. 1925, *Ekman H4625* (S). NORD: Massif du Nord, Le Borgne, top of Morne Darras, alt. c. 1175 m., 3 Sept. 1925, *Ekman H4772* (S, US). ARTIBONITE: La Brande to Mt. Balance, sunny hillside, alt. 3300 ft., 15 Aug. 1905, *Nash & Taylor 1718* (NY, LECTOTYPE; US, ISOTYPE); Mt. Bellance [Belanse], Gros-Morne, in open stony slopes, alt. 1000 m., 26 Sept. 1925, *Ekman H4915* (A, S). OUEST: Port-au-Prince, Morne Megi, Wegrand, alt. 1000 m., Aug. 1917, *Buch 1422* (GH, JAM).

This species, which in many ways is intermediate between *P. fuertesii* and *P. buchii*, is here retained only with the proviso that its status must be considered dubious. At first it seemed likely that *P. brachyphyllus* might represent merely a hybrid between those two species; but there are several circumstances which make it difficult to assign it outright hybrid status. It was hoped that examination of the pollen might prove decisive in interpreting the situation, but unfortunately pollen was not available from most collections, and the results of the observations that were made proved to be inconclusive. *Ekman H4772*, for instance, had only about 20 percent good pollen, as one might expect if it represented a hybrid; but *Buch 1422* yielded nearly 100 percent good pollen. Furthermore, some collections of *P. buchii* (such as *Ekman H8410*) had a high percentage of defective grains even though they appeared to represent the "pure" species. It still seems possible that study of the pollen can yield significant results, particularly if preserved material were available for cytological smears; but at present it must be admitted that no great help is forthcoming from this field.

Morphologically, *P. brachyphyllus* shows some features which cannot readily be dismissed as intermediate between *P. fuertesii* and *P. buchii*; the most important of these are the shorter branchlets, smaller leaves, and male flowers with a slightly longer staminal column and completely sessile horizontally dehiscing anthers. The known geographical distribution of *P. brachyphyllus* and its two possible parents is of little assistance, for the available specimens merely indicate a scattering of all three species over much of western Hispaniola. Thus although much suspicion attaches to the status of *P. brachyphyllus*, and its specific distinctiveness is very weak, it is here retained as a full species pending further investigation.

28. **Phyllanthus buchii** Urb. Symb. Ant. 3: 288–289. 1902. (PLATE XX, *fig. D*).

Subshrub c. 0.5–1.3 m. high, the sparsely branching main stems erect, smooth, terete, brownish, inconspicuously furrowed, mostly 1–2 mm. thick; internodes mostly 2–10 cm. long (becoming shorter at the tips). Cataphylls: stipules triangular-ovate, 1.2–1.9 (–2.3) long, 0.8–1.1 (–1.25) mm. broad, acute, conspicuously cordate-auriculate, subentire or crenately toothed, dark reddish becoming blackish and indurate; blade lanceolate, acuminate, 0.7–1.5 mm. long. Deciduous branchlets mostly 3.5–10 (–12) cm. long, 0.25–0.6 mm. thick, subterete, olivaceous, smooth, with (15–) 20–40 (–45) nodes; first internode 3–7 mm. long, median internodes 1.5–4 mm. long. Leaves: stipules persistent, lanceolate, 0.7–1.3 mm. long, 0.25–0.5 mm. broad, acuminate, entire, reddish when young, becoming reddish-black and indurate (sometimes with a very narrow whitish margin). Leaf-blades firm (subcoriaceous or coriaceous), smooth on both sides or scabridulous beneath (sometimes, scabridulous above), elliptic or oblong, mostly 3.5–8 mm. long, 1.5–3 mm. broad; above deep green or brownish, the midrib impressed, the laterals invisible; beneath olivaceous, paler, the midrib evident and continuing to the tip but scarcely raised, the laterals obsolete; margins thickened, often rim-like, smooth, plane.

Dioecious or subdioecious. Male branchlets with the (0–) 2–6 proximal axils barren, the racemiform cymules producing up to 5 or 6 male flowers and becoming almost 1 mm. long, the reddish-black entire somewhat indurate bracteoles persistent. Female branchlets with the proximal (3–) 6–16 axils barren, the flowers solitary at the succeeding nodes; occasional female flowers sometimes appearing on otherwise male branchlets.

Male flower: pedicel 0.5–1 mm. long. Calyx-lobes 6, subequal, elliptic to obovate, 0.8–1.1 mm. long, 0.6–0.8 mm. broad, obtuse or rounded at the tip, entire, yellowish-scarious, the midrib unbranched. Disk-segments 6, massive, conspicuously rugose-papillate, c. 0.15–0.25 mm. across. Stamens 3; filaments connate for most of their length into a stout column c. 0.3–

0.35 mm. high and 0.2–0.25 mm. broad; anthers short-stipitate to subsessile on the column, broadly ovate, blunt, 0.15–0.2 mm. long, 0.2–0.3 mm. broad; anther-sacs divergent, the slits apically confluent, dehiscing horizontally or obliquely; pollen grains finely reticulate, 21–30 μ long, 18–25 μ broad.

Female flower: pedicel becoming 1.5–2.5 mm. long, terete and reddish below, angled and olivaceous above. Calyx-lobes 6, subequal, elliptic or oblong to obovate, becoming 1.1–1.5 mm. long, 0.7–1.1 mm. broad, obtuse or rounded at the tip, entire, the yellowish- scarious margin conspicuous but not as broad as the olivaceous midstrip, the midrib pinnately branched but the veins all obscure. Disk 6-lobed, the lobes rather thick, obtuse, triangular. Styles ascending or spreading, somewhat thickened, 0.3–0.4 mm. long, parted ⅓ to ½ their length, the arms spreading, the slender unthickened tips recurved.

Capsule oblate, c. 2.5 mm. in diameter, shallowly sulcate, nearly smooth, yellowish-olivaceous, not veiny. Seeds trigonous, 1.3–1.4 mm. long, 0.9–1 mm. radially and tangentially, yellowish-brown, with c. 12 very tenuous longitudinal striae, transversely barred with slightly hygroscopic epidermal cells.

TYPE: Haiti, *Buch 251*.

DISTRIBUTION: mountainous areas, Hispaniola (MAP XIII).

HAITI. NORD: grassy slope, M. la Cidre, alt. 350 m., vicinity of St. Michel de l'Atalaye, 23 Nov. 1925, *Leonard 7402* (US). ARTIBONITE: Ennery, *Buch 251* (NY, LECTOTYPE; GH, ISOTYPE); hills near Ennery, low forest with some pines on soft limestone, alt. c. 600 m., 14 Nov. 1924, *Ekman H2466* (S, US); hills north of Ennery, pineland, alt. 550 m., 12 June 1927, *Ekman H8410* (S, US); vicinity of Ennery, Puilboreau road, alt. 325–900 m., 21 Jan. 1926, *Leonard 9061* (US), *9064* (GH, US). OUEST: Massif de la Selle, Ganthier, ridge of M. Vincent, above Source-Courty, alt. c. 1700 m., 2 Mar. 1927, *Ekman H7757* (S).

DOMINICAN REPUBLIC. SANTIAGO: Las Lagunas, hills at Arroyo Harenquillo, alt. c. 400 m., 20 Oct. 1930, *Ekman H16077* (S). BARAHONA: Aceitillar, Sierra de Bahoruco, 13 Nov. 1955, coll. Prof. Marcano, *Jiménez 3121* (US).

In its typical form, *P. buchii* is readily recognizable by virtue of its coriaceous leaves, darkened indurate branchlet stipules and male flowers with obliquely dehiscing anthers and rugose-papillate disk-segments. However, specimens intermediate between *P. buchii* and *P. fuertesii* occur (as

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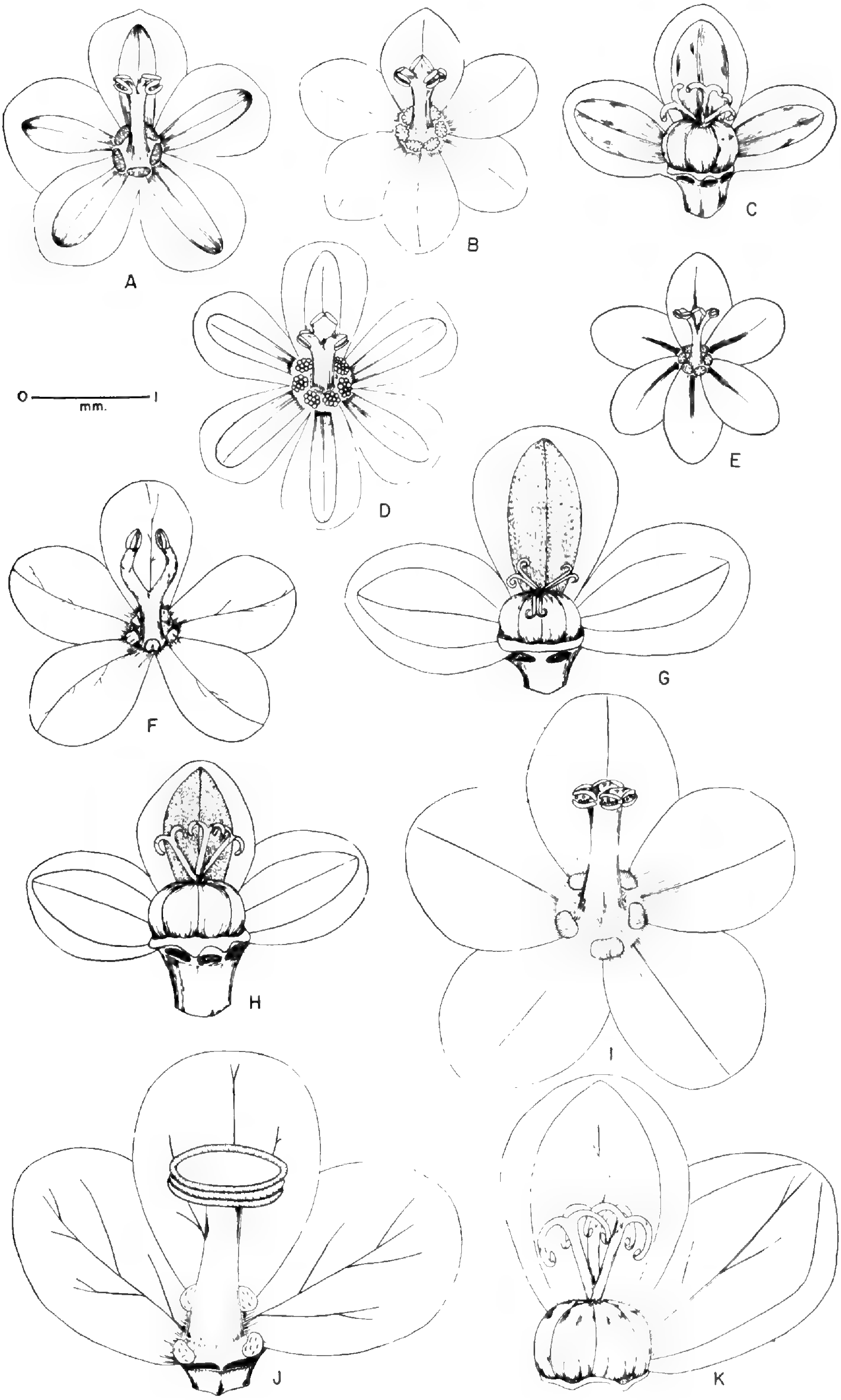
PLATE XX. FLOWERS OF SECT. *Phyllanthus*, SUBSECT. *Pentaphylli*.

FIG. A. *Phyllanthus micranthus* A. Rich. (*Linden 2074* [A]). FIGS. B-C. *Phyllanthus fuertesii* Urb. (*Fuertes 561* [GH]). FIG. D. *Phyllanthus buchii* Urb. (*Buch 251* [GH]). FIG. E. *Phyllanthus amnicola* Webster (*Ekman H12936* [S]). FIGS. F-G. *Phyllanthus maestrensis* Urb. (male, *Morton & Acuna 3825* [US]; female, *Ekman 7247* [S]). FIGS. H-I. *Phyllanthus leptoneurus* Urb. (*Ekman H11505* [S]). FIGS. J-K. *Phyllanthus dimorphus* Br. & Wils. (*Webster 4770* [GH]).



WEBSTER, WEST INDIAN PHYLLANTHUS

discussed under the latter species), and hybridization very probably plays a part in contributing to the difficulty in distinguishing *P. buchii* from its neighbors. Furthermore, considerable geographical variation is evident, which may be due largely to the fact that the species grows only in the mountains and is consequently broken up into many small populations on individual peaks. The specimen from Arroyo Harenquillo (*Ekman H16077*), which has a somewhat different aspect from the Haitian collections, has associated in a packet on the sheet a single seed 1.5 mm. long which is verruculose, with evenly spaced round points, rather than being striate, as in other collections of the species. If this seed really belongs with the plant, then *Ekman H16077* probably represents a distinct undescribed species; but since the collection shows no other really distinctive features, it is retained for the present within *P. buchii*.

29. **Phyllanthus amnicola** Webster, Contr. Gray Herb. 176: 54. 1955. (PLATE XX, *fig. E*).

Decumbent annual or short-lived perennial herb, the sparsely branching main stems c. 1.5–3 dm. long, 0.7–1.3 mm. thick, subterete, brownish, smooth on older portions, more or less roughened with minute pale ridges above; stems more or less rooting at the lower nodes; internodes mostly 0.5–2.5 cm. long. Cataphylls: stipules triangular, (1.2–) 1.5–2 mm. long, 0.7–0.8 mm. broad, short-acuminate, conspicuously auriculate at the base, entire or sparsely toothed, becoming blackish and indurate; blade linear-lanceolate, c. 0.5–1 mm. long. Deciduous branchlets (2–) 4–8 (–12) cm. long, 0.25–0.3 mm. thick, subterete, olivaceous, densely short-hispidulous, with mostly 20–50 (–70) leaves; first internode (1.5–) 2–4 (–5) mm. long, median internodes (1–) 1.5–2.5 (–3) mm. long. Leaves: stipules subpersistent, lanceolate, 0.5–0.8 mm. long, c. 0.3 mm. broad, acuminate, reddish-olivaceous becoming dark reddish-brown, scarious. Petioles 0.3–0.5 mm. long. Leaf-blades firmly chartaceous, oblong, usually somewhat falcate, c. 3–6 mm. long and 1.5–2.3 mm. broad, obtuse or rounded at the tip (mostly with no trace of an apiculum even when young), obtuse at the base; above plumbeous-olivaceous, minutely foveolate, plane or depressed along the midrib; beneath greyish-pulverulent, conspicuously hispidulous, the midrib prominent, the 2–4 pairs of laterals slightly raised, straight, not anastomosing; margins conspicuously thickened and revolute, smooth.

Dioecious. Male branchlets mostly with the proximal 1–4 nodes barren, the succeeding nodes with racemiform cymules of 3 or 4 male flowers; bracteoles reddish-brown, scarious. Female branchlets [only a few observed] with the proximal 7–10 nodes barren, the succeeding nodes with solitary female flowers.

Male flower: pedicel c. 0.8–1.3 mm. long. Calyx-lobes 6 (rarely 7), subequal, obovate, c. 0.7–0.9 mm. long, 0.5–0.75 mm. broad, rounded at the tip, entire, yellowish and scarious, the midrib unbranched. Disk-segments 6, concave, thin, crenulate or entire, roundish, not glandular, c. 0.15–0.2 mm. across. Stamens 3; filaments c. 0.4–0.5 mm. long, united in the lower half into a column; anthers nearly reniform in outline, very obtuse, c. 0.15 mm. long, 0.2–0.3 mm. broad; anther-sacs widely divergent, the slits confluent, dehiscing horizontally or somewhat obliquely; pollen grains finely reticulate, c. 18–22μ long, 15–18 μ broad.

Female flower [not seen at anthesis]: pedicel 1–1.2 mm. long, olivaceous, smooth or slightly roughened, subterete, gradually dilated from the base. Calyx-lobes 6, subequal, obovate, c. 1–1.2 mm. long, 0.6–0.8 mm. broad, rounded at the tip, entire, olivaceous with broad conspicuous whitish-scarious margins. Disk [as seen in fruit] parted into 6 linear-lanceolate subacute segments. Ovary and styles not seen.

Capsule not seen entire; valves c. 1.7–1.8 mm. long, olivaceous, smooth, not veiny; seeds c. 1.1 mm. long, 0.7–0.85 mm. radially and tangentially, yellowish-brown, finely striate longitudinally and transversely.

TYPE: Dominican Republic, Prov. Monte Cristi, Monción, at the junction of the Río Cenobí and the Río Cenobicito, edge of stream, alt. 700 m., 20 June 1929, *Ekman H12936* (S, HOLOTYPE; US, ISOTYPE).

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

This very distinctive species, named in allusion to its riparian habitat, may at once be distinguished from its relatives by its conspicuously hispidulous branchlets and lower leaf-surfaces, as well as by its only partially united stamens and dissected female disk. It is perhaps most closely related to *P. fuertesii*, some forms of which (e.g., *Ekman H10223*) also grow in stream-beds and have a similar habit; but these lack the characteristic vegetative and floral characters of *Ekman H12936* from Monción. Consequently, it seems evident that *P. amnicola* is a distinct species rather than merely an ecological variant of *P. fuertesii.*

30. **Phyllanthus maestrensis** Urb. Symb. Ant. 9: 193. 1924.
(PLATE XX, *figs. F-G*).

Suffruticose glabrous perennial 0.5–1.5 m. high, the main stem erect, stiff or wand-like, simple or sparsely branched above, greyish and sometimes sulcate above, smooth and brownish below; internodes mostly 2–6 cm. long. Cataphylls: stipules triangular, (1–) 1.2–1.8 (–2) mm. long, 0.5–1 mm. broad, acute to acuminate, conspicuously auriculate at the base, entire or more often denticulate towards the base (sometimes with conspicuous lateral teeth near the apex), reddish-brown becoming indurate and blackened; blade lanceolate, 0.8–1.5 mm. long, 0.2–0.3 mm. broad. Deciduous branchlets mostly 7–15 cm. long, 0.25–0.4 (–0.5) mm. thick, terete or obscurely angled, smooth, brownish or greenish, with mostly 30–50 leaves; first internode 3–12 (–16) mm. long, median internodes 2–4 (–5.5) mm. long. Leaves: stipules lanceolate, 0.9–1.5 mm. long, 0.25–0.4 mm. broad, acuminate or attenuate-acuminate, basally dilated, reddish becoming blackened in the distal half, scarious, entire. Petioles 0.3–0.7 mm. long. Leaf-blades membranous to chartaceous, oblong or elliptic-oblong, 6–13.5 mm. long, 2–5 mm. broad, obtuse or rounded to subtruncate and usually apiculate at the tip, tapering more or less evenly at the base; above olivaceous, the midrib and laterals usually slightly raised (at least proximally); beneath pale yellowish- or greyish-green, the midrib raised, the laterals (c. 5–8 on a side) plane but dark and conspicuous, the delicate tertiaries visible or obsolete; margin scarcely thickened, plane, smooth.

Monoecious or exceptionally subdioecious, the male and female flowers usually on the same branchlets; (0–) 2–15 (–20) proximal nodes barren, succeding (5–) 10–20 (–25) nodes with racemiform cymules of 3–7 male flowers, distal nodes with solitary female flowers.

Male flower: pedicel 0.5–0.7 mm. long. Calyx-lobes 5, broadly obovate to spathulate, (0.8–) 1–1.2 mm. long, 0.6–0.9 (–1.1) mm. broad, broadly obtuse or rounded at the tip, entire, yellowish-scarious with an olivaceous median area, the midrib unbranched or with 1 or 2 ascending lateral veins. Disk-segments 5, more or less elliptical, 0.15–0.25 mm. across, smooth, subentire. Stamens 2; filaments 0.5–0.75 mm. long, fused in the lower ⅓ to ⅔ their length into a stout column c. 0.25–0.3 mm. thick; anthers introrse, erect, 0.2–0.3 mm. long, 0.3–0.35 mm. broad; anther-sacs somewhat divergent, contiguous apically and thus usually with an apically confluent slit, dehiscing vertically and laterally; pollen grains finely reticulate, 23–28 μ long, 18–23 μ broad.

Female flower: pedicel 1.5–2.5 mm. long. Calyx-lobes 5 (rarely 6), elliptic-obovate or spathulate, (1.1–) 1.3–2 (–2.3) mm. long, 0.9–1.1 mm. broad, obtuse or rounded at the tip, olivaceous with broad conspicuous yellowish scarious margins, the unbranched midrib slightly carinate dorsally. Disk rather massive, more or less minutely foveolate, obtusely 5-lobed or cut into 5 distinct segments. Styles free, ascending or at length spreading, 0.35–0.4 mm. long, bifid 1/4 to 2/5 their length, the branches spreading and recurving with tapering blunt or minutely uncinate tips.

Capsules not seen entire; valves yellowish-brown, smooth, not veiny. Seeds acutely trigonous, 1.2–1.4 mm. long, 0.9–1.1 mm. radially, 0.85–1.15 mm. tangentially, pale yellowish-brown, with c. 9–12 delicate longitudinal striae; epidermal cells not hygroscopic.

Collected in flower and fruit April throughout September.

TYPE: Cuba, Sierra Maestra, *Ekman 7247*.

DISTRIBUTION: endemic to Cuba (MAP XII).

CUBA. PINAR DEL RÍO: Pinar del Río, among tall grasses in thickets surrounded by pine woods, *Wright 3684* ex p. (P, S; mixed with *P. procerus*); Arroyo del Sumidero, rocks near water, *Shafer & León 13584* (NY); Vinales, Sitio del Infierno, in pineland hills, *Ekman 16713* (S); San Diego de los Banos, *Britton et al. 6799* (NY), *León & Hioram 4443* (NY), *Palmer & Riley 650* (NY, US). ORIENTE: Sierra Maestra, La Bayamesa, banks of the Río Oro, alt. 400 m., *Ekman 7247* (S, HOLOTYPE), *Webster 4119* (MICH); banks of Guama River, near Santiago de Cuba, *Clemente 3409* (MICH).

A specimen from the Sierra Maestra, Pinar de Papayo (*Ekman 9267*

[S]), has male flowers with introrse anthers and is therefore referable to *P. maestrensis*, but it has not been accounted for in the description since it is aberrant in several respects: branchlets only 3.5–7.5 cm. long, leaves 4.5–6 mm. long, plants dioecious, filaments completely united and anthers sessile. It appears to be intermediate between *P. maestrensis* and *P. micranthus* and perhaps represents a hybrid between these two species.

Phyllanthus maestrensis is immediately distinguishable from its West Indian congeners by its introrse anthers, which in fact appear to be unique in the genus. Vegetatively, it perhaps most closely resembles *P. dimorphus* and *P. leptoneurus*; but in Cuba, it is most apt to be confused with either *P. procerus* or *P. micranthus*. Probably its closest relationship is with the latter species, but it apparently may hybridize with either. The apparent cross with *P. micranthus* has been noted above, and a specimen from Pinar del Río (*Ekman 17875* [S]) intermediate between *P. maestrensis* and *P. procerus* has already been noted under the latter.

31. **Phyllanthus leptoneurus** Urb. Symb. Ant. 7: 246–247. 1912.
(PLATE XX, *figs. H–I*; PLATE XXII, *fig. A*).

Phyllanthus trigonus Urb. & Ekm. Ark. Bot. **20A**(15): 46–47. 1926.

Subshrub up to c. 7.5 dm. high, the subsimple main stem brownish, sometimes shiny, usually terete or obtusely angled (rarely with sharp decurrent ridges from the nodes), nearly smooth or with minute greyish longitudinal ridges, c. 1.5–2 mm. thick, internodes mostly 0.5–2 cm. long, or up to 5 cm. below. Cataphylls: stipules triangular-ovate or triangular-lanceolate, (1.2–) 1.5–2 mm. long, (0.6–) 0.8–1.2 mm. broad, acuminate, conspicuously auriculate at the base, entire or sparingly toothed, becoming reddish-black and indurate; blade linear-lanceolate, 0.9–1.5 mm. long. Deciduous branchlets mostly 5–15 (–18) cm. long (occasional ones shorter), (0.2–) 0.3–0.5 mm. thick, olivaceous or brownish, subterete or obtusely angled, proximally roughened with minute points or ridges (particularly on the first internode) or less commonly the entire length, with mostly 20–50 (–85) leaves; first internode (2.5–) 4–8 (–10) mm. long, median internodes 1.5–4.5 mm. long. Leaves: stipules persistent or subpersistent, ovate-lanceolate to linear-lanceolate, (0.5–) 0.7–1.2 mm. long, acuminate, olivaceous becoming more or less dark reddish and scarious (particularly at the tip). Petioles 0.3–0.7 mm. long. Leaf-blades membranous to chartaceous, elliptic to oblong, (4–) 5–11 (–13) mm. long, 2–4 (–5) mm. broad, mostly obtuse to truncate and apiculate at the tip, cuneate to obtuse at the base; above dark olivaceous, the midrib pale and conspicuous but not much raised, the laterals not visible; beneath distinctly paler, the midrib prominent and slightly raised, the laterals (c. 5–7 on a side) conspicuous and enclosing a fine reticulum, or sometimes obscure; margins scarcely or not at all thickened, plane, smooth or slightly roughened.

Dioecious. Male branchlets often longer than the female, the proximal (1–) 2–5 (–7) nodes barren, the succeeding nodes with racemiform cymules of 3–10 flowers, bracteoles yellowish-white or reddish-tinged.

scarious (not indurate), subpersistent. Female branchlets with the proximal 3–16 nodes barren, the succeeding nodes with solitary female flowers.

Male flower: pedicel (0.5–) 0.9–1.2 mm. long. Calyx-lobes 6 (less commonly 5), obovate to spathulate, c. 1.2–1.5 (–1.7) mm. long, 0.7–1.5 mm. broad, rounded at the tip, entire, yellowish-scarious, the midrib unbranched. Disk-segments 6 (5), roundish, rather thin, flat or slightly concave, entire, not glandular, mostly 0.2–0.3 mm. across. Stamens 3; filaments completely united into a column (0.5–) 0.7–0.9 mm. long and c. 0.2–0.3 mm. thick; anthers sessile, more or less connate back-to-back by the connectives, triangular to ovate, subacute or obtuse, 0.2–0.3 mm. long, 0.35–0.5 mm. broad; anther-sacs dorsiventrally compressed, divergent, the slits confluent, dehiscing horizontally; pollen grains coarsely reticulate (the brochi 1.5–3 μ across), nearly spheroidal, 24–30 μ long, 21–27 μ broad.

Female flower: pedicel becoming (1.5–) 1.8–2.5 mm. long, olivaceous, smooth or obscurely roughened, gradually dilated from the base, angled above or throughout. Calyx-lobes 6 (occasionally 5), subequal, obovate or sometimes spathulate, c. (1.2–) 1.3–1.8 mm. long, 0.9–1.4 mm. broad, rounded at the tip, entire, olivaceous with conspicuous pale scarious margins, midrib unbranched or with a few obscure steeply ascending lateral veins. Disk shallowly cupuliform, subentire or obscurely and obtusely 6-lobed. Styles erect or ascending, c. (0.3–) 0.5 mm. long, slender, parted ¼ to ⅓ their length, the arms divergent, the slender tips recurved.

Capsule oblate, trigonous, c. 2.5 mm. in diameter, smooth, yellowish-brown, not veiny. Seeds plumply trigonous, c. 1.2 mm. long and 0.8 mm. radially and tangentially, pale yellowish-brown, with 8-10 plane longitudinally darker bands and many fine transverse striae.

TYPE: Dominican Republic, *Türckheim 3187.*

DISTRIBUTION: mountainous areas, Hispaniola (MAP XIV).

HAITI. NORD: near Port Margot, Morne Maleuvre, shrubby grassy slopes, alt. 800–1000 m., 8 Dec. 1924, *Ekman H2792* (S, HOLOTYPE of *P. trigonus*). ARTIBONITE: Massif des Matheux, Grand-Bois, Morne Moitié-Duporté, on the high ridge, "Laubwald", limestone, alt. 1850–1875 m., 16 Mar. 1926, *Ekman H5731* (A, S).

DOMINICAN REPUBLIC. DUARTE [formerly in Pacificador]: Loma Quita Espuela, vicinity of San Francisco de Macorís, alt. 400–1000 m., 5–17 Apr. 1922, *Abbott 2132* (US), *2138* (NY, US); top of Loma Quita Espuela, alt. 930 m., 25 Apr. 1929, *Ekman H12288* (S). LA VEGA: Constanza, Valle Nuevo, Kiefernwald unterhalb, alt. 1700 m., Apr. 1910, *Türckheim 3187* (BR, LECTOTYPE). TRUJILLO VALDEZ [formerly in Azua]: Sierra de Ocoa, San Jose de Ocoa, Bejucal, Loma de los Palos Mojados, alt. c. 1650 m., in pinelands, 13 Mar. 1929, *Ekman H11919* (S, US). SANTO DOMINGO: top of Loma La Campana (west of La Cumbre), alt. c. 1100 m., 11 Feb. 1929, *Ekman H11505* (S).

This robust species is usually recognizable as distinct from its Hispaniolan congeners by virtue of its longer branchlets with more leaves which are usually truncate at the tip, larger male flowers, with completely united filaments, and banded rather than striate seeds. Actually its coarsely reticulate pollen grains are its most characteristic feature, and examination of these will always permit discrimination of the present species from superficially similar forms of *P. fuertesii.* It is possible that hybridization may occasionally occur between these two species, as a rather intermediate specimen from San Jose de Ocoa (*Türckheim 3688*; listed under *P. fuertesii*) suggests. There can be no doubt, however, that the only near relative of *P. **leptoneurus*** is the following species, *P. **dimorphus***, which also has coarsely reticulate pollen grains and is very similar in its vegetative parts and flowers as well.

32. **Phyllanthus dimorphus** Br. & Wils. Mem. Torr. Bot. Club **16**: 75. 1920. (PLATE XX, *figs. J–K*).

Subshrub c. 0.5–1.5 m. high, the erect main stem subsimple, 1.5–2.5 mm. thick, terete or nearly so, brownish and smooth on older basal portions, plumbeous with many fine pale longitudinal ridges above; internodes c. 3–7 cm. long below, 0.5–2 cm. above. Cataphylls: stipules ovate-lanceolate, 1.5–2.5 (–3) mm. long, 1–1.5 (–2) mm. broad, acuminate, conspicuously auriculate at the base, subentire, blackish and indurate; blade lanceolate, more or less reflexed, c. 0.8–1.5 (–2) mm. long, 0.3 mm. broad. Deciduous branchlets (4–) 5–15 (–22) cm. long, 0.4–0.7 mm. thick, subterete, plumbeous or brownish, more or less roughened with minute ridges on the main stem (especially so on the first internode), with 25–75 (–95) leaves; first internode 1.5–4.5 mm. long, median internodes (1–) 1.5–3.5 mm. long. Leaves: stipules persistent, triangular-lanceolate, 0.7–1.5 (–2.2) mm. long, 0.3–0.7 mm. broad, acuminate, dark reddish-brown to black, more or less indurate. Petioles 0.4–0.5 mm. long. Leaf-blades subcoriaceous, linear-oblong, 6–11 mm. long, 1.5–4 (–5) mm. broad, obtuse to rounded and apiculate at the tip, obtuse at the base; above deep olivaceous, smooth, the midrib plane, the laterals invisible, beneath brownish with minute white flecks or greyish, the midrib prominently raised, the laterals (c. 3–6 on a side) rather obscure or obsolete; margins thickened, plane, smooth or minutely roughened, more or less reddish-tinged.

Dioecious or rarely monoecious (but then the branchlets unisexual). Lower branchlets of male plant with c. 10–40 barren proximal nodes, upper with c. 5–8 such barren nodes, the succeeding nodes with racemiform cymules of 3 or 4 flowers; bracteoles reddish-brown, scarious, subpersistent. Female branchlets with c. 15–25 barren proximal nodes, the succeeding nodes with solitary female flowers.

Male flower: pedicel c. 0.7–1.8 mm. long. Calyx-lobes 5, subequal, elliptic-obovate, c. (1.4–) 1.7–2 (–2.3) mm. long, 0.9–1.7 (–2) mm. broad, broadly rounded at the tip, entire, yellowish-scarious, the midrib unbranched or nearly so. Disk-segments 5, trigonous, fleshy and massive, subentire, not evidently glandular, c. 0.25–0.4 mm. across. Stamens 3, completely fused into a synandrium as in sect. *Cyclanthera*, the column 1.1–1.3 mm. high, c. 0.35 mm. thick at the dilated base, tapering above; common connective of the synandrium plane or with the slight central umbo, peltate on the column, c. 0.5 mm. across (the entire synanther c. 0.7–1 mm. across); anthers horizontal, confluent into a circumscissile rim encircling the connective; pollen grains coarsely reticulate, 20–25 μ long, 19–24 μ broad.

Female flower: pedicel becoming (2.2–) 2.5–2.8 (–3.1) mm. long, subterete, smooth, olivaceous or reddish-brown. Calyx-lobes 5, elliptic to obovate, 1.6–2.5 mm. long, 1–1.6 mm. broad, rounded at the tip, entire, with fairly broad yellowish-scarious margins, the midrib apparently unbranched (the lateral veins completely obscure), not dorsally carinate. Disk saucer-shaped, obscurely 5-lobed or 5-angled, entire. Styles erect, 1.1–1.7 mm. long (much longer than the ovary), parted ¼ to ⅓ their length, the branches divergent, the slender recurved tips 0.4–0.7 mm. long.

Capsule oblate, 2.8–3 mm. in diameter, shallowly sulcate, olivaceous, obscurely rugulose, not veiny; seeds plumply trigonous, 1.2–1.3 mm. long, 1–1.1 mm. radially and tangentially, light yellowish-brown, lucent, with c. 10–12 fine longitudinal scarcely raised striae, finely transversely striate.

TYPE: Cuba, Trinidad Mountains, *Britton & Wilson 5350*.

DISTRIBUTION: endemic to the Trinidad Mountains, Cuba (MAP XII).

CUBA. LAS VILLAS: Trinidad Mountains, El Porvenir to Aguacate, grassy hill, alt. 700–900 m., 10 Mar. 1910, *Britton & Wilson 5350* (NY, HOLOTYPE; F, US, ISOTYPES); Buenos Aires, alt. c. 2500 ft., 6 Dec. 1928, *Jack 6849* (A, F, US; flowers abnormal), 6 Mar. 1929, *7003* (A); same locality, 12 Mar. 1930, *Hunnewell 11571* (GH); Loma del Campo, Buenos Aires, grassy shrubby area, 19 July 1953, *Webster 4770* (GH).

The floral morphology of this species was completely misinterpreted by Britton & Wilson, who described the flowers as having the styles slender and forked in some plants and united in a column with a peltate stigma in others. Since in the latter instance they were actually describing the characteristic androecium of the species, their epithet *dimorphus* is unfortunately inappropriate and erroneous.

The synandrium of this species superficially closely resembles that of species in sect. *Cyclanthera*, and Alain (Fl. Cuba 3: 56. 1953) has in fact combined *P. dimorphus* with *P. cyclanthera* [i.e., *P. lindenianus*]. However, the pollen grains and stipules clearly demonstrate that the plant of the Trinidad Mountains belongs to subsect. *Pentaphylli* of sect. *Phyllanthus*. Furthermore, the coarsely reticulate ornamentation of the pollen, as well as vegetative features, show that *P. dimorphus* is much more closely related to *P. leptoneurus* of Hispaniola than it is to any of the Cuban species.

33. **Phyllanthus junceus** Muell. Arg. in DC. Prodr. 15(2): 411–412. 1866. (PLATE XXI, *figs. A–B*).

Phyllanthus pruinosus var. ? *subnudus* Wright ex Griseb. Cat. Pl. Cub. 16. 1866.
Phyllanthus squamatus Wright, Anal. Acad. Ci. Habana **7**: 109–110. 1870.
Diasperus junceus (Muell. Arg.) O. Ktze. Rev. Gen. **2**: 599. 1891.

Perennial herb, main axis a slender more or less gnarled woody caudex bearing at ground level several clustered wand-like branches mostly 1–3.5 dm. high, 0.5–1 (1–1.3) mm. thick, stramineous to pale reddish-brown, smooth, terete, sulcate, with (3–) 5–7 (–10) nodes, the internodes mostly 2–6 (–8) cm. long. Cataphylls: stipules ovate, 1.2–1.8 mm. long, 0.6–1.1 mm. broad, acute or acuminate at the tip, basal auricle very large (and often overlapping so that stipule appears peltate) and denticulate, brownish-black and indurate; blade lanceolate, 0.5–0.8 mm. long. Deciduous branchlets mostly 2–7 (–8) cm. long, 0.2–0.4 mm. thick, light brownish, somewhat pruinose, smooth, terete, with c. (6–) 10–20 (–30) leaves; first internode (6–) 10–18 (–25) mm. long, median internodes 2–4 (–6) mm. long. Leaves: stipules mostly ovate-lanceolate, 0.6–0.8 (–1.1) mm. long, 0.25–0.4 mm. broad, acute or acuminate at the tip, entire, dark brown to blackish and more or less indurate. Petioles 0.3–0.6 (–0.8) mm. long. Leaf-blades chartaceous to subcoriaceous, elliptic to obovate, mostly 5–8 (–10) mm. long and 2–5 mm. broad, obtuse or rounded at both ends; above olivaceous, minutely but usually distinctly areolate-foveolate, the midrib inconspicuous, the laterals obscure; beneath minutely pulverulent-scabridulous (glabrate with age), the midrib raised, the laterals obsolete; margins thickened, smooth, sometimes more or less revolute.

Dioecious or subioecious, the branchlets never bisexual; proximal 1–3 axils barren, or all nodes floriferous; male flowers c. 7–10 in racemiform cymules which become 1–1.5 mm. long, the bracteoles subindurate; female flowers solitary.

Male flower: pedicel c. 1.2–2.2 mm. long. Calyx-lobes 5, elliptic to spathulate, 1–1.5 (–1.7) mm. long, 0.6–0.9 (–1) mm. broad, obtuse or rounded at the tip, entire, yellowish, the herbaceous median area narrower than the broad scarious margins, the midrib unbranched. Disk-segments 5, squarish or broadly obcuneate, c. 0.2–0.3 mm. across, thin, subentire, usually standing erect. Stamens 2 (rarely 3, or with the rudiment of a third); filaments united into a colmun (0.4–) 0.5–0.6 (–0.75) mm. high, gradually tapering from the strongly dilated base to the apex; anthers sessile or subsessile atop the column, discrete or sometimes slightly connate by the connectives, 0.2–0.3 mm. long, 0.25–0.4 mm. broad; anther-sacs divergent, confluent at the apex, dehiscing more or less horizontally; pollen grains finely reticulate, 23–27 μ long, 18–22 μ broad.

Female flower: pedicel becoming (2.2–) 2.5–3 (–4) mm. long, more or less terete below, angled and thickened above. Calyx-lobes 5 (rarely 6), elliptic to spathulate, becoming 1.5–1.8 (–2) mm. long, (0.75–) 0.9–1.5 mm. broad, rounded or obtuse at the tip, with broad scarious margins, the midrib raised dorsally and ventrally, the lateral veinlets usually quite inconspicuous. Disk 5-lobed or nearly divided into 5 (6) suborbicular segments, somewhat fleshy, entire, sometimes pitted. Styles free, ascending, 0.3–0.45 mm. long, parted only ¼ their length, the more or less flattened and dilated style-branches recurved.

Capsule [rarely seen entire] c. 3.5 mm. in diameter, smooth, light brownish, not veiny. Seeds (1.35–) 1.5–1.7 (–1.8) mm. long, c. 1–1.2 mm. radially and tangentially, golden- or chestnut-brown, transversely barred with overlapping rows of more or less hygroscopic cells which spread as brownish setae when wetted, the longitudinal striae very inconspicuous or invisible.

Collected in flower and fruit November to July; perhaps flowering throughout the year.

TYPE: Cuba, Pinar del Río, *Wright 1937*.

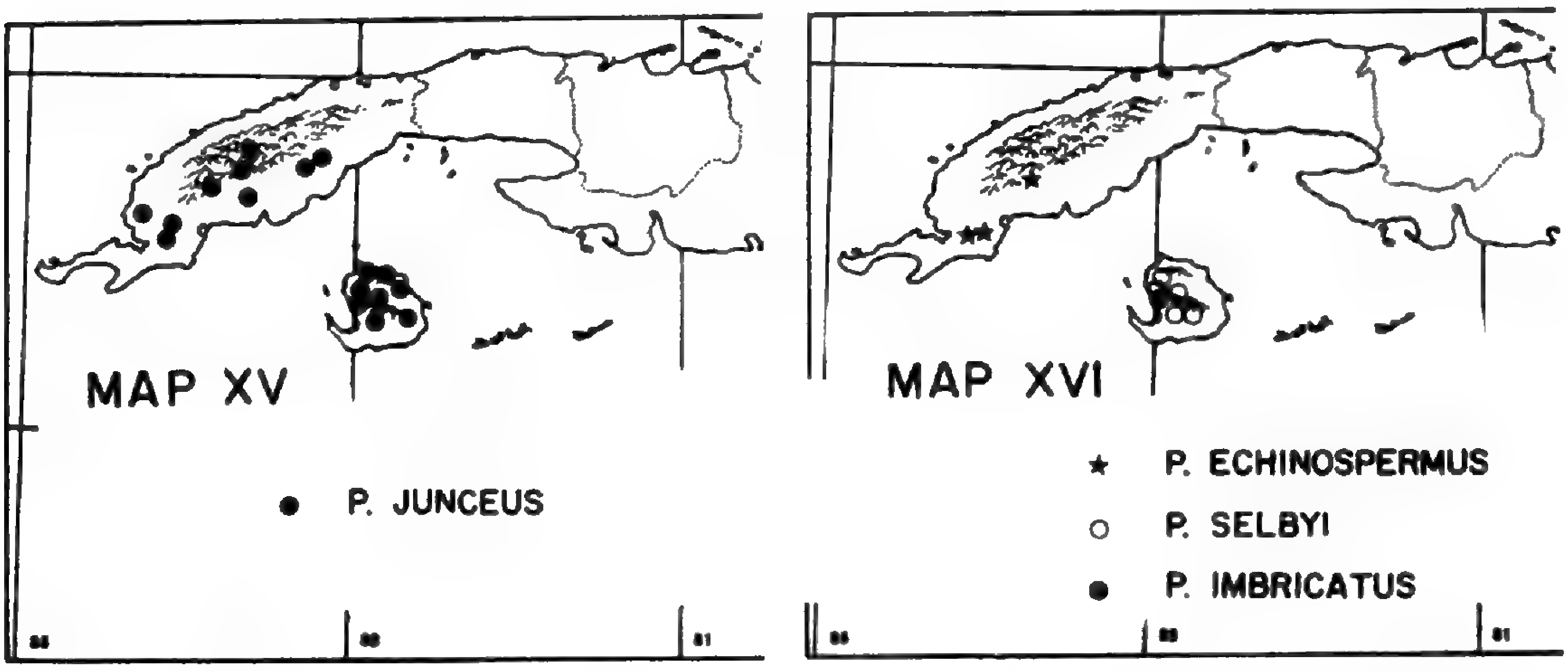
DISTRIBUTION: endemic to western Cuba and the Isle of Pines (Map XV).

CUBA. PINAR DEL RÍO: Arroyo Mantua, Damují, in savannas near salt water, *Ekman 11067* (S); palm-barrens west of Guane, *Shafer 10628* (NY); Laguna Jovero to Mendoza, in sand, *Shafer 10875* (NY); cut-over pineland between Pinar del Río City and Sumidero, *Webster 4671* (GH); pinelands near Pinar del Río, *Wright 3685* (GH, NY; type collection of *P. squamatus*); pinelands near San Luis, south of Pinar del Río, *León et al. 19589* (MICH); savanna 10.5 km. south of Pinar del Río, *Proctor 16329* (JAM); white sands near lagoons, between Pinar del Río and La Coloma, *Webster 4675* (GH); between Vinales and Pinar del Río, serpentine bank, *Webster 4669* (GH); Vinales, Sitio del Infierno, in pineland hills, *Ekman 16722* (S); Herradura, pinelands, *Baker 3503*, *Britton et al. 6448*, *Earle 642* (NY); between Los Palacios and Herradura, savanna, *Shafer 11704* (NY); Pinales Almácigos, *Wright 1937* (G, HOLOTYPE; GH, MO, ISOTYPES); without locality, *Wright* (MO, S; probably *Wright 3685*). ISLA DE PINOS: white-sand savannas, Santa Barbara, *Alain & Killip 2120*, *2146* (US), *Killip 42666*, *42695* (US); pinelands south of Santa Barbara, *Killip 44112* (US); near Nueva Gerona, *Curtiss 422* (G, L, NY, P), *Jennings 648* (NY); pineland savannas, Río Júcaro region, *Killip 42947* (US); savannas, Cemetario de Columbia, *Killip 43586* (US); grassy pinelands, San Francisco de las Piedras, *Killip & Swetland 41634* (US); barrens near Majagua River north of Los Indios, *Jennings 408* (GH, NY); pinelands, San Pedro and vicinity, *Britton & Wilson 14323* (NY); savannas between Santa Fe and San Juan, *Killip 43926* (US).

This species characteristic of savannas and pinelands in western Cuba is easily distinguishable by its large floral and fruiting parts, as well as by the areolate pattern of its upper leaf-surface. Although the total area of the distribution of the species is not very large, it appears to be very common within this range and indeed ubiquitous in favorable localities. It is very similar in habit to *P. pentaphyllus* ssp. *pentaphyllus* and may be regarded as more or less coordinate in ancestry. Unlike *P. pentaphyllus*, *P. junceus* appears to prefer siliceous soil and is never found on calcareous substrates; this may partially account for its more restricted over-all range.

34. **Phyllanthus pentaphyllus** Wright ex Griseb. Goett. Nachr. **1865**: 167. 1865.

A highly variable perennial herb becoming 0.2–3 dm. high, with the main axis often abortive, the branches becoming clustered on a caudex and themselves more or less diffusely branching; flowering the first year, thus simulating an annual (and perhaps occasionally an annual in fact under difficult conditions); main stems erect or spreading, stramineous or greyish becoming dark brown in age, smooth or rarely minutely scabridulous, often somewhat channelled, c. 0.5–2 mm. thick; internodes (except in very depauperate plants) mostly 2–5 cm. long. Cataphylls: stipules ovate-triangular, mostly 0.9–1.3 mm. long, 0.5–0.7 mm. broad, acute to acuminate at the tip (or the lateral teeth sometimes obscuring the apex), entire to more commonly conspicuously dentate or lacerate, conspicuously auriculate at the base, dark reddish becoming blackish and indurate; blade linear-lanceolate. Deciduous branchlets (0.5–) 1–3 (–6) cm. long, 0.2–0.3 mm. thick, terete, furrowed, olivaceous or stramineous, smooth or rarely scabridulous, with 5–20 (–35) leaves; first internode (2.5–) 5–15 mm. long, second internode often very short and first two leaves hence subopposite, median internodes c. 0.5–1.5 (–2) mm. long. Leaves: stipules subpersistent, lanceolate, 0.4–0.8 (–1) mm. long, acuminate, olivaceous or sometimes reddish-tinged, entire, scarious (the proximal ones sometimes becoming reddish-black and indurate). Petioles 0.3–0.4 mm. long. Leaf-blades membranous to subcoriaceous, elliptic to mostly obovate or suborbicular, (1.5–) 2.5–7.5 (–8.5) mm. long, (0.75–) 1.5–4 (–5.5) mm. broad, mostly obtuse or rounded and often apiculate at the tip, acute to obtuse or rounded at the base; above smooth, deep green, the midrib inconspicuous; beneath smooth or minutely scabridulous, greyish or brownish, the midrib prominent, the laterals invisible to conspicuous and reticulate; margins plane or slightly reflexed, sometimes slightly thickened, smooth or roughened.



Maps XV and XVI. Distribution of some species of subsect. *Pentaphylli* in Cuba.

Monoecious (in the West Indies; only rarely and exceptionally dioecious); male flowers 5–25 in racemiform cymules, the scarious yellowish-white bracteoles more or less persistent after fall of the flowers; female flowers solitary in the distal axils.

Male flower: pedicel mostly 0.4–0.8 mm. long. Calyx-lobes 5, subequal, rather strongly imbricate, obovate, (0.4–) 0.5–1 mm. long, (0.3–) 0.4–0.75 mm. broad, obtuse at the tip, entire to crenulate, yellowish and scarious, the midrib unbranched. Disk-segments 5, roundish or squarish, flat, subentire, not evidently glandular, c. 0.1–0.15 mm. across. Stamens 2; filaments connate beyond the middle into a column c. 0.2–0.3 mm. high; anthers short-stipitate or subsessile atop the column, discrete (rarely united at the base), c. 0.1–0.2 mm. long, 0.15–0.3 mm. broad; anther-sacs divergent, the slits confluent, dehiscing obliquely to horizontally; pollen grains finely reticulate, 21–25 μ long, 16–20 μ broad.

Female flower: pedicel becoming (0.8–) 1.2–2 (–2.7) mm. long, terete or sometimes obscurely angled, slender, tapering only slightly upwards, olivaceous, smooth. Calyx-lobes 5, subequal, elliptic to mostly obovate, becoming 0.8–1.2 mm. long and 0.5–0.75 mm. broad, subacute to rounded at the tip, entire or occasionally obscurely crenulate, herbaceous with broad whitish scarious margins, the midrib unbranched. Disk variable: cupuliform and merely angled, 5-lobed, or parted into 5 linear segments. Styles spreading or somewhat ascending, c. 0.15–0.2 mm. long, parted (¼–) ⅓ to ½ their length, the style-arms divergent, the slender tips recurving.

Capsule oblate, rounded, c. 1.7–1.9 mm. in diameter, smooth, stramineous or olivaceous, the veins obscure. Seeds acutely trigonous, 0.8–1 mm. long, 0.7–0.8 mm. radially and tangentially, light brown, with 6–8 delicate but often obscure slightly raised longitudinal striae on the back, transversely barred on the back with slightly hygroscopic epidermal cells.

Collected flowering and fruiting throughout the year.

This highly variable species has a broad range embracing most of the West Indies but with many lacunae as regards its local distribution. It shows close relationships to *P. junceus* on the one hand and to *P. pulverulentus* and *P. echinospermus* on the other; all four of these species have in common a more or less acaulescent habit which is associated with an unusual degree of development of branches from collateral buds, both at the cotyledonary and at subsequent nodes. The result is that the plants have clusters of rather wand-like stems either at the swollen end node of the original main axis or one of the branches.

Ecologically, *P. pentaphyllus* is well separated from *P. junceus* and *P. echinospermus* by its preference for calcareous habitats; but it is merely geographically isolated from *P. pulverulentus*, which grows on precisely the same sort of littoral coral platforms that *P. pentaphyllus* does. It is hardly surprising that of these three species related to *P. pentaphyllus*, the least distinctive is *P. pulverulentus*, which has the earmarks of a subspecies showing geographical replacement; but in the present treatment, *P. pulverulentus* is retained at specific rank because of its reasonably well-marked characters.

KEY TO THE SUBSPECIES

Leaves subcoriaceous, broadly obovate to suborbicular (1.2–1.7 times as long as broad), the lateral veins very obscure or invisible beneath; disk (at anthesis) 5-angled or shallowly and obtusely 5-lobed; plants stiffly erect. . . ssp. *polycladus*.

Leaves membranous to chartaceous, more narrowly obovate (1.7–2.5 times as long as broad), the lateral veins and tertiary reticulum usually prominent beneath; disk of female flower deeply 5-lobed or parted into 5 linear segments; plants with usually more flexible, often spreading, stems . . . . ssp. *pentaphyllus*.

34a. **Phyllanthus pentaphyllus** ssp. **pentaphyllus** (PLATE XXI, *figs. C–D*).

Phyllanthus niruri ζ radicans Muell. Arg. Linnaea **32**: 44. 1863; DC. Prodr. **15**(2): 407. 1866.
Phyllanthus radicans (Muell. Arg.) Small, Fl. S.E. U. S. 692. 1903.
Phyllanthus polycladus var. γ *curassavicus* Urb. Symb. Ant. **5**: 384. 1908.

Perennial or sometimes appearing annual, stems smooth or rarely scabridulous, rather flexuous, upright or spreading. Deciduous branchlets (0.5–) 1–3.5 (–6) cm. long, with (5–) 8–25 (–35) leaves. Leaf-blades membranous or chartaceous, flexible or brittle, obovate to spathulate, sometimes quite narrow, (1.5–) 3–6 (–8.5) mm. long, (0.75–) 1–3.5 (–5) mm. broad, mostly 1.7–2.5 times as long as broad; lateral veins usually rather conspicuous beneath, a reticulum of delicate veinlets often visible; margins rather clearly demarcated, thicker than the blade, more or less roughened by projecting cell walls.

Monoecious (very rarely dioecious); proximal 0–2 axils barren, succeeded by 2–4 axils with cymules of (5–) 10–25 male flowers; cymule often with twin axes (the first branching being dichasial), or sometimes cristate and developing into a thick cluster of flowers.

Male flower: calyx-lobes entire, obovate, 0.4–0.7, mm. long, 0.3–0.5 mm. broad; staminal column c. 0.2–0.25 mm. high. Female flower: pedicel (0.8–) 1.2–2 (–2.7) mm. long; calyx-lobes 0.5–1.2 mm. long, 0.25–0.6 mm. broad; disk deeply 5-lobed or parted into 5 lanceolate to linear segments.

TYPE: Cuba, Pinar del Río, Santa Cruz, on rocks in the river, 8 April 1863, *Wright 1938* ex p. (GOET, HOLOTYPE; GH, MO, NY, S, US, ISOTYPES). Wright's collection is a mixture of plants from at least two different localities; the citation of type locality is the result of matching the data on the Goettingen and Gray Herbarium specimens. The other locality, the label for which is also on the Gray Herbarium sheet, is Lagunillas, River San Sebastian, and is presumably also in Pinar del Río, although it has not been located on any map. There are two rather distinctive forms represented in the type collection, one with shorter branch internodes and monoecious inflorescences, the other with longer branch internodes and dioecious inflorescences (this latter form occurring on the New York and Stockholm sheets). Various circumstances suggest that the monoecious form was collected at Santa Cruz and the dioecious form probably at Lagunillas, so that the nomenclatural type fortunately must be associated with the far more common monecious plant.

DISTRIBUTION: ssp. *pentaphyllus* comprises two varieties: var. *pentaphyllus,* which is very widespread in the West Indies, and var. *floridanus*, which is restricted to southern Florida (MAP X).

BAHAMAS. GREAT BAHAMA: pinelands, Eight Mile Rocks, *Britton & Millspaugh 2381* (F, NY). ELEUTHERA: Governor's Harbor and vicinity, sandy soil, *Britton & Millspaugh 5514* (F, NY). MARIGUANA [Mayaguana]: 5 mi. west of Southeast Point, *Wilson 7552* (F, NY).

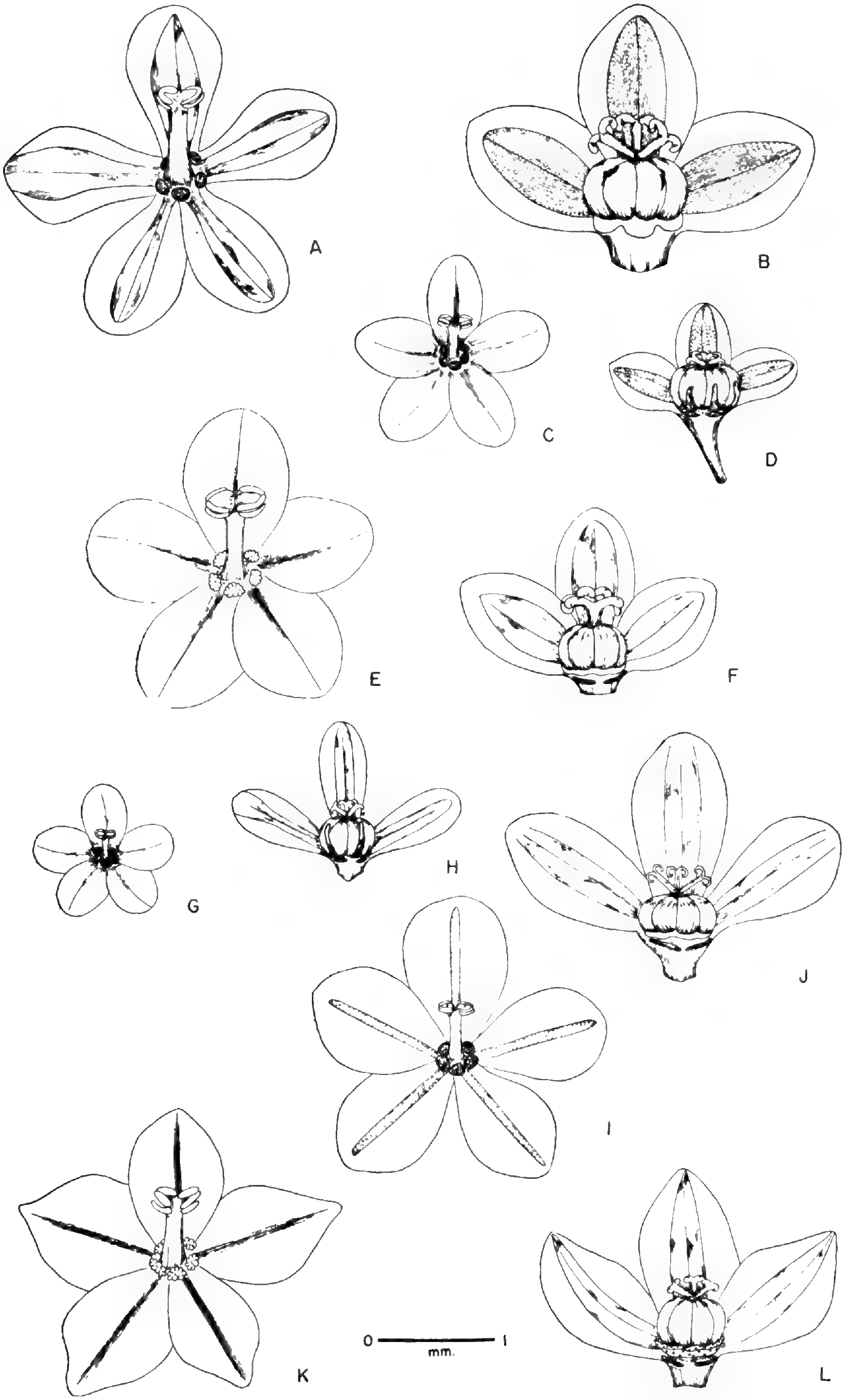
CUBA. PINAR DEL RÍO: Arroyo del Sumidero, dry rocks above the water, *Shafer & León 13587* (NY); Pinar del Río City, Mateo Sanchez, moist places, *Ekman 17933* (MICH, S); Sierra de los Organos, San Diego de Tapía, at the edge of the Río Maní-Maní, *Ekman 12679* (S); La Cajálbana, La Mulata, *Acuña* (SV 18221); La Cajálbana, La Palma, *Acuña & Alain* (SV 15812); Santa Cruz, on rocks in the river, *Wright 1938* ex p. (GOET, HOLOTYPE; GH, MO, NY, S, US, ISOTYPES); River San Sebastian, Lagunillas, *Wright 1938* ex p. (GH, and perhaps some of the other isotype sheets); bay of Mariel, *Britton & Earle 7597* (F, NY), *7610* (NY, US); Mariel, Tinaja, towards Río Dominica, *Ekman 12882* (S); without specific locality, *Wright* "48" (GOET, probably *Wright 1938*). ISLA DE PINOS: Nueva Gerona, near the marble quarry at the foot of Sierra Las Casas, on shaded rocks, *Ekman 12571* (S). HABANA: Havana, *Hermann 62* (F, NY); Vedado, *Ekman 149* (S); prope Morro in rupibus, *Ekman 1164* (S); Playa de Jaimanitas, *León 6294* (NY); Cabana Fortress, *León 11396* (NY); Playa de Baracoa, *León 8440* (NY); Cuabal de Jesus Maria near Minas, *León 4781* (NY, SV). MATANZAS: Boca de Canasí, on limestone rocks, *León 13172* (NY); coral rocks, playa, Matanzas,, *Britton et al. 92* (NY); Matanzas, among bushes and grass near the bay, *Wright* "123" (GOET); Canimar, *Otto 51* (W); shore of Matanzas Bay, limestone ledges near Canimar Bridge, *Webster 4800* (GH). LAS VILLAS: Trinidad Mountains, Hanabanilla Falls, rocky river bed, *Britton et al. 4850* (F, NY).

HAITI. OUEST: Pte.-á-Raquettes, Ile Gonave, *Ekman H8879* (S, US), *Eyerdam 272* (F, GH, NY, US).

DOMINICAN REPUBLIC. PUERTO PLATA: Sosúa, rock fissures on coral reef, *Ekman H14481* (S). BARAHONA: sea-shore, *Fuertes 1078* (A, F, GH, US); bei Paraíso, *Fuertes 961* (A, NY, P, W).

PLATE XXI. FLOWERS OF SECT. *Phyllanthus*, SUBSECT. *Pentaphylli.*

FIGS. A-B. *Phyllanthus junceus* Muell. Arg. (male, *Killip 43926* [US]; female, *Killip 42947* [US]). FIGS. C-D. *Phyllanthus pentaphyllus* Wright ex Griseb. ssp. *pentaphyllus* (male, *Eyerdam 272* [GH]; female, *Ekman 1164* [S]). FIGS. E-F. *Phyllanthus pulverulentus* Urb. (male, *Webster 3981* [GH]; female, *Webster 3937* [GH]). FIGS. G-H. *Phyllanthus echinospermus* Wright (*Ekman 18131* [S]). FIGS. I-J. *Phyllanthus selbyi* Br. & Wils. (*Britton & Wilson 14157* [MO]). FIGS. K-L. *Phyllanthus imbricatus* Webster (*Britton & Wilson 14192* [GH]).



Webster, West Indian Phyllanthus

CURAÇAO. CURAÇAO: *P. E. Benzon* (C); Ft. Nassau, calcareous land, *Suringar 2* (L, type collection of *P. polycladus* var. *curassavicus*); limestone rocks near Willemstad, *Britton & Shafer 2948* (F, US). BONAIRE: *Boldingh 7278* (C, L).

Although this very polymorphic population could perhaps be subdivided further into varieties, the present broad circumscription seems the most practicable. Actually, the only additional entity recognized within ssp. *pentaphyllus*, var. *floridanus*, is very weakly defined; it differs from var. *pentaphyllus* mainly in its dioecious inflorescence, but dioecious individuals do occur (though rarely) in the Cuban population. Consequently, if any taxonomic adjustments are made, the result may prove to be the deletion of the two varieties now existing rather than the erection of additional ones.

The distribution of ssp. *pentaphyllus* appears to be curiously disjunct, and it appears doubtful that future collecting will appreciably narrow the gaps. It might be supposed that such a distant station as that in Curaçao might show appreciable taxonomic differences, but there do not appear to be any significant differences between the plants from the Dutch islands and those from Cuba. The absence of ssp. *pentaphyllus* from eastern Cuba may be accounted for by its replacement by *P. pulverulentus*, and its apparent rarity in Hispaniola may simply reflect inadequate collecting; but the spotty distribution in the Bahamas is more difficult to explain. The plants from the Lesser Antilles (Guadeloupe), which show a much closer approach to ssp. *pentaphyllus* than one would expect from their proximity to ssp. *polycladus*, also pose a problem in relationships that cannot be resolved at this time.

34b. **Phyllanthus pentaphyllus** ssp. **polycladus** (Urb.) Webster, Contr. Gray Herb. **176**: 56. 1955. (PLATE XXII, *fig. C*).

Phyllanthus polycladus Urb. Symb. Ant. **1**: 333. 1899.
Phyllanthus polycladus β *guadeloupensis* Urb. ibid.

Perennial, woody at the base, branches mostly stiffly erect (at least below). Deciduous branchlets 0.7–1.5 (–2.7) cm. long, with (4–) 5–12 leaves. Leaf-blades subcoriaceous, broadly ovate to suborbicular, 2.5–5 (–6) mm. long, 2–4 mm. broad, mostly 1.2–1.7 times as long as broad; lateral veins inconspicuous or invisible; margins not clearly demarcated except by color (scarcely thicker than the blade), smooth.

Monoecious, the proximal 0–1 nodes barren, the succeeding 2–4 nodes with racemiform male cymules.

Male flowers: calyx-lobes more or less crenulate, broadly obovate, 0.7–1 mm. long, 0.65–0.75 mm. broad; staminal column 0.2–0.35 mm. high. Female flower: pedicel 0.8–1.8 mm. long; calyx-lobes 0.8–1.2 mm. long, 0.5–0.7 mm. broad; disk cupuliform and merely 5-angled or shallowly and obtusely 5-lobed.

TYPE: Puerto Rico, *Sintenis 3440*.

DISTRIBUTION: Puerto Rico and the Lesser Antilles (MAP X).

PUERTO RICO. MAYAGUEZ: limestone east of Guayanilla, *Britton & Britton*

9141 (F, NY); prope Guanica in rupibus litoralibus ad salinas, *Sintenis 3440* (NY, LECTOTYPE; A, F, GH, L, MO, NY, P, US, W, ISOTYPES); rocky coastal thicket, Guanica and vicinity, *Britton & Shafer 1912* (NY, US); salinas de Guanica, *Britton, Cowell, & Brown 4913* (F, NY, US). PONCE: Cayo Muertos, coastal limestone rocks, *Britton, Cowell, & Brown 4998* (F, MO, NY, US); crevices of rocks near Ponce, *Underwood & Griggs 696* (NY, US). HUMACAO: Icacos Cay, limestone rocks, *Britton 7171* (NY, US).

LESSER ANTILLES. ANEGADA: rocky plain near settlement, *Britton & Fishlock 1000* (F, MO, NY, US). GUADELOUPE: Vieux-Fort, champs de manioc, endroits secs, sablonneux, *Duss 209* (P); hauteurs de Vieux-Fort, abondant dans le terrain rocailleux et sec, *Duss 2443* (F, GH, NY, US).

A collection purportedly from St. Thomas, in the Virgin Islands (*Friedrichsthal 383* [W]), is not listed above because its characters on the whole agree better with ssp. *pentaphyllus* and also because it seems rather unlikely that the plant has not been recollected on such a comparatively well-known island as St. Thomas. It must be granted, however, that since the plants from Guadeloupe also approach ssp. *pentaphyllus,* there is a possibility that the populations east of Puerto Rico may ultimately prove not to belong to ssp. *polycladus*; in such an event, Friedrichsthal's record would no longer be surprising. A careful search for *P. pentaphyllus* on St. Thomas is highly desirable.

Two collections from Indiera Fria, Maricaco, Aquadilla Province, Puerto Rico (*Stevens & Hess 3328, 3347* [NY]), are too fragmentary to be positively identified, but may represent an aberrant form of ssp. *polycladus.* They differ in having branchlets up to 4.2 cm. long with narrow leaves, and in being apparently dioecious. Additional specimens will have to be procured from this population in order to ascertain its exact affinity.

In his original publication of *P. polycladus,* Urban merely referred it to sect. *Euphyllanthus* and remarked it as distinct by its two stamens, without discussing its relationships. Subsequently (on labels) he applied the name *P. polycladus* to individuals of ssp. *pentaphyllus* from Cuba and Hispaniola, so that evidently he did not appreciate the fact that Wright had already described the species nor that any real differences existed between the plants of Cuba and those of Puerto Rico. Careful study of all available collections demonstrates, however, that the species may be divided into two subspecies which are so distinctive that they might appear to merit specific rank. The intermediate nature of the plants from Guadeloupe suggests on the contrary that the two populations have not yet attained specific distinctiveness, and confirmation of Friedrichsthal's collection from St. Thomas would strengthen this point of view. In any event, there appears to be no necessity for designating or recognizing any further subspecific taxa, such as Urban's var. *guadeloupensis.*

35. **Phyllanthus pulverulentus** Urb. Symb. Ant. 9: 192. 1924. (PLATE XXI, *figs. E–F*).

Suffruticose perennial c. 1–3 dm. high, copiously branching from a woody base; branches erect or spreading, terete, stramineous or brownish, smooth or minutely scabridulous, c. 0.5–0.6 mm. thick; internodes c. 0.5–3 (–4.5) cm. long. Cataphylls: stipules deltoid-ovate, 0.8–1.2 mm. long, 0.6–0.9 mm. broad, acute to acuminate at the tip, conspicuously auriculate at the base, entire to conspicuously dentate (sometimes distally several-toothed, with a definite apex), becoming reddish-black and indurate; blade linear-lanceolate, 0.5–0.8 mm. long. Deciduous branchlets (1–) 1.5–3 (–4) cm. long, 0.2–0.3 mm. thick, subterete, olivaceous, smooth to densely scabridulous, with mostly 7–25 leaves; first internode (1–) 1.5–7 (–8) mm. long, median internodes 1–3 (–4) mm. long. Leaves: stipules more or less deciduous, lanceolate, c. 0.5–0.9 mm. long, acuminate, entire, yellowish, scarious. Petioles 0.25–0.5 mm. long. Leaf-blades firmly chartaceous, scabridulous on both sides but more conspicuously so beneath, elliptic or oblong to obovate or sometimes suborbicular, c. (2.5–) 3–5 (–6) mm. long, (1.5–) 2–3 mm. broad, obtuse to rounded or occasionally subacute at the tip, obtuse or rounded at the base; above greyish-green, the midrib obscure, the laterals invisible; beneath yellowish-green, the midrib raised, the laterals obscure or invisible; margins somewhat thickened, plane, scabridulous.

Monoecious or subdioecious. Branchlets of 3 types: (1) bisexual, the proximal 1–3 nodes barren, the succeeding 3–9 nodes with cymules of male flowers, the distal with solitary female flowers; (2) predominantly male, with no barren nodes, the proximal 10–14 nodes with male flowers, the 1 or 2 distal nodes with or without female flowers; and (3) female, never with any male flowers, the proximal 5–6 nodes barren. Male cymules with c .5 or 6 flowers, monochasial or dichasial at the first branching; bracteoles yellowish-white, scarious, persistent.

Male flower: pedicel c. 0.5–0.8 mm. long. Calyx-lobes 5, subequal, obovate, 0.9–1.2 mm. long, 0.6–0.9 mm. broad, obtuse or rounded at the tip, entire, yellowish-scarious, the midrib usually unbranched (that of larger lobes occasionally with a few obscure branches). Disk-segments 5, plane or concave, roundish, c. 0.2 mm. across, subentire or crenulate, not conspicuously glandular. Stamens 2 (rarely 3); filaments completely united into a column (0.3–) 0.4–0.5 mm. long; anthers sessile atop the column, more or less fused back-to-back, often unequal, c. 0.2 mm. long and 0.25–0.3 mm. broad; anther-sacs widely divergent, the slits confluent, dehiscing more or less horizontally; pollen grains finely reticulate, 21–26 μ long, 16–20 μ broad.

Female flower: pedicel becoming (0.7–) 1.2–1.8 (–2.2) mm. long, olivaceous, terete, gradually dilated from the base, smooth. Calyx-lobes 5 (rarely 6), subequal, obovate, c. 1.2–1.7 mm. long, 0.8–1.2 mm. broad, rounded at the tip, entire, with yellowish-scarious margins, the midrib branched but the laterals quite obscure. Disk shallowly cupuliform, thin, the 5-angled rim undulate or crenulate. Styles spreading or ascending, c. 0.3–0.4 mm. long, parted c. ⅓ their length, the branches divergent, the slender blunt tips recurved.

Capsule oblate, c. 2.2–2.4 mm. in diameter, shallowly sulcate, smooth, yellowish-brown, not veiny. Seeds trigonous, c. 1–1.1 mm. long, 0.85–

0.9 mm. radially and tangentially, pale to dark brown, with c. 12–14 delicate longitudinal striae and transversely barred by non-hygroscopic epidermal cells.

TYPE: Cuba, *Ekman 7736.*

DISTRIBUTION: Coastal terraces, southeastern Oriente Province, Cuba (MAP X).

CUBA. ORIENTE: between Santiago de Cuba and El Morro, on coral, 25 Sept. 1916, *Ekman 7736* (S, HOLOTYPE); limestone rocks at El Morro, steep slopes facing the sea, 6 July 1924, *Ekman 19197* (MICH, NY, S); vicinity of Guantánamo, limestone hills along the coast between Escondido Bay and the Río Yateras, 28 July 1951, *Webster 3937* (GH, MICH, NY); coastal limestone terrace between the Río Yateras and Baitiquirí, 31 July 1951, *Webster 3981* (GH, MICH, NY).

This species, with its rigid stems and leaves, appears to be a local woodier representative of the widespread Caribbean species *P. pentaphyllus*, which it indeed replaces in Oriente. It would be possible to regard *P. pulverulentus* as merely a subspecies of the wide-ranging plant, and the disposition made above of the Puerto Rican ssp. *polycladus* might appear to justify such a point of view. However, although the criteria are admittedly subjective, the Oriente population, with its larger male flowers and distinctive leaves, appears to be well-marked enough to stand at the specific level, whereas the Puerto Rican plant does not.

36. **Phyllanthus echinospermus** Wright, Anal. Acad. Ci. Habana 7: 108. 1870. (PLATE XXI, *figs. G–H*).

Phyllanthus minimus Wright, idem 108–109.

Slender depauperate herb, flowering precociously and appearing as if an annual, but at length perennial, the primary axis becoming abortive or confounded with numbers of more or less procumbent branches c. 2–5 (–10) cm. long, 0.3–0.6 (–0.9) mm. thick, smooth, terete, light brown, with internodes c. (0.5–) 1–1.5 (–2) cm. long. Cataphylls: stipules deltoid-ovate, 0.8–1.1 mm. long, 0.4–0.6 mm. broad, acute, auriculate at the base, entire or somewhat denticulate, reddish-brown becoming dark brown or blackish and indurate. Deciduous branchlets 1–2.5 cm. long, 0.15–0.2 mm. thick, smooth, terete, reddish-brown, with c. 10–15 leaves; first internode mostly 3–7 mm. long, median internodes c. 0.8–1 mm. long. Leaves: stipules linear-lanceolate, 0.5–1 mm. long, 0.15–0.2 mm. broad, attenuate-acuminate, reddish with narrow whitish scarious margins. Petioles c. 0.3–0.4 mm. long. Leaf-blades thin, elliptic or elliptic-obovate, (1.5–) 2–4 mm. long, 1–2 mm. broad, obtuse or rounded at the tip, obtuse often somewhat inequilateral at the base, minutely scabridulous on both sides (but more conspicuously so beneath); above green or reddish-tinged, midrib impressed and rather inconspicuous, the laterals invisible; beneath often reddish, the midrib conspicuous and raised, the laterals scarcely or not at all visible; margins plane, slightly thickened, smooth, more or less reddish-tinged.

Monoecious; proximal (0–) 1–3 (–4) nodes barren; succeeding (1–) 2–4 (–6) nodes with racemiform cymules (less than 0.5 mm. long) of 3–5 male flowers; distal axils with solitary female flowers.

Male flower: pedicel 0.3–0.7 mm. long. Calyx-lobes 5, suborbicular, equal, c. 0.4–0.5 mm. long, 0.25–0.4 mm. broad, obtuse or rounded at the tip, entire, yellowish, subhyaline, obscurely carinate along the unbranched midrib. Disk-segments 5, roundish, thin, more or less entire, c. 0.1 mm. across. Stamens 2; filaments completely connate into a column 0.15–0.2 mm. high; anthers sessile atop the column, c. 0.2 mm. long and 0.3 mm. broad; anther-sacs divergent, the slits apically confluent, dehiscing more or less horizontally; pollen grains finely reticulate, 21–24 μ long, 16–19 μ broad.

Female flower: pedicel (0.5–) 0.9–1.2 mm. long, more or less angled and reddish-tinged. Calyx-lobes 5, becoming definitely spathulate in fruit, 0.9–1.2 (–1.5) mm. long, 0.4–0.5 (–0.6) mm. broad, rounded at the tip, entire, the scarious margins broader than the narrow herbaceous midstrip, dorsally carinate along the unbranched midrib, often conspicuously reddish-tinged. Disk parted into 5 distinct linear, subulate segments c. 0.25–0.3 mm. long. Styles ascending, rather fleshy, c. 0.15–0.2 mm. long, bifid, the branches reflexed.

Capsule oblate, rounded-trigonous, c. 1.4–1.5 mm. in diameter, smooth, stramineous or brownish, the veins completely obscure. Seeds trigonous, 0.6–0.7 mm. long, 0.4–0.55 mm. radially and tangentially, brownish, transversely barred with hygroscopic epidermal cells which recurve as clavate brown-stained trichomes (the longitudinal striae completely obscure).

Collected in November and December.

TYPE: Cuba, Pinar del Río, *Wright 3687.*

DISTRIBUTION: endemic to the lagoon area, western Pinar del Río (MAP XVI).

CUBA. PINAR DEL RÍO: Laguna Jovero, sandy soil, *Shafer 10774* (NY); Laguna Jovero to Laguna del Bufeo, in wet sand, *Shafer 10996* (NY); Laguna Santa Barbara, in the *Paurotis*-belt, sandy places, *Ekman 18112* (S); Laguna Alcatraz Grande, in white sand, *Ekman 18131* (S); Laguna de la Máquina de Tarafa, *Wright 3686* (F, GH, NY, P, US;type collection of *P. minimus*), *3687* (GH, LECTOTYPE; F, NY, US, ISOTYPES); same locality, steep sides of a small brook, *Ekman 17903* (S); Pinar del Río City, between Laguna de la Máquina and Laguna de Junio, in somewhat moist places, *Ekman 17907* (S).

This species, which is one of the most diminutive in the West Indies, is easily recognizable by its leaves scabridulous on both sides, its spathulate usually reddish-tinged fruiting calyx-lobes, and its linear female disk-segments. Its habit is precisely like that of very depauperate individuals of *P. pentaphyllus*, and it does indeed appear to be closely related to that species. Ecologically, the two are well separated, since *P. echinospermus* is found on sand usually at the edge of lagoons, while *P. pentaphyllus* is a calciphile growing in stream-beds or along the seacoast.

Specimens of the proposed species *P. minimus*, described by Wright from individuals collected at the same locality, differ in no way from *P. echinospermus* except that they represent very young individuals, some of which are flowering at the third or fourth branchlet while the cotyledons are still attached. In combining the two species, it seems appropriate to conserve the epithet *echinospermus* for the aggregate concept, since the hygroscopic cells of the very small seed are a characteristic feature of the species.

37. **Phyllanthus selbyi** Br. & Wils. Mem. Torr. Bot. Club **16**: 74. 1920. (PLATE XXI, *figs. I–J*; PLATE XXII, *fig. D*).

Erect perennial herb (but flowering first year and then appearing as if annual) with dendroid form, the main stem sparingly to copiously branching above, becoming 2–4 dm. high, terete, rather woody, with bark becoming blackened and fissured in age; internodes of main stem mostly 0.5–2 cm. long. Cataphylls: stipules ovate-lanceolate, 1.2–1.5 mm. long, 0.5–0.7 mm. broad, acuminate, auriculate at the base, entire or conspicuously dentate, becoming blackish and indurate; blade linear-lanceolate, 0.6–1.1 mm. long, 0.1–0.15 mm. broad. Deciduous branchlets (1–) 2–3 (–3.5) cm. long, 0.15–0.3 mm. broad, terete, smooth, reddish-brown or stramineous and more or less pruinose, with mostly (15–) 20–30 (–35) leaves; first internode c. 3.5–6 mm. long, median internodes 0.6–1.3 mm. long. Leaves: stipules linear-lanceolate, 0.5–0.7 mm. long, 0.15–0.2 mm. broad, acuminate, distally scarious-tipped, reddish-tinged with entire whitish scarious margins. Petioles c. 0.2–0.3 mm. long. Leaf-blades rather thick, elliptic or oblong to obovate, 2–3 mm. long, 1–1.8 mm. broad, acute or obtuse at the tip, rounded at the base; pale green and somewhat pruinose above and below, the veins invisible except for the rather faint midrib; margins plane, more or less reddish-tinged, smooth or sometimes slightly roughened.

Dioecious or subdioecious; male branchlets normally with the proximal 6–10 nodes barren, succeeding ones with racemiform cymules (up to 0.5 mm. long) of 3–7 flowers; female branchlets with the proximal 10–17 nodes barren, followed by solitary flowers; occasional male branchlets producing a single distal female flower.

Male flower: pedicel 0.4–0.7 mm. long. Calyx-lobes 5, elliptic to obovate, unequal, the longer c. 0.7–1.2 mm. long and 0.6–0.75 mm. broad, the shorter c. 0.6–0.9 mm. long and 0.5–0.7 mm. broad, obtuse or rounded at the tip, yellowish-scarious except for the narrow herbaceous area along the dorsally carinate unbranched midrib. Disk-segments 5, transversely elongate, not conspicuously glandular, c. 0.1–0.2 mm. across. Stamens 2; filaments completely united into a column 0.3–0.4 mm. high; anthers sessile atop the column, 0.2–0.3 mm. long, 0.25–0.4 mm. broad; anther-sacs divergent, the slits apically confluent, dehiscing obliquely; pollen grains finely reticulate, 22–24 μ long, 18–20 μ broad.

Female flower: pedicel (0.6–) 1–1.4 mm. long, terete, smooth, olivaceous, angled. Calyx-lobes 5 (rarely 6), elliptic to obovate, subequal, 1–1.4 mm. long, 0.6–0.8 mm. broad, obtuse or rounded at the tip, with yellowish scarious margins broader than the greenish midstrip, dorsally carinate along the unbranched midrib. Disk variable, usually deeply 5-lobed, sometimes merely with 3–5 notches, the thin lobes squarish or triangular. Styles ascending, 0.25–0.35 mm. long, bifid ¼ their length or less, the very short unthickened branches recurved.

Capsules not seen entire; valves stramineous, the veins obsolete. Seeds sharply trigonous, c. 0.9 mm. long, 0.65–0.75 mm. radially and tangentially, dark brown, the longitudinal striae very obscure or invisible, transversely barred by hygroscopic cells which project as slightly clavate setae when moistened.

Collected in flower or fruit November to May; perhaps flowering throughout the year.

TYPE: Cuba, Isle of Pines, *Britton et al. 14157.*

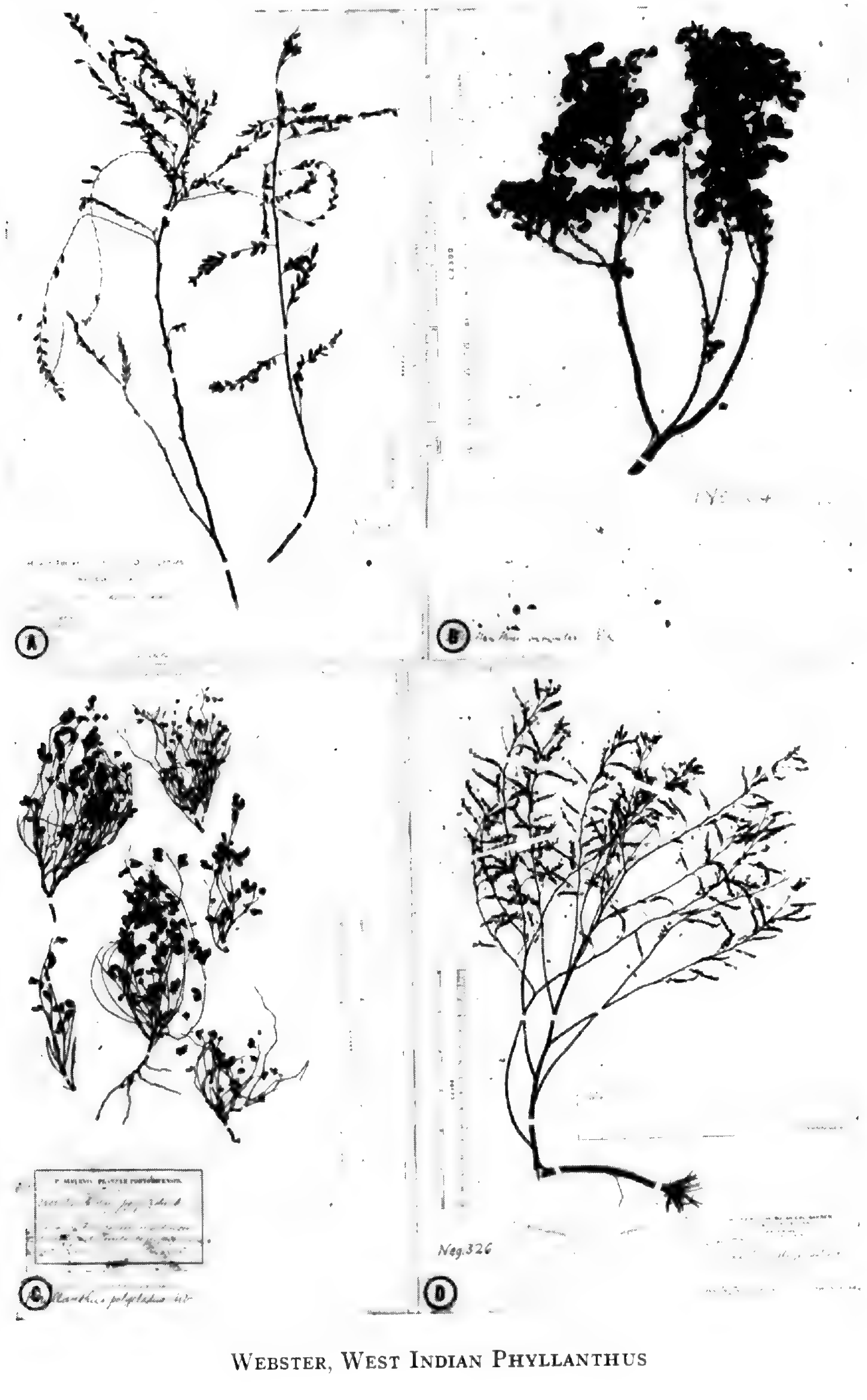
DISTRIBUTION: endemic to the Isle of Pines (MAP XVI).

CUBA. ISLA DE PINOS: Santa Barbara, *Alain & Killip 2120*, *Killip 42666* (US); between San Francisco de las Piedras and Cerro la Canada, *Killip 44633* (US); between Mina de Oro and Playa del Soldado, *Killip 43896* (US); Los Indios, *Alain & Killip 2174* (US), *Ekman 12159* (S); Siguanea, *Killip 44055* (US); San Pedro and vicinity, *Britton, Wilson, & Selby 14157* (NY, HOLOTYPE; F, GH, MO, US, ISOTYPES); Las Tunas rivulet, *León & Marie-Victorin 17892* (MICH).

This species, characterized by its resemblance to a miniature tree, is strikingly microphyllous, like many of its neighbors on the white sands of the Isle of Pines. Occasionally individuals of *P. selbyi* may produce a few branches from near the base; and in a collection from Santa Barbara (alkali flats on white sand, *Ekman 12063* [NY, S]), not enumerated above, the plants are copiously branched from a basal caudex and, at first sight, appear completely different from *P. selbyi*. Urban proposed on the basis of this collection a new species, *P. pinosius*, supposedly differing from *P. selbyi* in having two stamens instead of three. Urban was here misled by Britton and Wilson, who either erred in recording the stamen number of *P. selbyi* or else happened to dissect by chance a rare flower with three stamens (only two stamens were observed in repeated dissections of the flowers of the species). The Ekman collection differs not only in its habit but also in its longer (1.5–1.8 mm.) female calyx-lobes; but in most other respects it is essentially identical with typical individuals of *P. selbyi*. Since *P. selbyi* may sometimes produce basal branches as well, it seems probable that the plants described as *P. pinosius* are outstanding because of some environmental modification rather than any significant genetic diversity.

PLATE XXII. TYPES OF GROWTH FORM IN SECT. *Phyllanthus*.

FIG. A. *Phyllanthus leptoneurus* Urb. (*Turckheim 3187* [BR, lectotype]). FIG. B. *Phyllanthus fadyenii* Urb. (*Macfadyen* [K, holotype]). FIG. C. *Phyllanthus pentaphyllus* Wright ssp. *polycladus* (Urb.) Webster (*Sintenis 3492* [US]). FIG. D. *Phyllanthus selbyi* Br. & Wils. (*Britton, Wilson, & Selby 14157* [NY, holotype]).



WEBSTER, WEST INDIAN PHYLLANTHUS

The only species very closely related to *P. selbyi* is *P. imbricatus*, which is clearly a further reduced derivative species with a distribution even more narrowly restricted on the Isle of Pines. Evidently related also is *P. echinospermus*, which has a similar hygroscopic seed-coat, and which occupies somewhat similar habitats in western Pinar del Río.

38. **Phyllanthus imbricatus** Webster, Contr. Gray Herb. **176**: 56. 1955. (PLATE XXI, *figs. K–L*).

Phyllanthus nanus Millsp. Bull. Torr. Bot. Club **43**: 464–465. 1916; non *P. nanus* Hook. f. Fl. Br. Ind. **5**: 298. 1887.

Diminutive perennial herb; branches (0.5–) 1–2 (–5) cm. long, clustered on a caudex, usually prostrate and more or less buried in sand, sometimes considerably ramified, bearing branchlets above-ground at the tips, smooth and reddish-brown, above, becoming blackened in age; internodes c. 0.1–0.8 cm. long, 0.5–1 mm. thick. Cataphylls: stipules triangular-ovate, 1–1.3 mm. long, 0.7–1 mm. broad, acuminate, auriculate at the base, entire or the auricle toothed, becoming blackened and indurate and persisting on underground parts; blade linear-lanceolate, 0.7–1.1 mm. long, 0.15–0.2 mm. broad. Deciduous branchlets mostly 1–2 cm. long, 0.2–0.3 mm. thick, angled, smooth, stramineous or reddish-brown, with mostly 10–25 (–35) leaves; first internode mostly 4–7 mm. long, subsequent internodes only 0.3–0.9 mm. long, usually only half the length of the leaves, which thus overlap extensively. Leaves: stipules linear-lanceolate, 0.6–1 mm. long, 0.2 mm. broad, acuminate, stramineous with brownish tips, scarious (those at the proximal nodes often becoming indurate). Petioles 0.2–0.25 mm. long. Leaf-blades thick, ovate, 1.5–2 (–2.5) mm. long, 1.1–1.8 mm. broad, obtuse or subacute at the tip, cordate or subcordate at the base, pruinose, smooth or obscurely alveolate on both sides, the veins invisible above and below except for the faint midrib; margins somewhat thickened, plane, smooth or minutely roughened, sometimes reddish-tinged.

Monoecious or dioecious; proximal (3–) 5–10 (–12) nodes barren, succeeding nodes with cymules of 2–7 male flowers or solitary female flowers; bisexual branchlets entirely male except for 1 or 2 distal female flowers.

Male flower: pedicel only 0.2–0.3 mm. long. Calyx-lobes 5, elliptic, unequal, the longer c. 1.2–1.5 mm. long and 0.7–1 mm. broad, the shorter 0.9–1 mm. long and 0.5–0.7 mm. broad, rounded at the tip, yellowish and scarious except for the olivaceous dorsally carinate midstrip along the unbranched midrib. Disk-segments 5, squarish, c. 0.2 mm. across, conspicuously papillate-rugose. Stamens 2 (sometimes a rudimentary third anther developed); filaments completely connate into a column c. 0.2 mm. high; anthers sessile atop the column, c. 0.25 mm. long. 0.3–0.4 mm. broad; anther-sacs with apically confluent slits, dehiscing horizontally or somewhat obliquely; pollen grains finely reticulate, c. 21–24 μ long, 17–19 μ broad.

Female flower: pedicel only 0.2–0.3 mm. long. Calyx-lobes 5, elliptic (or becoming obovate in fruit), subequal, 1.2–1.5 mm. long, 0.6–0.8 mm. broad, narrowed to an obtuse or subacute tip, with yellowish scarious margins as broad as or broader than the olivaceous midstrip, dorsally carinate along the unbranched midrib. Disk undivided, 5-angled, obscurely and minutely crenulate. Styles free, ascending, c. 0.2 mm. long, reddish-tinged at first, bifid, the unthickened branches recurved.

Capsule c. 1.5 mm. in diameter, smooth, brownish-tinged, the veins completely obscure. Seeds sharply trigonous, 0.8–0.85 mm. long, 0.6–0.65 mm. radially and tangentially, dark brown, with 3 or 4 very inconspicuous longitudinal striae and many fine presumably hygroscopic barred epidermal cells on the back.

TYPE: Isle of Pines, *Britton, Britton, & Wilson 14192.*

DISTRIBUTION: endemic to the white sand areas, southwestern coast of the Isle of Pines (MAP XVI).

CUBA. ISLA DE PINOS: white-sand savannas, Los Indios, 27 Dec. 1951, *Alain & Killip 2205* (US); same locality, 13 Feb. 1916, *Britton, Britton, & Wilson 14192* (F, HOLOTYPE; GH, US, ISOTYPES); same locality, 8 Nov. 1920, *Ekman 12144* (S).

This pygmaean species, with its prostrate partially buried stems and very short branchlets with small closely overlapping cordate leaves, is vegetatively the most highly specialized species of subsect. *Pentaphylli.* It is also one of the most narrowly endemic in range, since it does not appear to occur anywhere except in the white sands area of the Los Indios region, whereas its sister species *P. selbyi* is distributed much more widely in the Isle of Pines. It seems reasonable to regard *P. imbricatus* as a more or less dwarfed derivative of *P. selbyi*, for the close affinity between the two is very apparent. Nevertheless, *P. imbricatus* is unquestionably a perfectly distinct species which is easily distinguished from *P. selbyi* both by its habit and by its subsessile flowers, the male with papillate disk-segments.

Subgenus V. **Eriococcus** (Hassk.) Croiz. & Metc. Jour. Arnold Arb. 23: 32. 1942.

Eriococcus Hassk. in Hoeven & De Vriese, Tijdschr. **10:** 143. 1843.

Subshrubs or shrubs with phyllanthoid branching; monoecious. Male flower: calyx-lobes 4–6, entire to conspicuously lacerate; disk cupuliform or of distinct segments; stamens 2 or 3, filaments connate; anthers dehiscing vertically to horizontally; pollen grains globose, porate. Female flower: calyx-lobes 4–6; disk patelliform to urceolate; ovary of 3–8 carpels, smooth or hirsute; styles bifid or entire, free or connate. Fruit capsular; seeds smooth.

In addition to the typical section *Eriococcus*, this entirely Old World subgenus includes sects. *Emblicastrum, Eriococcodes*, and *Scepasma*. These latter three sections, all monotypic when established, are open to the suspicion that they represent merely individual species with striking "key" characters; a recasting of subg. *Eriococcus* along phylogenetic lines may result in radical changes in the circumscription of the constituent taxa.

The majority of the species of subg. *Eriococcus* may be easily recognized by virtue of their lacerate calyx-lobes, distinctive androecium of two stamens, and porate pollen grains. The pollen has been examined in relatively few species, however, and should be checked in any whose exact affinities are being considered.

Sect. 12 **Eriococcus** (Hassk.) Muell. Arg. Linnaea 32: 46. 1863; DC. Prodr. 15(2): 420. 1866.

Eriococcus Hassk. in Hoeven & De Vriese, Tijdschr. 10: 143. 1843.
Reidia Wight, Icon. Pl. Ind. Or. 5(2): 27. *pls. 1903, 1904.* 1852.
Epistylium sect. *Eriococcus* (Hassk.) Baill. Etud. Gen. Euphorb. 648. 1858.

Shrubs with phyllanthoid branching, the stems often hirsutulous with reddish hairs. Monoecious; cymules unisexual. Male flower: calyx-lobes 4, decussate, margins more or less lacerate; disk-segments 4, large, petaloid; stamens 2, filaments connate; anthers dehiscing horizontally; pollen grains porate. Female flower: calyx-lobes 4–6, more or less fimbriate or lacerate along the margins; disk cupuliform; ovary of 3 carpels, smooth [in West Indian species]; styles more or less free, spreading, bifid.

TYPE SPECIES: *Eriococcus gracilis* Hassk. [= *Phyllanthus gracilipes* (Miq.) Muell. Arg.].

Section *Eriococcus* is an entirely Asiatic group of about 25 species which extend from southern India and Ceylon to Malaysia and the Philippines. Although it is evidently a natural group, its limits are rather hard to define, for the fimbriate calyx-lobes and vestite ovary of the type species do not occur in all of its relatives. There do not appear to be any close relatives of the section in the New World; although some of the species of sect. *Hemiphyllanthus* have similar rusty pubescence and oblique leaf-bases, their flowers are very different.

39. **Phyllanthus pulcher** Wall. ex Muell. Arg. Linnaea 32: 49. 1863; DC. Prodr. 15(2): 421. 1866; J. J. Sm. Add. Cog. Fl. Arb. Jav. 12: 94–97. 1910. (PLATE XXIII, *figs. A–B*).

Diasperus pulcher ("Wall.") O. Ktze. Rev. Gen. 2: 600. 1891.

A small shrub c. 0.5–1.5 m. high; main stem slender, sparsely branched, c. 3–5 mm. thick, younger parts covered with reddish-brown dendritic hairs. Cataphylls persistent: stipules triangular-lanceolate, mostly 3–4 mm. long and 1.5–2 mm. broad, acuminate, basally dilated but scarcely auriculate, entire or obscurely denticulate, reddish-brown, scarious, hirsutulous at the base; blade lanceolate, often narrowly so, c. 3–4 mm. long. Decidu-

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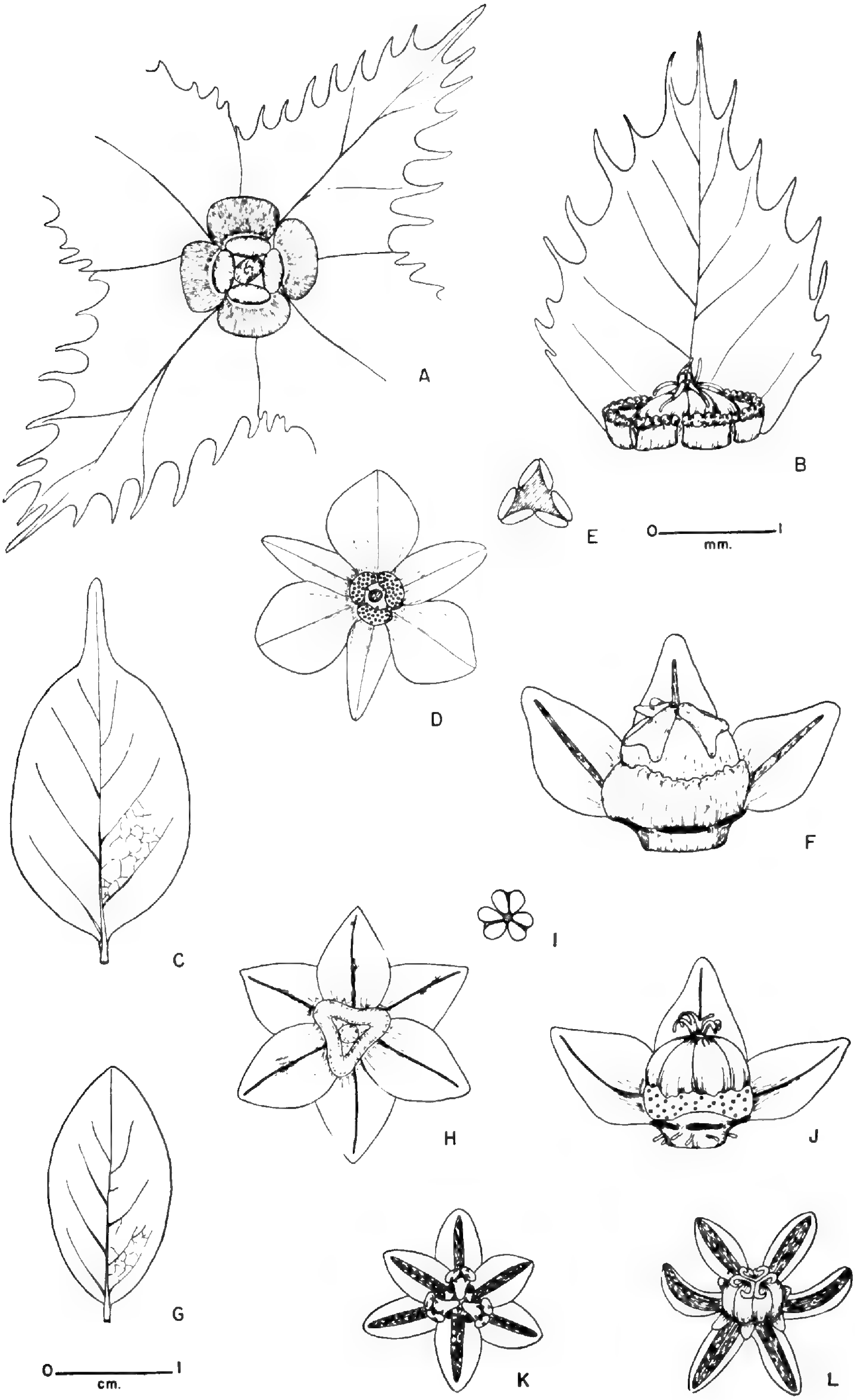
PLATE XXIII. FLOWERS AND LEAVES OF SUBG. *Ericoccus* AND SUBG. *Conami*. FIGS. A-B. *Phyllanthus pulcher* Wall. ex Muell. Arg. (*Britton 1554* [GH]). FIGS. C-F. *Phyllanthus acuminatus* Vahl (*Baker 104* [GH]). FIGS. G-J. *Phyllanthus subglomeratus* Poir. (*Duss 2446* [GH]). FIGS. K-L. *Phyllanthus orbiculatus* L. C. Rich. (*Broadway 5564* [S]). (The androecia of *P. acuminatus* [fig. E] and *P. subglomeratus* [fig. I] are shown as removed to one side and seen from above).



WEBSTER, WEST INDIAN PHYLLANTHUS

ous branchlets steeply ascending, mostly 10–15 (–18) cm. long, 0.7–1 mm. thick, subterete, reddish-brown, hirsutulous as on the main stem, with c. 15–30 leaves; first internodes 5–10 mm. long, median internodes 5–7 mm. long. Leaves: stipules persistent, triangular-lanceolate, 2.5–4 mm. long and 0.9–1.2 mm. broad, acuminate, subentire, dark brown with lighter scarious margins. Petioles flattened, 0.8–1 mm. long. Leaf-blades membranous, glabrous, asymmetrically oblong to elliptic, mostly 18–28 mm. long and 8–14 mm. broad, abruptly pointed with a scarious tip, strongly inequilateral at the base (one side obtuse, the other acute); above olivaceous, sublucid, the slightly raised midrib and lateral veins not very conspicuous; beneath greyish, the midrib and laterals (c. 4–6 on a side) slightly raised, the laterals forming an irregular intramarginal loop with the reticulum of tertiary veinlets more or less conspicuous on both sides; margins plane, smooth, not thickened.

Monoecious; proximal axils of branchlet with cymules of several male flowers, the female flowers solitary in the distal axils; bracteoles conspicuously hirsutulous-ciliate.

Male flower: pedicel capillary (3–) 5–10 mm. long. Calyx-lobes 4 [rarely 5, ex Smith], decussate, subequal, triangular-ovate, c. 2.5–3 mm. long and 1.5–2 mm. broad, acuminate, conspicuously lacerate, the midrib sparsely branched or simple. Disk-segments 4, reniform or orbicular, thin and flat, smooth and entire, subpetaloid, c. 0.5–0.7 mm. broad. Stamens 2 [sometimes with the rudiment of a third, ex Smith]; filaments completely united into a very short column c. 0.1 mm. high, the anthers thus appearing sessile; connectives of anthers fused into a central knob; anthers 0.2–0.25 mm. long, 0.5–0.6 mm. broad; anther-sacs divergent, discrete (the androecium seemingly of 4 one-celled anthers), dehiscing horizontally; pollen grains spheroidal, reticulate, with a few scattered pores, c. 22–24 μ in diameter.

Female flower: pedicel 15–23 mm. long, capillary (slightly thickened above), subterete, smooth. Calyx-lobes 6, similar to those of the male but larger (to 3–3.5 mm. long) and the midrib regularly branched. Disk patelliform, with a thickened and fleshy somewhat pitted rim, enclosing the base of the ovary, becoming more or less split into discrete lobes. Ovary oblate, smooth, shallowly sulcate; styles free, spreading, alternating at the base with 3 erect blunt projections, bifid nearly to the base, the slender gradually tapered branches 0.3–0.4 mm. long.

Fruits not seen.

Flowering throughout the year, according to Smith.

TYPE: Malay Peninsula, Pulo-Penang, *Wallich 7908* (G, HOLOTYPE).

DISTRIBUTION: native to Malaysia, introduced into the West Indies.

ST. VINCENT: old clearings, alt. 500 ft., *H. H. & G. W. Smith 522* (NY). TRINIDAD: Port of Spain, *Wall* (S); Maracas, path to falls, *Baker* (TRIN 15037), *Broadway 5459* (A, MO, S); Caura River valley, *Britton 1554* (GH).

This exotic ornamental species is a relative newcomer to the West Indies.

having been first collected in St. Vincent in 1889 by the Smiths and in Trinidad in 1920 by Britton. Smith, who observed the plant in the living condition in Java, noted that it never produced any fruit; and Hooker (Fl. Br. Ind. **5**: 302. 1887) also did not see any capsules. Evidently the plant spreads by vegetative means, perhaps by root-sprouts in the manner of *P. emblica* or *Breynia disticha*.

Among the West Indian species of *Phyllanthus, P. pulcher* is easily recognizable by the dark red lacerate calyx-lobes, the "cruciform" androecium of the male flower, and the dendritic trichomes on the axes.

Subgenus VI. **Conami** (Aubl.) Webster, Jour. Arnold Arb. **37**: 345. 1956.

Conami Aubl. Hist. Pl. Guian. Fr. 926–927, *pl. 354.* 1775.

Herbs, shrubs, or trees with phyllanthoid branching, the branchlets pinnatiform or bipinnatiform. Monoecious or dioecious, cymules usually bisexual. Male flower: calyx-lobes 6; disk cupuliform or of discrete segments; stamens 3, filaments free or connate; anthers dehiscing more or less horizontally; pollen grains globose, echinulose, porate or brevicolpate. Female flower: calyx-lobes 6; disk cupuliform or of discrete segments; ovary of 3 carpels; styles more or less free. Fruit capsular; seeds smooth or verruculose.

The present interpretation of subg. *Conami* must be regarded as provisional, since it is based mainly on the few West Indian representatives and does not take into account the rather considerable number of South American species which may eventually prove to belong here. "Typical" members of sect. *Nothoclema*, which numerically predominate in the subgenus, are distinctive because of their bipinnatiform branchlets, echinulose pollen grains, and slenderly pedicellate flowers with hexamerous calyces. However, the type species of the subgenus, *P. brasiliensis* (Aubl.) Poir., has branchlets with very few lateral axes which approach the pinnatiform condition. There is still a very large gap between this species and *P. orbiculatus* of sect. *Apolepis*, but the latter has such similar pollen grains that there appears to be no alternative to considering it a reduced derivative of sect. *Nothoclema*.

KEY TO THE SECTIONS

Shrubs or trees with bipinnatiform branchlets; pollen grains brevicolporate; filaments united; seeds smooth. . . . . 13. **Nothoclema**

Herbs with pinnatiform branchlets; pollen grains porate; filaments free; seeds verruculose. . . . . 14. **Apolepis**

Sect. 13. **Nothoclema** Webster, Contr. Gray Herb. **176**: 56. 1955.

Shrubs or trees with phyllanthoid branching; branchlets bipinnatiform, both ultimate and penultimate axes bearing leaves. Monoecious or dioecious; cymules with 1 or 2 female flowers and many males. Male flower: calyx-lobes 6; disk cupuliform or of 3 duplex segments: stamens 3, filaments completely united into a short column; anthers dehiscing horizontally; pollen grains globose, echinulose (i.e., the exine with sculpturing of clavate projections), brevicolporate, the colpi each with two ora. Female flower: calyx-lobes 6; disk cupuliform, sometimes lobed; styles free, spreading, slender or dilated, bifid to lacerate. Capsule conspicuously veined; seeds plano-convex, essentially smooth (colliculose).

TYPE SPECIES: *Phyllanthus acuminatus* Vahl

Of the sections of *Phyllanthus* restricted to the New World, sect. *Nothoclema* is probably outstanding in the taxonomic difficulties which its representatives present. About 15 to 20 species have been proposed, but these are very poorly distinguished, and the identifications of South American specimens are almost wholly untrustworthy. Fortunately the two species in the West Indies are quite distinct and offer no problems in determination.

The origin and relationships of sect. *Nothoclema* are obscure; no other group, unless it possibly be the next section, appears to be at all closely related. Some affinity with sect. *Elutanthos* is suggested by general similarities in gross floral structure; but the species of that section differ strongly in their non-phyllanthoid branching and areolate pollen grains. Sect. *Hemiphyllanthus* includes some species which resemble sect. *Nothoclema* in having bipinnatiform branchlets, but they have areolate pollen grains and further differ in details of leaves, styles, and capsules. Similar floral structure is evident in sect. *Ciccopsis*, and although this group is obviously rather distant in affinity — as is indicated by its simply pinnatiform branchlets, free stamens, and tricolporate pollen grains — it possibly comes closer to representing the ancestral line to sect. *Nothoclema* than any other group in the West Indies.

The relationship of the following section, *Apolepis*, appears reasonably evident on the hypothesis that it is a reduced herbaceous derivative of sect. *Nothoclema*. The pollen grains of sect. *Apolepis* could be easily derived from those of *Nothoclema* by a simple reduction of the already short colpi to single pores. It must be granted, however, that in some characters, particularly the free disk-segments and stamens, sect. *Apolepis* is less specialized than sect. *Nothoclema*.

KEY TO THE WEST INDIAN SPECIES

Flowers borne mainly on ultimate axes of branchlet (the primary axis with 0–2 nodes bearing flowers, the distal nodes bearing only ultimate axes); leaf-blades ovate, abruptly cuspidate-acuminate; male flower with 3 reniform disk-segments; anthers acute; pedicel of female flower glabrous or scabridulous below. .... 40. *P. acuminatus*

Flowers borne at all nodes of both ultimate and primary axes of branchlet; leaf-blades elliptic, acute; male flower with cupuliform disk; anthers emarginate; pedicel of female flower hirsutulous. .... 41. *P. subglomeratus*

40. **Phyllanthus acuminatus** Vahl, Symb. 95. 1791; Muell. Arg. in

DC. Prodr. **15**(2): 381. 1866; Fawc. & Rend. Fl. Jam. **4**(2): 254. 1920. (PLATE XXIII, *figs. C-F*).

Phyllanthus conami Sw. Prodr. 28. 1788 (as to description, not as to type).
Diasperus acuminatus (Vahl) O. Ktze. Rev. Gen. **2**: 598. 1891.
Conami conami (Sw.) Britton, Sci. Surv. Porto Rico **5**(4): 475. 1924 (as to description).
Phyllanthus brasiliensis sensu Alain, Fl. Cub. **3**: 52. 1953; not *P. brasiliensis* (Aubl.) Poir.

A slender rather sparsely branching shrub or small tree 2–8 m. high, the leafy branches with somewhat the aspect of fern-fronds. Older branches straight, subterete or bluntly angled, light brownish, the lenticels not conspicuous, mostly 3–5 mm. in diameter, the internodes c. 2–3.5 cm. long. New permanent branches not clustered at the apices of old branches but rather springing from the axils of deciduous branchlets of the previous year (and thus spaced 2–3.5 cm. apart), each producing during the season c. 3–6 deciduous branchlets. Cataphylls inconspicuous; stipules triangular-lanceolate, c. 1.4–1.5 mm. long and 1.3 mm. broad, not auriculate at base, entire, pale and scarious; blade c. 1.3 mm. long and 0.7 mm. broad; blade and sometimes also the stipules deciduous, or the thickened bases persistent. Deciduous branchlets bipinnatiform (except for the first branchlet of a new branch, which is usually simply pinnatiform); primary axis (15–) 20–50 cm. long, (1–) 2–3 mm. broad, green, smooth on the ventral (upper) side but usually scabridulous or hirsutulous dorsally, more or less tetragonous, the dorsal and ventral angles blunt but the lateral angles sharply winged and dilated just below the nodes; nodes of primary axis (5–) 9–18 (–21), first internode mostly 2–5 cm. long, distal internodes (1–) 1.5–3 cm. long. Ultimate axes leafy and floriferous, similar to the primary axis in form and texture but more flattened, (5–) 7–20 cm. long, with (5–) 7–15 (–22) leaves; first internode 1.2–3 cm. long, distal internodes (0.5–) 1–2.5 cm. long. Leaves on both primary and ultimate axes similar but averaging somewhat larger on the primary: stipules triangular-lanceolate, blunt, not auriculate, entire, more or less persistent and becoming thickened and scarious (though often the tip deciduous), sometimes reflexed, those of the primary axis up to c. 1.3 mm. long and 1.1 mm. broad, those of the ultimate axes c. 0.7–1 mm. long and 0.4–0.7 mm. broad (or sometimes about as large as those of the primary axis). Petioles flattened and densely scabridulous or hirsutulous adaxially, convex and nearly smooth abaxially, 1.5–3 mm. long. Leaf-blades membranous to chartaceous, ovate or elliptic (sometimes very broadly so), (1.5–) 2.2–4.5 cm. long, (0.7–) 1.2–2.5 cm. broad, rather abruptly and bluntly cuspidate-acuminate at the tip, usually obtuse at the base; above olivaceous, lucid as though varnished (under a bright light), more or less scabridulous-roughened (often conspicuously so on the midrib), the midrib raised proximally but obscure toward the tip, the laterals (c. 5 or 6 on a side) only slightly raised; beneath pale and greyish, smooth except for the veins, the midrib prominently raised and running to the tip, the laterals also raised, connecting with the tertiaries to form an irregular reticulum; margins scarcely thickened, definitely roughened, plane.

Monoecious; primary axis producing flowers at the 1 or 2 proximal nodes but not at the subsequent nodes with ultimate axes (and thus entirely nonfloriferous when the first node occasionally bears an ultimate axis) except for the simple branchlet at the beginning of the year's growth; this latter, and the ultimate axes, usually floriferous at every node. Flowers in contracted bisexual cymules, the peduncle becoming up to 1 mm. long, the female flower central and solitary (rarely accompanied by a second), the male flowers lateral, usually 6–20.

Male flower: pedicel capillary, smooth, 3–4.5 mm. long. Calyx-lobes 6, biseriate, 1-nerved, with green midrib and broad whitish hyaline margins; outer lobes narrowly oblong, slightly carinate dorsally, the acutish tip slightly inflexed, c. 0.9–1 mm. long and 0.4–0.6 mm. broad; inner lobes obovate (almost flabellate), flaring outwards from about the middle, c. 0.9–1. 2 mm. long and broad. Disk-segments 3, massive, subcubical with a deep adaxial channel (and thus more or less reniform), glandular-pitted but smooth in outline, c. 0.3–0.35 mm. broad. Stamens 3, filaments completely united into a short column c. 0.15–0.3 mm. high; anthers triangular-ovate, acutish, usually minutely apiculate, flattened, sessile atop the column, the bases contiguous and the common connective thus more or less triangular, c. 0.3–0.4 mm. long and broad; anther-sacs contiguous but not confluent across the tip, dehiscing horizontally; pollen grains globose, somewhat angular, with 3 short diorate colpi, c. 19–20 μ in diameter.

Female flower: pedicel (5–), 7–12 mm. long [in West Indian populations], slender, obscurely to conspicuously angled, scabridulous (sometimes smooth above) but not hirsutulous. Calyx-lobes 6, biseriate, 1-nerved, greenish-herbaceous with rather narrow scarious whitish entire margins, never hirsutulous dorsally; outer lobes elliptic or triangular-elliptic, c. 1.1–1.4 mm. long and 0.5–0.9 mm. broad; inner lobes broadly ovate, c. 1.5–1.7 mm. long and 1–1.13 mm. broad. Disk cupuliform, massive, more or less 3-lobed (as though formed of 3 reniform segments as in the male), inconspicuously pitted, the rim minutely crenulate. Ovary oblate, trigonous, deeply sulcate between the locules. Styles free, flattened, appressed and spreading (the tips sometimes upcurving), 0.4–0.6 mm. long, divided ¼ to ½ their length; style-branches subterete or flattened, subparallel, sometimes dilated and again lobed.

Capsule oblate, olivaceous, rather conspicuously veiny, 4.5–5 mm. in diameter. Columella massive, conical, c. 2 mm. long. Seeds plano-convex, often coherent in pairs, (2.2–) 2.5–2.8 mm. long, (1.7–) 1.8–2 mm. broad, reddish-brown, sometimes mottled, smooth with a honeycomb pattern imparted by the epidermal cells; hilum elliptic, c. 0.5–0.6 mm. long; micropylar end sometimes with rudimentary elliptic corneous caruncular swellings.

Collected in flower [in West Indies] May through November, in fruit July through December.

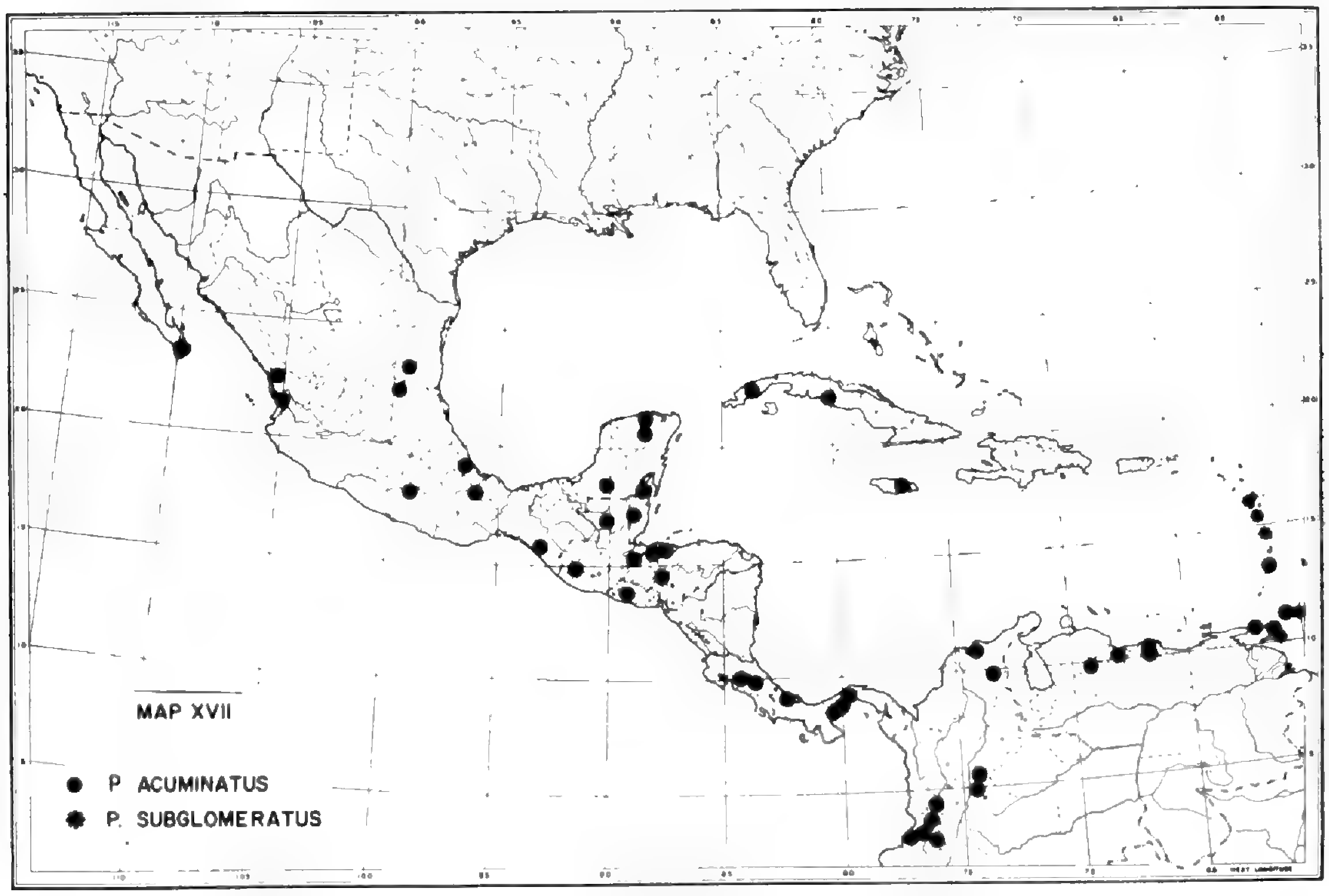
TYPE: Trinidad, *Ryan* (C, HOLOTYPE).

DISTRIBUTION: widespread from northern Mexico (Tamaulipas) south to northern Argentina (Jujuy, Salta), Paraguay, and central Brazil (Minas Geraes); range discontinuous in the West Indies (MAP XVII).

CUBA. PINAR DEL RÍO: Pinar del Río City, in thickets at Laguna Gauyabo, *Ekman 18245* (S); Baños San Vicente, *Britton, Britton, & Gager 7487* (NY); Viñales, near Pan de Azúcar, *Alain 4435* (GH); Viñales, Palmarito, in thickets at a brook, *Ekman 16624* (S); San Diego de los Baños, in pinelands, at a brook, *Ekman 17769* (S); San Diego, *Van Hermann 3219* (NY). HABANA: Santiago de las Vegas [cult.], *Baker 104* (C, NY, P). LAS VILLAS: Trinidad Mountains, scrubby woods near the top of Pico Sombrero, *Webster 4769* (GH).

JAMAICA. ST. MARY: near Castleton, *Harris 8409* (F, JAM, NY); Wag Water Valley, near Castleton, *Harris 11147* (F, JAM, NY, US).

LESSER ANTILLES. ST. VINCENT: 1816, *Caley* (G, P). TOBAGO: Easterfield, *Broadway 4555* (C, L, MO). TRINIDAD: *Ryan* (C); thicket, Port-of-Spain, *Britton 990* (GH); ad Caroni flumen, in sylvestribus, *Eggers 1428* (C); Arima, in sylvis, *Eggers 1184* (P, W); Laventille, *D. W. Alexander* (TRIN 4378, 4555); savannah, road to Lambie, *Finlay* (TRIN 2464); Santa Cruz, among cocoa, *Broadway 2659* (MO).



MAP XVII. Caribbean distribution of the West Indian representatives of sect. *Nothoclema.*

Phyllanthus acuminatus, in contrast to most of the other taxa in sect. *Nothoclema*, is a clearly circumscribed species and is as readily indentifiable as it is widely distributed. Its characteristic leaves with roughened upper surface and abruptly narrowed tip, male disk of 3 segments, and non-hirsutulous female pedicel together make its recognition easy. Furthermore, it appears to be exceptional in that it is never used as a fish-poison in the manner of the majority of species of sect. *Nothoclema*. The prevalent confusion (in herbaria and in the literature) of *P. acuminatus* with *P. brasiliensis* may ultimately be attributed to the misconception of Swartz, who mistakenly assumed the Jamaican representative of sect. *Nothoclema* to be conspecific with Aublet's *Conami brasiliensis* and proposed the name *Phyllanthus conami* to include both plants. This proposal of the new epithet *conami* is of course illegitimate under the present rules, since Aublet's type was included in Swartz's specific concept; consequently, the combination *P. brasiliensis* (Aubl.) Poir. has been applied by various authors to the species here called *P. acuminatus*. However, there is no doubt that the plant described by Aublet is quite distinct from *P. acuminatus* and in fact is much more closely related to the other West Indian member of the section, *P. subglomeratus*. In contrast to *P. acuminatus*, *P. brasiliensis* does not occur outside of South America.

The spotty distribution of *P. acuminatus* in the West Indies is striking, for its geographical pattern is not duplicated by any other species. The plant does not appear to be particularly common anywhere in the West Indies (except possibly in Trinidad) and in Jamaica and Cuba is comparatively rare and local. This sporadic occurrence, and the fact that there is no evident morphological variation among the various insular populations, make it appear likely that the range of *P. acuminatus* within the West Indies is the result of relatively recent dispersal. The absence of the species from the central Caribbean, especially Hispaniola and Puerto Rico, can perhaps be best explained on the assumption that it has invaded the West Indies from two separate points, Cuba and Jamaica being colonized from Central America and Trinidad and Tobago from northeastern South America.

41. **Phyllanthus subglomeratus** Poir. Encycl. Method. **5**: 304. 1805 (as *P. subglomerata*). (PLATE XXIII, *figs. G-J*).

Phyllanthus brasiliensis β oblongifolius Muell. Arg. Linnaea 32: 27. 1863; DC. Prodr. **15**(2): 383. 1866.
Phyllanthus conami sensu Duss, Fl. Phan. Ant. Fr. 22. 1896; non Sw.

A shrub or small tree 2–4 m. high, with the habit of *P. acuminatus*, the main branches often tortuous and knotted (Duss). Branches subterete, sparsely hirtellous but becoming smooth with age; branchlets probably borne in the manner of *P. acuminatus*, but apparently all bipinnatiform. Cataphylls of permanent branches becoming thickened and persistent: stipules broadly ovate-triangular, c. 1.7–2 mm. long and broad, bluntly pointed, more or less auriculate at the base, entire, dark reddish-brown in the center and scarious at tip and margins, persistent; cataphyll blade c. 1.3 mm. long, deciduous. Deciduous branchlets apparently always bipinnatiform with both flowers and ultimate axes produced at all the nodes of the primary axis. Primary axis 15–40 cm. long, c. 1.8–3.5 mm. thick, drying brownish, ventrally smooth and dorsally hirsutulous as in *P. acuminatus*, proximally more or less terete, becoming tetragonous distally but not sharply wing-angled, with c. 10–25 nodes; first internode mostly (15–) 20–40 mm. long, distal internodes (10–) 15–25 (–30) mm. long. Ultimate axes floriferous and leafy precisely as the primary axis but more flattened, 7–16 cm. long, with c. 15–25 leaves; first internode mostly 5–10 (–13) mm. long, distal internodes (2–) 4–9 mm. long. Leaves similar on both primary and ultimate axes: stipules triangular-lanceolate, bluntly acute or acuminate, subauriculate, entire, dark and thickened at the base, paler and scarious at tip and margins, more or less persistent, those of the primary axis c. 1.3–1.7 mm. long and nearly as broad, those of the ultimate axes 1–1.4 mm. long, 0.7–1.1 mm. broad. Petiole flattened and densely hirsutulous adaxially, convex and nearly smooth abaxially, 1.2–1.5 mm. long. Leaf-blade membranous, elliptic, (12–) 14–26 mm. long, (5–) 6–9 (–11) mm. broad, gradually narrowing to an acute tip (this sometimes slightly constricted but never attenuate), cuneate at the base; above olivaceous, rather dull, never appearing varnished under a bright light, smooth and glabrous (the midrib excepted), midrib slightly raised and hirsutulous proximally, smooth and becoming obscure toward the tip, laterals (3–5 on a side) smooth, not conspicuous; beneath paler, smooth, the midrib rather prominently raised, slightly hirsutulous proximally, running to the tip, the laterals and tertiaries forming a fine reticulum; margins smooth, plane, unthickened.

Monoecious; flowers produced only on deciduous branchlets; primary axis producing flowers at all the nodes, including those bearing ultimate axes (sometimes a few proximal axils barren?). Flowers in contracted bisexual cymules, the peduncle becoming c. 0.5–0.7 mm. long; female flower central and solitary, male flowers lateral and numerous.

Male flower: Pedicel capillary, smooth, mostly 5–6 mm. long. Calyx-lobes 6, rather unequal but the inner series not sharply different from the outer, triangular, 0.8–1 mm. long, 0.5–0.7 mm. broad, obtuse or subacute, 1-nerved, with greenish herbaceous area around midrib (brownish in dried specimens) and narrow hyaline scarious entire margins. Disk a shallow cup with a rather narrow subentire rim, not evidently glandular, c. 0.8 mm. across. Stamens 3; filaments united into a very short column c. 0.15 mm. high, the discrete anthers thus appearing nearly sessile on the receptacle; anthers with constricted connectives, emarginate, not flattened, c. 0.2–0.25 mm. long and 0.3–0.35 mm. broad; anther-sacs subglobose, dehiscing horizontally, the slits completely confluent. Pollen grains globose, echinulose as in *P. acuminatus* but the germ-pores obscure, c. 19–22 μ in diameter.

Female flower: Pedicel [in flower] c. 1.5 mm. long, terete below, becoming angled above, hirsutulous the entire length. Calyx-lobes 6, biseriate but about equal in size, triangular-lanceolate, 1–1.2 mm. long and 0.7–0.8 mm. broad, bluntly pointed, 1-nerved with an herbaceous mid-area and narrow scarious minutely denticulate margins. Disk cupuliform, 6-angled, covering less than ⅓ the height of the ovary, glandular-pitted, the rim minutely crenulate. Ovary subglobose, smooth, sessile, not angled or deeply sulcate. Styles free, spreading or commonly more or less ascending, c. 0.3–0.35 mm. long, divided ⅓ to ⅔ their length; style-branches more or less divergent but not recurved, tapering to blunt tips.

Fruit not seen; apparently never produced by West Indian plants. Flowering throughout the year.

TYPE: Martinique, *Herb. Lamarck* (P, HOLOTYPE).

DISTRIBUTION: probably native to South America, but exact range and origin not yet determined (MAP XVII).

LESSER ANTILLES. GUADELOUPE: Matouba, *Duss 212* (P), *2446* (GH, MO, US); Grande Terre, *L'Herminier* (A, P); haies, St. Claude, *R. P. Quentin 527* (P); chemin de la Regrettée, Trois-Rivières, *R. P. Quentin 671* (P); chemin de la Soufrière, St. Claude, subspontané, *Stehlé 63* (A). DOMINICA: in fruticetis ad Grande Bay, *Eggers 662* (GH, GOET, L, W); *Imray s.n.* (GOET), *97* (GH). MARTINIQUE: St. Pierre, *Belanger 294* (G, P), *283*, *832* (P); Ajoupa-Bouillon, Marin, &c., *Duss 2047* (NY); *Hahn 322* (G, GH, L, P, W); *Mouret 109* (P); *Plée* (P); *Herb. Richard* (P); *Ryan* (C); *Sieber Fl. Martin. 223* (GH, GOET, L, MO, W). TOBAGO: Valencia road, roadside, *Baker* (TRIN 14864). TRINIDAD: *Ryan* (C).

Although *P. subglomeratus* is thus far known only from the Lesser Antilles (including Trinidad), it cannot with any confidence be classed as a species endemic to this region. Several collectors have noted that the plant occurs both cultivated and in a semi-wild state, and Plée has described (in the notes accompanying his specimens in the Paris Museum) the utilization of the plant for fishing in Martinique in 1820: dams were thrown across streams to form pools and the leafy branches of *P. subglomeratus* were simply tossed into the water; in a few minutes the larger fish were stunned so that they could be easily caught, while the smaller ones were killed. The common native usage of the plant, and the circumstance that not a single fruit is present on any of the specimens, strongly suggests that the present distribution of *P. subglomeratus* in the Lesser Antilles is largely affected by the activities of man.

The status of *P. subglomeratus* has been confused since its publication, probably because Poiret cited *P. acuminatus* Vahl, with a question mark, as a synonym of his new species. It might be argued that *P. subglomeratus* is therefore only a superfluous name for *P. acuminatus*, but the manner in which Poiret cited the latter suggests rather that he was merely raising the possibility that Vahl's species was the same as his, and he definitely did not refer to any plant except the type specimen from Martinique. Mueller, perhaps influenced by Poiret's citation, incorrectly referred *P. subglomeratus* to the synonymy of *P. acuminatus* but at the same time listed specimens of the former (collected on Martinique by Plée and Sieber) under his *P. brasiliensis* var. *oblongifolius*. Mueller's interpretation of these collections as representing a variety of the South American *P. brasiliensis* is not unreasonable, for these two plants are undoubtedly closely related. The latter, originally named *Conami brasiliensis* by Aublet, was based on a cultivated shrub observed by Aublet in French Guiana, but said by the natives to have been introduced from Pará in Brazil. This plant too was used in stunning fish and, in fact, "Conami" according to Aublet was an aboriginal generic name for fish-poisoning plants. However, while the plant observed by Aublet is doubtless a near relative of *P. subglomeratus*, it differs in its more sparsely ramified (sometimes simple) branchlets, broadly ovate leaves, and hirsutulous ovary. It is conceivable that *P. subglomeratus* may represent a clone derived from some aberrant population of *P. brasiliensis* (or from one of the several closely related species), but for the time being the definite morphological features of the Antillean plant would appear to justify maintaining it at specific rank.

Further investigations of *P. subglomeratus* might be of ethnobotanical interest, since it seems probable that the plant was introduced into the Antilles by the Carib Indians and its history may be connected with the migrations of these tribes.

Sect. 14. **Apolepis,** sect. nov.[18]

Herbs with phyllanthoid branching, the branchlets pinnatiform. Monoecious; cymules bisexual. Male flower: calyx-lobes 6; disk-segments 6; stamens 3, filaments free; anthers emarginate, dehiscing horizontally; pollen grains globose, echinulose, porate. Female flower: calyx-lobes 6; disk-segments 6; styles free, bifid. Capsule not veiny; seeds verruculose.

TYPE SPECIES: *Phyllanthus orbiculatus* L. C. Rich.

It is with some reluctance that another monotypic section is described within a genus that is already overburdened with them; but although *P. orbiculatus* superficially resembles members of sect. *Phyllanthus*, its pollen grains are so different that it cannot be closely related. On the other hand, its bisexual cymules and slenderly pedicellate flowers, as well as its pollen grains, show such a resemblance to those of sect. *Nothoclema* that *P. orbiculatus* seems best placed in subg. *Conami* rather than in subg. *Phyllanthus*. However, the simply pinnatiform branchlets, herbaceous habit, and free stamens of *P. orbiculatus* are so discordant with the characters of sect. *Nothoclema* that it would seem preferable to create a new section rather than to modify unduly the limits of sect. *Nothoclema*.

42. **Phyllanthus orbiculatus** L. C. Rich. Act. Soc. Hist. Nat. Paris **1**: 113. 1792. (PLATE XXIII, *figs. K–L*).

Phyllanthus nummulariaefolia Poir. Encycl. Method **5**:302. 1804 (as to Guiana collection, not as to type).

Phyllanthus poiretianus Muell. Arg. Linnaea **32**: 39. 1863.

Phyllanthus orbiculatus α *genuinus* Muell. Arg. in DC. Prodr. **15**(2): 401. 1866.

Diasperus orbiculatus (Rich. "emend.") O. Ktze. Rev. Gen. **2**: 600. 1891.

Annual herb c. 1–5 dm. high, main stem c. 0.5–1.5 mm. thick, un-

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[18] Sect. **Apolepis**, sect. nov. Herbae monoicae, ramificatione more sectionis *Phyllanthi*, ramulis simpliciter pinnatiformibus, cymulis bisexualibus; flore masculo lobis calycis 6, staminibus 3, filamentis liberis, antheris plusminusve horizontaliter dehiscentibus, granis pollinis globosis echinulosis; flore femineo laciniis calycis 6, segmentis disci 6, stylis liberis bifidis; capsula non venosa, seminibus verruculosis. — Species typica *Phyllanthus orbiculatus* L. C. Rich.

branched or sparsely branched, brownish, terete, smooth; internodes c. 0.3–2 cm. long. Cataphylls: stipules oblong-lanceolate, (0.5–) 0.7–0.9 mm. long, 0.25–0.35 mm. broad, acute (often abruptly so) at the tip, truncate at the base, entire or sometimes with one or two teeth near the apex, reddish-brown, scarious; blade linear, 0.6–0.9 mm. long, 0.1–0.15 mm. broad, sometimes fused with the stipules in the lower third. Deciduous branchlets (3–) 5–10 (–12) cm. long, c. 0.15–0.25 mm. thick, olivaceous, smooth, subterete, with (7–) 9–20 (–25) leaves, often somewhat zigzag; first internode (6–) 9–13 (–16) mm. long, median internodes mostly 2–5 mm. long. Leaves: stipules ovate, 0.4–0.7 mm. long, 0.2–0.3 mm. broad, acute or acuminate, entire, reddish with indistinct yellowish margins, scarious. Petioles 0.3–0.6 mm. long. Leaf-blades membranous to chartaceous, orbicular or broader than long, mostly 5–10 mm. long and about as broad, broadly obtuse and usually apiculate at the tip, obtuse at the base; above olivaceous, smooth or minutely wrinkled, the midrib evident but not raised, the laterals obscure; beneath pale, more or less greyish, the midrib salient and running to the tip, the laterals (c. 3 or 4 on a side) slightly raised, the tertiary veinlets evident or obscure; margins plane, scarcely thickened, smooth or obscurely roughened.

Monoecious; cymules bisexual, of a single female and 1 or 2 male flowers.

Male flower: pedicel capillary, becoming mostly 2.5–4 mm. long. Calyx-lobes 6, elliptic-oblong, c. 0.6–0.8 mm. long and 0.3–0.4 mm. broad, narrowed to an acute tip, entire, thin and subhyaline, the midrib unbranched. Disk-segments 6, subentire, more or less concave, only 0.1–0.15 mm. across. Stamens 3, filaments free; anthers c. 0.15–0.2 mm. long, 0.3 mm. broad, emarginate between the discrete anther-sacs, dehiscing horizontally; pollen grains nearly spherical, echinulose, porate, c. 16–17 μ in diameter.

Female flower: pedicel becoming c. 2.5–3 mm. long, terete, olivaceous, minutely scabridulous below. Calyx-lobes 6, linear-oblong, 0.7–0.8 mm. long, 0.25–0.3 mm. broad, acute, entire, olivaceous with yellowish scarious margins, the midrib unbranched. Disk dissected into 6 discrete segments, these elliptic-oblong to obovate, entire, rather thin, c. 0.2 mm. long. Ovary deeply sulcate, smooth; styles free except at the very base, spreading and appressed to the top of the ovary, c. 0.15–0.2 mm. long, divided c. ½ their length, the branches circinately recurving, the slender tips curled inwards.

Capsule trigonous, smooth, c. 2.5 mm. in diameter, stramineous, not veiny. Columella slender, c. 0.75–0.8 mm. long. Seeds trigonous, becoming fuscous, c. 1.1–1.25 mm. long, 1–1.1 mm. radially and tangentially, verruculose with more or less transversely elongated dots arranged in irregular longitudinal rows on the back and sides.

TYPE: French Guiana, Cayenne, *Leblond* (P, HOLOTYPE; C, ISOTYPE).

DISTRIBUTION: widespread in South America from Bolivia and Paraguay north to Colombia and Venezuela, reaching its northeastern limit in Trinidad.

TRINIDAD: San Juan, roadside, *Broadway 5564* (S), stony grassy lands, 1928, *Broadway* (MO, S); Cedros, prospect near the lagoon, *Broadway* (TRIN 8540); Icacos, *Broadway* (TRIN 7404, 8539); Icacos, near the sea, sandy land, St. Quinton, *Broadway 7833* (MO).

Phyllanthus orbiculatus appears to be a taxonomically isolated species, the relationships of which need to be further investigated. Although it has the general aspect of species of sect. *Phyllanthus*, it stands out even superficially by its elongated pedicels and broad leaves and, of course, it differs esentially in its inflorescence and pollen grains. Mueller (DC. Prodr. **15**[2]: 401. 1866) placed it between *P. subemarginatus* and *P. claussenii* in the group of sect. *Euphyllanthus* having widely separated anther-sacs. However, the anthers of *P. claussenii* are very different from those of *P. orbiculatus* in that the anther-sacs are much more widely separated and completely discrete as though the filament terminated in two one-celled anthers, whereas the anthers of *P. orbiculatus* are merely deeply emarginate. Furthermore, the pollen grains of *P. claussenii* and its Brazilian relatives are more or less typical of those in sect. *Phyllanthus* and appear very different from those of *P. orbiculatus*.

It is rather curious that none of the older collectors encountered *P. orbiculatus* in Trinidad, the earliest record apparently being the collection made at Icacos in 1915 by Broadway (TRIN 7404). This suggests that the species is either a newcomer to the island or at least has been extending its range in recent times.

(*To be continued*)

ADDITIONAL NOTES ON THE VESSELLESS DICOTYLEDON, AMBORELLA TRICHOPODA BAILL.

I. W. BAILEY

With two plates

IN OUR ORIGINAL INVESTIGATION of *Amborella* (Bailey and Swamy, 1948), the largest stem available was seven millimeters in diameter, obtained from a specimen in the Gray Herbarium, *Vieillard 3149*. Recently, I have received a larger, much older stem from H. S. McKee. The field notes accompanying the specimen are as follows:

> "McKee 5617; western slope of Plateau de Dogny, La Foa District, [New Caledonia,] Oct. 25, 1956; shrub 3 to 8 meters high with several stems from common base, some branches pendent especially in older plants; bark light brown, rough; leaves dark glossy green above, slightly lighter below; fruits red. A very common plant between about 600 m. and 800 m." Largest stem seen about 10 cm. in diameter.

The dried section of stem sent to me is asymmetrical in cross section owing to severe injury on one side. It has a large pith 12 mm. in diameter. The longest radius of secondary xylem is 3.5 cm., the shortest 1.6 cm. The bark is very thin, having contracted to approximately one millimeter in thickness. Owing to incipient decay in much of the secondary xylem and to excessive contraction of the bark in drying, it is essential to embed the material in celloidin in order to obtain sections suitable for microscopic study and photomicrography. However, the specimen is of considerable significance, since it enables one to compare the structure of a relatively mature vegetative axis with that of the previously investigated, slender, flowering and fruiting twigs, and to determine that *vessels are absent* in the later-formed xylem of mature stems.

PITH AND BARK

Although the diameter of the pith in McKee's specimen is approximately eight times as broad as that of the slender flowering twigs of *Vieillard 3149* and of other herbarium collections, the structural differences are largely quantitative rather than qualitative. In both cases, the pith is relatively homogeneous, being composed of moderately thick-walled, conspicuously pitted parenchyma and being devoid of idioblasts, nests of stone cells or sclerenchymatous diaphragms. Slender, vertically elongated strands of parenchyma are largely confined to the perimedullary region in close proximity to the elements of the primary xylem.

The softer parts of the secondary phloem in McKee's specimen are badly collapsed and distorted, but the thin-walled parenchymatous cells obviously contained the same dark, amber-colored, colloidal substance that occurs in the cortex and first-formed phloem of *Vieillard 3149*. However, the later-formed secondary phloem differs from the first-formed phloem in having aggregations of "hippocrepiform" sclereids that appear to have been formed by modification of the cells of the multiseriate rays. There are no fibers in the bark of either young or old stems. Between the outer peridermal layers and the secondary phloem of the large stem, there is a relatively broad zone of a somewhat sclerenchymatous nature. The cells of this layer have moderately and uniformly thickened walls, in contrast to those of the narrow layer of hippocrepiform sclereids that is formed during the early stages of the growth of the stem (compare Bailey and Swamy, 1948, fig. 31). The first-formed narrow zone of sclereids appears to be disrupted during enlargement of a stem, clusters of dissociated hippocrepiform sclereids being incorporated in the subsequently formed broad zone of thick-walled tissue.

XYLEM

The primary xylem of the broad cylindrical eustele of McKee's specimen is distributed in a large number of strands of fluctuating size and conspicuousness (*Fig. 1*). The interfascicular parts of the eustele likewise vary markedly in width and distinctness. In the large stem, as in the slender flowering twigs of Vieillard's collection, there are numerous rents or conspicuous cavities in many of the strands of primary xylem (*Fig. 1*). Without freshly collected and adequately preserved material, it is not possible to determine whether these lacunae form during normal growth and enlargement of a stem or are artifacts produced during the drying and contraction of the vascular tissues.

The rays of the first-formed secondary xylem which extend outward from the fascicular parts of the eustele are uniseriate or biseriate (*Fig. 1*). In addition, there are multiseriate rays which extend outward from conspicuous interfascicular gaps in the eustele (*Fig. 1*). These multiseriate rays vary in number, not only being less numerous in slender flowering twigs, but also being more widely spaced and less numerous in certain parts of the circumference of the McKee specimen than in others (compare *Figs. 1 & 3*). However, in the outermost secondary xylem of the large stem (*Fig. 2*), the multiseriate rays are more abundant and uniformly distributed, their numbers having been augmented in part by enlargement of uniseriate and biseriate rays of the first-formed secondary xylem. The changes in the height and form of the rays and of their constituent cells during lateral enlargement of the stem closely parallels those which have been shown by Barghoorn (1940), Bailey and Howard (1941), and others to occur characteristically in dicotyledonous woods having the primitive, so-called Heterogeneous Type I form of ray structures (Kribs, 1935). In such secondary xylem, both the narrow rays and the multiseriate ones are vertically extensive in the first-formed tissue but become dissected into lower rays during their subsequent extension outward. The elongated cells of the narrow rays maintain their original markedly "erect" orientation except where the rays widen to form multiseriate rays. On the contrary, the outward extensions of the original multiseriate rays (and of subsequently developing wide rays) are composed of a higher proportion of isodiametric or more or less "procumbent" cells. Although the rays of *Amborella* are of the general primitive heterogeneous form, there are evidences of incipient reduction in the number of multiseriate rays in the first-formed secondary xylem, particularly of slender flowering twigs.

As previously noted (Bailey and Swamy, 1948) the tracheids in the secondary xylem of slender flowering twigs are very long, and obviously are formed as in other primitively vesselless dicotyledons by a primitive type of cambium having long fusiform initials with extensively overlapping ends. The length of the tracheids in the inner and outer parts of the secondary xylem of the McKee specimen are recorded in *Table I*. In each case, the figures given are based upon the measurement of 100 cells.

TABLE 1, SHOWING LENGTH OF TRACHEIDS IN MICRA

	INNERMOST MILLIMETER	OUTERMOST MILLIMETER
Minimum length	1730	1930
Average length	2850	3140
Maximum length	3860	4660

The fusiform cambial initials and tracheids of *Amborella* are of comparable length to those that occur in stems of equivalent diameter of the primitively vesselless dicotyledons, *Tetracentron*, *Trochodendron*, *Sarcandra* and the Winteraceae, and are much longer than those which occur in comparable tissue of vessel-forming dicotyledons. In *Amborella*, the fusiform cambial initials and their tracheary derivatives become longer during increase in circumference of the stem. However, the length of the cells in the outermost part of the McKee specimen is considerably less than that ultimately attained in large stems of arboreal representatives of the Winteraceae, *Tetracentron* and *Trochodendron*. In comparisons between the tracheids of vesselless dicotyledons and gymnosperms it is essential to deal with stems of equivalent ages or diameters; see Bailey and Tupper (1918), Bailey (1920), Bailey (1944), Swamy (1953).

The tracheids of *Amborella*, as seen in transverse section (*Fig. 4*), are characterized by having a strongly angular external outline but their lumina are smoothly circular or oval. This is due to inequalities in the thickness of the secondary wall which tends to be much thicker in the angles of the cells. The bordered pits are restricted to the thinner parts of the radial and tangential walls, being abundantly developed in the radial facets and sporadically and sparsely developed in the tangential ones. A majority of the tracheids have circular bordered pits, 7–10 μ in diameter, in their radial surfaces. In most cases, these pits are arranged uniseriately, but transitions to a biseriate condition are of not infrequent occurrence. Transitions to scalariform pitting (such as were illustrated by Bailey and Swamy, 1948, fig. 39) are of sporadic and irregular distribution, as in many of the Winteraceae.

Concentric zones of radially narrower tracheids or of wood parenchyma strands occur in parts of McKee's specimen (*Fig. 3*). It is not possible to determine with certainty to what extent these zonal variations may have been induced by injuries in the stem. The distribution of wood parenchyma external to these zones is scanty diffuse.

SUMMARY AND CONCLUSIONS

The chief significance of the McKee specimen is in demonstrating that no vessels are present in the outermost secondary xylem of mature stems, and that the rays of *Amborella* are fundamentally of the primitive Heterogeneous Type I form. It is evident, accordingly, that the cambia and secondary xylem of all of the known primitively vesselless dicotyledons are consistently similar, regardless of whether the plants are small, short-lived shrubs (*Sarcandra*), large shrubs (*Amborella*) or trees (*Tetracentron*, *Trochodendron*, and various representatives of the Winteraceae). In all cases, the cambium is of the long-celled form that occurs throughout the gymnosperms, with the exception of the vessel-forming Gnetales. Wherever vessels appear in the vascular land plants (*Selaginella*, *Pteridium*, Gnetales, monocotyledons and dicotyledons) there is a conspicuous reduction in length of the constituent cells of the xylem. Furthermore, where vessels are eliminated from the secondary xylem of dicotyledons, e.g. certain Cactaceae, and where they are replaced by so-called vascular tracheids, the remaining tracheary cells are short, and the xylem is unlike that of the primitively vesselless gymnosperms and dicotyledons. In addition, it is significant that where such reductions or eliminations occur in extreme xerophytes, aquatics, etc., there are obvious physiological factors involved in their reduction or elimination. Therefore, to assume that the primitively vesselless dicotyledons formerly had vessels and subsequently lost them is purely gratuitous and scientifically unjustifiable.

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EXPLANATION OF PLATES

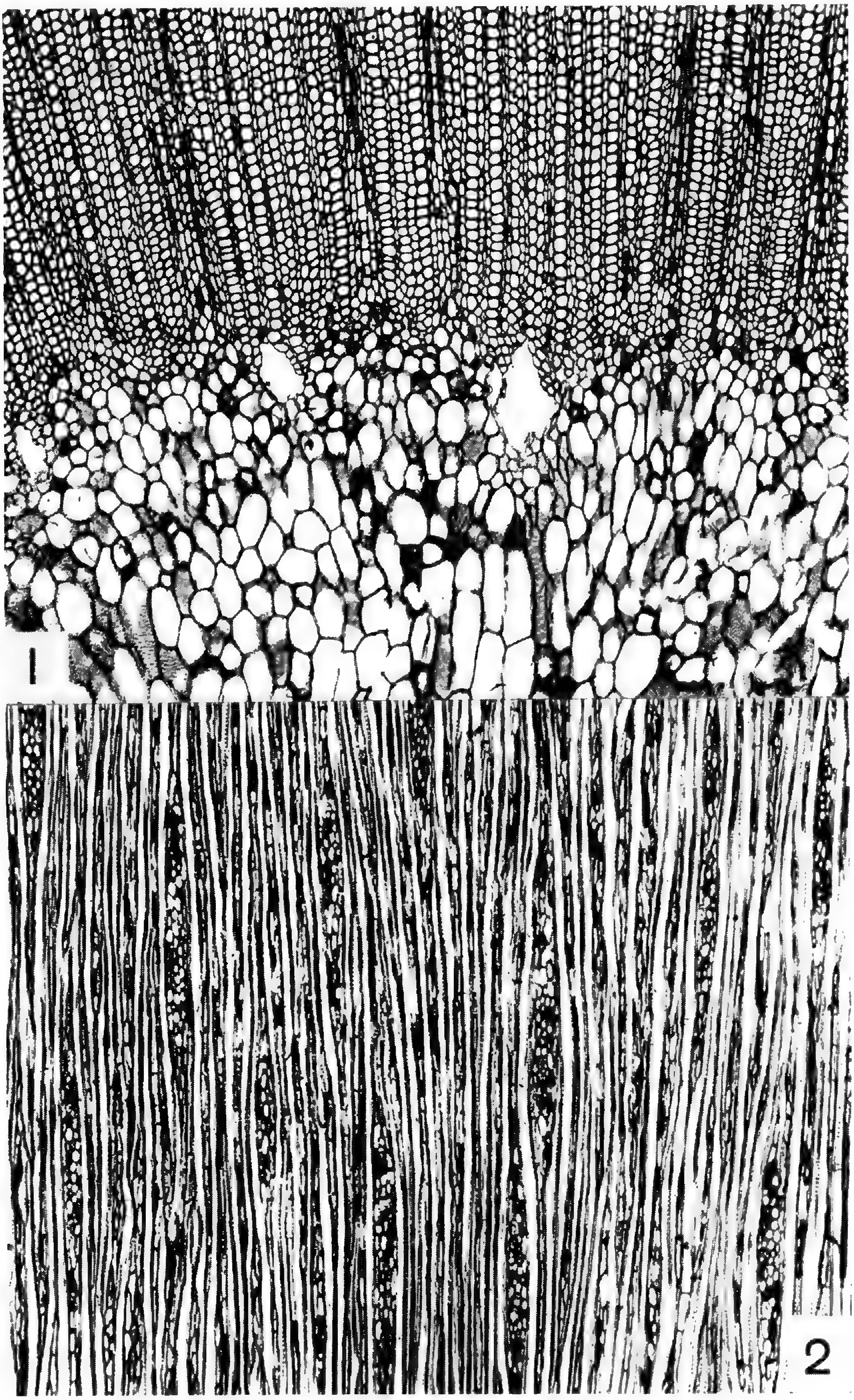
AMBORELLA TRICHOPODA BAILL. (*McKee 5617*).

PLATE I

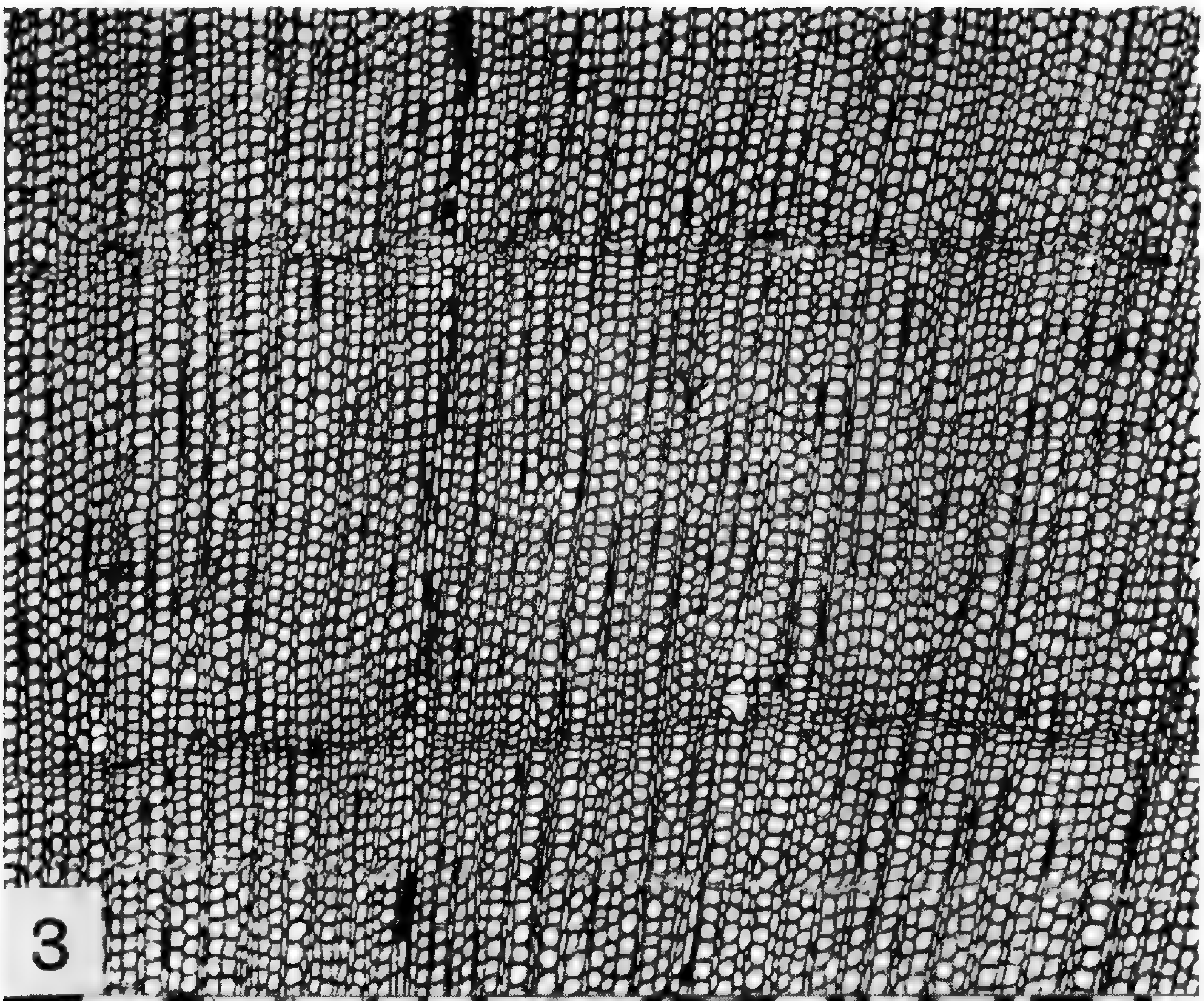
FIG. 1. Transverse section of the stem, showing part of pith and secondary xylem. × 40. FIG. 2. Tangential longitudinal section of the outermost secondary xylem of the stem. × 40.

PLATE II

FIG. 3. Transverse section of the secondary xylem, showing two arcs of wood parenchyma. × 40. FIG. 4. Transverse section of the secondary xylem, showing form of the tracheids in sectional view. × 250.



BAILEY, NOTES ON AMBORELLA



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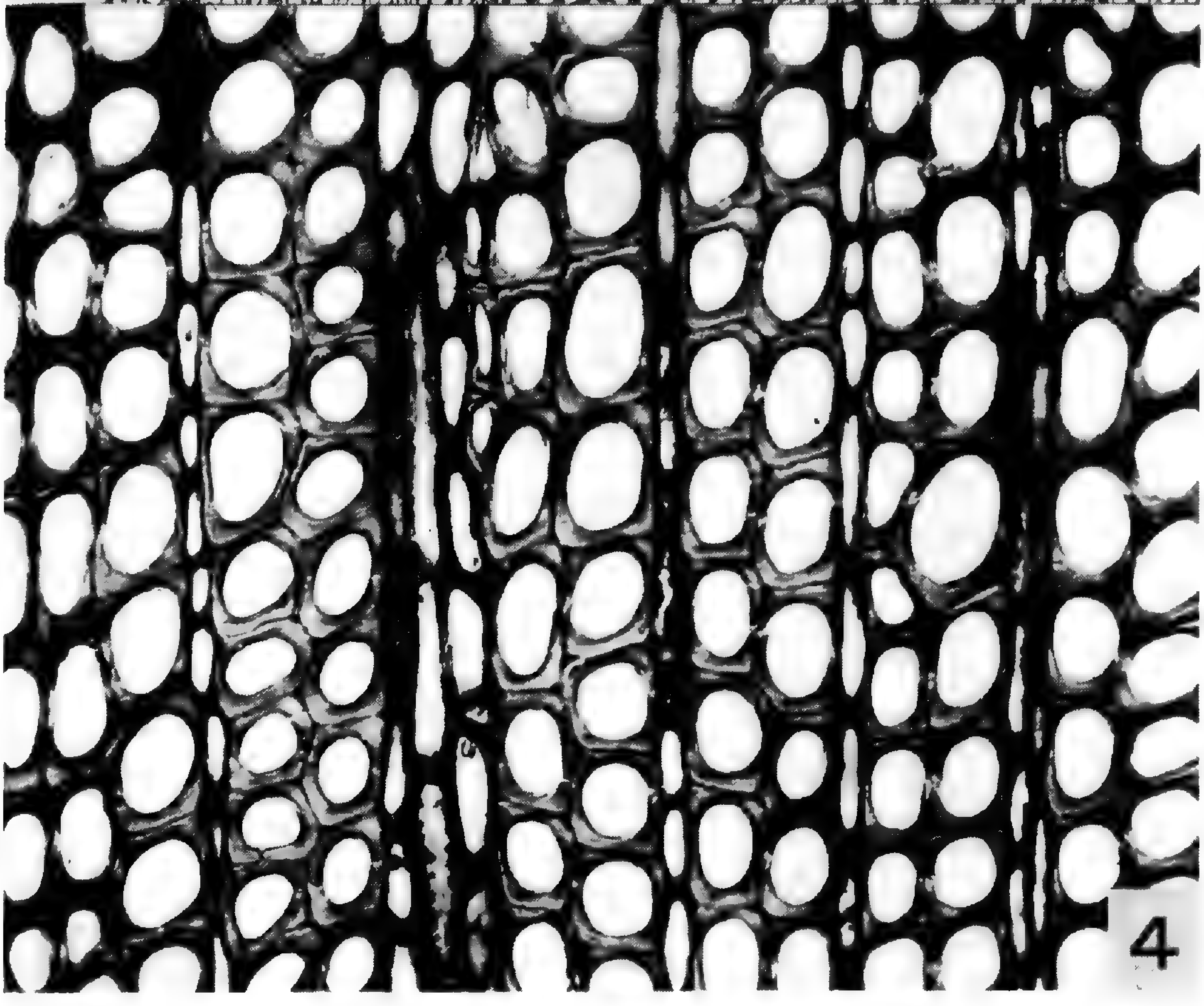

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Bailey, Notes on Amborella

CYTOTAXONOMY OF POTENTILLA FRUTICOSA, ALLIED SPECIES AND CULTIVARS [1]

WRAY M. BOWDEN [2]

With one plate

DURING THE PAST SIX YEARS, a large collection of shrubby potentillas has been assembled at The Dominion Arboretum at Ottawa. Mr. H. L. J. Rhodes was responsible for collecting much of the material and for the taxonomic study; the author make chromosome-number determinations on some of the accessions. After Mr. Rhodes left the staff in 1956, the author assembled voucher specimens for the plants examined cytologically and inquired into the taxonomy of the group in order to classify the specimens as accurately as possible.

The shrubby potentillas are a very difficult group from a taxonomic viewpoint. A thorough study is needed of synonymy, type-specimens, morphological characteristics and range of variation. An adequate taxonomic treatment is not yet available for all of the species and cultivars. The cytological results presented in this paper should prove helpful for future taxonomic treatments.

All the specimens listed below are deposited in The Herbarium of the Botany and Plant Pathology Division (DAO). The chromosome-numbers were determined in permanent section-smears of root tips prepared by schedule B of Bowden (1949) except that the prefixation treatment in cold water was omitted. The slides are deposited in the permanent slide-files of the Cytogenetic Section. The chromosomes of these potentillas are small but distinct, well-fixed and well-stained and are ideal for making accurate counts.

Potentilla fruticosa L., *sensu stricto*

Collections from Northern Europe; tetraploid, $2n = 28$. **England:** Teesdale, below Cronkle Scar on the River Tees, transplanted to Cambridge; Arboretum plots, *Bowden*, July 8, 1957, two cuttings. **Sweden:** Öland, transplanted to Göteborg, *C. Blom*, Sept. 1953; Arboretum plots, *Bowden*, June 15 and Aug. 9, 1956, $2n = 28$ determined on five seedlings. Turesson (1938) also found the tetraploid number in plants from Öland.

Collections of cultivated plants, presumably of European origin; tetraploid, $2n = 28$. *P. fruticosa grandiflora* from the Arnold Arboretum, Arboretum plots, *Rhodes 9198* and *Bowden*, June 14 and Aug. 9, 1956. *P. fruticosa micranda* from Louis Frères, France, *J. M. Gillett*, June 27, 1939; *B. O'Connor*, July 3, 1953, and *Bowden*, June 19, July 16 and Aug. 9,1956; *P. fruticosa micranda* from

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[1] Contribution No. 1606 from the Botany and Plant Pathology Division, Science Service, Canada Department of Agriculture, Ottawa, Ontario.

[2] Botanist (Cytogenetics).

Späth, Germany, *J. M. Gillett*, July 22, 1939 and *Bowden*, June 19, July 13 and Aug. 9, 1956. Material of *P. fruticosa* of European origin was consistently tetraploid, $2n = 28$.

"**Potentilla fruticosa,**" North American Collections

Field collections; diploid, $2n = 14$. **United States:** NEW YORK: Seneca Co.: Junius Bog, *Rhodes 4126*. **Canada:** NOVA SCOTIA: Halifax Co.: Higginsville, *I. V. Hall 53–479–1*; Inverness Co.: Black River, *E. C. Smith et al 10261*. QUEBEC: Matepedia: Lac au Sauman: *Mulligan & Bassett 1338*. ONTARIO: Carleton Co.: Lavergne Bay, *Rhodes & Calder 3746, 3736, 3738*; Mud Lake, *Rhodes & Boivin 4134*. Lanark Co.: McGowan Lake, *Dore 14523*. Renfrew Co.: McNeill Bay, *Rhodes & Rae 4182*, and Arboretum plots, *Rhodes & Drummond 9112*. Bruce Co.: Southampton, *Rhodes & Rae 4300*; Manitoulin Island: South Bay Mouth, *Rhodes & Rae 4297*; Murphy Point, *Rhodes & Rae 4295 & 4296*; Thunder Bay: Schreiber, *Rhodes 8554*. Norfolk Co.: Vittoria, *Bowden 55–53–1*. MANITOBA: 5 miles east of Dauphin, *Rhodes 4739*; 7 miles east of Roblin, *Rhodes & Skinner 4740*; 8 miles east of Eriksdale, *Rhodes 4400*; Ricker, *Rhodes 4368*; Stony Mountain, *Rhodes 4380*, Poplarfield, *Rhodes 4407*; Neepawa, *Rhodes 5159*; Experimental Station, Morden, cultivated plants originally from north of The Pas, *Rhodes 51–249–23*. SASKATCHEWAN: Big Muddy Valley, 20 miles from Montana border, *Rhodes 4938*; Cypress Hills Park, *Rhodes 8553* and three specimens, Arboretum plots, *Bowden*, June 21, July 13 and Aug. 9, 1956. ALBERTA: Junction of Hy. 1 with Hy. from Radium Hot Springs, *Rhodes 8549*, and two specimens, Arboretum plots, *Bowden*, June 14 and Aug. 9, 1956. MACKENZIE: Arboretum plots grown from plant collected at Yellowknife by W. J. Cody, *Bowden*, June 11, 1956. BRITISH COLUMBIA: Kinbasket River delta on ne. side of Kinbasket Lake, *Calder & Savile 11952* and Arboretum plots, *Bowden*, June 18, 1956; Mt. Cheam near Rosedale, *Rhodes & Bitterlick 8268* and Arboretum plots, *Bowden*, July 13, 1956; Bridesville, *Rhodes 8543*; 21 miles east of Golden, *Rhodes 8545* and Arboretum plots, *Bowden*, June 19 & Aug. 9, 1956; Dempster Creek, 8 miles west of Field, *Rhodes 8546*; Kicking Horse Pass, 10 miles east of Field, *Rhodes 8547* and Arboretum plots, *Bowden*, June 12, 1956. **Alaska:** Kenai Peninsula, about 2 miles east of Hope, *Calder 5236*.

All of these plants were diploid, $2n = 14$. Meiosis was studied in the pollen mother cells of *Rhodes 8545*, from 21 miles east of Golden, B. C.; there were regularly 7 bivalents ($n = 7$).

Cultivated collections from the Dominion Arboretum plots, presumably of North American origin; diploid, $2n = 14$. From unknown source, grown since 1889, *Rhodes & Mills 2311*; four different accessions from the Montreal Botanical Garden (MTJB *6668, 11196, 3987*, and *407*), *Bowden*, June 14, June 18, June 21 and July 13, 1956, respectively; from the Arnold Arboretum, *Bowden*, June 21, 1956.

Plants of *P. fruticosa* from North America thus proved to be consistently diploid, $2n = 14$. The diploid chromosome-number was found in material from Edmonton, Alberta, by Turesson (1938) and in plants from several populations in Manitoba by Löve (1954).

From these data, it is clearly established that North American populations of *P. fruticosa* are diploid, while the plants from Öland, Sweden, and

Teesdale, England, are tetraploid. Raven and Walters (1956) have pointed out that there are only a few localities in Northern Europe where *P. fruticosa* exists in the wild. Juzepczuk (1941) states that the species grew from European USSR to Western and Eastern Siberia. Rydberg (1908) gave the range as "Labrador to Alaska, California, New Mexico, and New Jersey; also in Siberia and Western Europe." There is considerable variation in the morphology of the North American plants of this species and there is some variability in the European material. Some of the minute morphological differences between the European plants and the North American plants are very likely associated with the difference in chromosome-number; for example, the petals and peduncles of the European plants are thicker. However, when many specimens were examined it was difficult to find consistent morphological differences by which the diploid North American specimens could be distinguished from the tetraploid European plants. Perhaps the tetraploid European populations evolved from a diploid closely related to the diploid yellow-flowered North American plants and, for that reason, it is difficult to obtain strong morphological differences. However, later workers may still find some satisfactory morphological differences between the diploid North American specimens and the tetraploid European populations. If such differences can be found, the diploid North American plants would deserve taxonomic recognition as a distinct taxon, either a distinct species, or a subspecies of *P. fruticosa.*

In the Hortus Cliffortianus, Linnaeus (1737) listed several localities where this species grew in England and Sweden. He included ". . . in Anglia ad ripam meridionalem Tesae fluvii infra vicum Thorp . . . & in Oelandiae Sueciae insula proveniat." Linnaeus (1745) stated that the species occurred in southern Öland. Linnaeus (1753) recorded that *P. fruticosa* was found in "Eboraco [York], Anglia, Oelandia australi, Sibiria." In the Linnaean Society Herbarium in London, one of Linnaeus' specimens of *P. fruticosa* is preserved; it is Savage Catalogue no. 655.1 and on the back of the sheets is written "Sibiria." In the British Museum collection of specimens from the Clifford Herbarium (Hortus Cliffortianus), there is a well-preserved specimen that has large flowers similar to specimens from Teesdale, England and Öland, Sweden. Rydberg (1908) listed the type locality of the species as "England." The name *P. fruticosa* L., *sensu stricto*, applies to the tetraploid plants from Teesdale and Öland. Until the taxonomy and nomenclature of the North American populations can be clarified, the present author lists them as "*P. fruticosa*," diploid North American collections.

Potentilla parvifolia Fisch. in Lehm.

Cultivated plants in the Dominion Arboretum, from various sources, originally from Eastern Asia; diploid, $2n = 14$. Two different accessions from the Montreal Botanical Garden: MTJB *3433, Bowden*, June 21, 1956, *Rhodes 4004*; and MTJB *254, Bowden*, June 19, 1956; Experimental Station, Morden, Man., *Rhodes 4358*; A. M. Cocks & Sons, Winona, Ont., *Rhodes 4001*; Sheridan Nurseries, received as 'Gold Drop', *Rhodes 4003*; Woodland Nurseries, Cooksville, Ont., received as

'Woodland Gold', *Bowden*, June 21, 1956 and *Rhodes 3731*; Hillier & Sons, Winchester, England, *Bowden*, June 19, 1956 and *Rhodes 9205*; Hillier & Sons, from Prof. Lyttol's Garden, *Bowden*, June 19, 1956; Hillier & Sons, Forrest col., *Bowden*, June 18, 1956.

There is general agreement concerning the taxonomy of this small-leaved species with bright yellow flowers; cf. Fletcher (1950), Handel-Mazzetti (1939), Juzepczuk (1941) and Rhodes (1954). The chromosome-number of *P. parvifolia* suggests that it is a segregate diploid species in Eastern Asia.

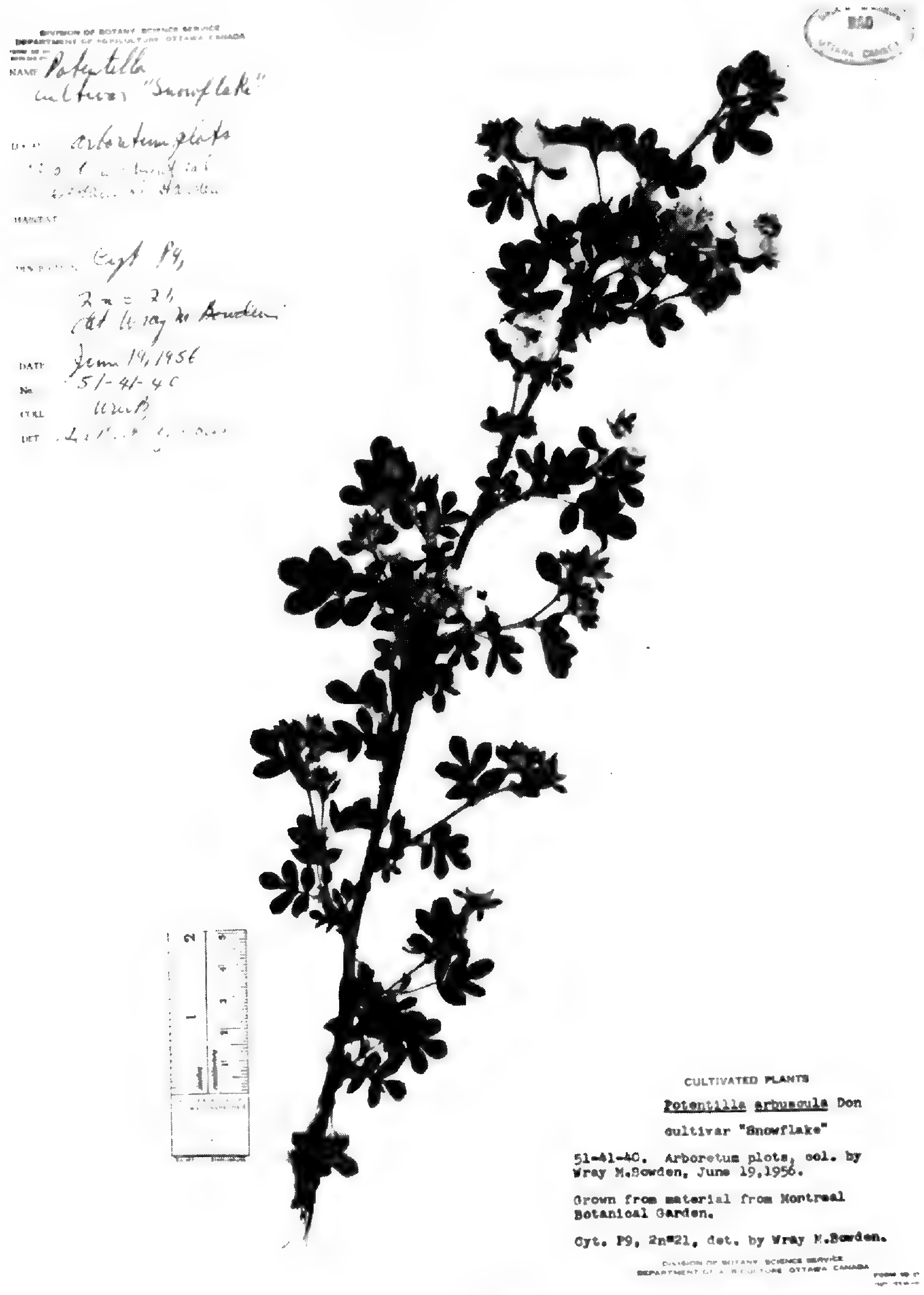
Potentilla davurica Nestl. (= *P. glabra* Lodd.)

Cultivated plants in the Dominion Arboretum, originally from Eastern Asia; diploid, $2n = 14$. Sheridan Nurseries, Ont., specimen with glabrous leaves, without flowers, four-year-old dwarf plant, *Bowden*, Aug. 28, 1956; Hillier & Sons, Winchester, England, received as *P. glabra* Lodd. (typical), specimen with glabrous leaves, without flowers, four-year-old dwarf plant, *Bowden*, Aug. 28, 1956; Hillier & Sons, received as *P. glabra rhodocalyx*, almost glabrous leaves, *Bowden*, Aug. 28, 1956; Hillier & Sons, received as *P. glabra* Lodd. var. *kansu* collected by Farrer, some hairs on leaves, etc., and numerous white flowers on dwarf shrub, *Rhodes 9114* and *Bowden*, June 12, 1956.

There is considerable confusion concerning the application of the name *P. davurica* Nestl. The leaves of Nestler's plants were glabrous ("utrinque glabra") and the plant came from Eastern Asia ("Hab. in Davuria"). Loddiges' *P. glabra* was said to be a native of Siberia, was glabrous ("perfectly smooth in all its parts") and presumably had white flowers (received by him as *P. fruticosa alba*). Handel-Mazzetti (1939) thought that *P. davurica* was a hybrid (*P. glabra* × *P. parvifolia*). Fletcher (1950) used the name *P. glabra* Lodd. for the white-flowered plant. In Rhodes' key (1954), *P. davurica* (typical) was applied to plants with "leaves glabrous; plant dwarf." The above specimens are listed under *P. davurica* to indicate that they are more glabrous than the other collections from Eastern Asia. Since only some of the plants have bloomed, I do not know if all the collections will have white flowers or if some are yellow-flowered. The first two collections had very glabrous leaves and were dwarf shrubs; they were so distinct from all the other collections that they seemed to me to merit recognition. A much more detailed study is needed on these and the next collections listed before the taxonomy of these plants can be precisely known. Hara (1952) has already discussed the taxonomic problems of these Eastern Asiatic taxa.

Potentilla arbuscula D. Don

Cultivated plants in the Dominion Arboretum, originally from Eastern Asia; diploid; $2n = 14$. Hillier & Sons, Winchester, England, received as *P. glabra* var. *mandshurica*, *Bowden*, June 15 and June 21, 1956; Hillier & Sons, received as *P. arbuscula* erect form, *Bowden*, June 11, 1956; The Montreal Botanical Garden, MTJB *4444*, received as *P. fruticosa mandshurica*, *Bowden*, June 19,



Herbarium specimen of the triploid ($2n = 21$) *Potentilla arbuscula* 'Snowflake,' Montreal Botanical Garden No. 1324–45; photograph by W. J. Cody.

1956; Hillier & Sons, received as "*veitchii*," *Bowden*, June 11, 1956; and Hillier & Sons, received as *P. rigida*, specimen without flowers, *Bowden*, Aug. 28, 1956.

Except for the last, all the specimens have white flowers. The leaves are characteristically pubescent, with long, white, silky hairs on the upper surfaces and also some pubescence on the lower surfaces, although Fletcher (1950) stated that "the typical plant is glabrous on the lower leaf-surface." Hara (1952) reported $2n = 14$ in plants listed as *P. fruticosa* L. var. *arbuscula* (D. Don) Maxim. from Honshu.

Potentilla arbuscula 'Snowflake'

Cultivated plants in the Dominion Arboretum; triploid, $2n = 21$. This is the first triploid reported in the genus. Dansereau (1955) gave a review-list of chromosome numbers in *Potentilla* and stated that no triploids had been recorded.

Specimens preserved: Montreal Botanical Garden, MTJB *1324–45*, *Rhodes 1775* and Arboretum plots, *Rhodes & Vrugtman 9134* and *Bowden*, June 19, 1956 (Plate 1). Open-field-pollinated seed of a plant of cultivar 'Snowflake' from Sheridan Nurseries, Toronto, was grown. Several specimens of the parental plant were preserved (*Rhodes 4002* and *6156*) but a chromosome-count was not made on the plant. Of four seedlings studied, two were diploid, $2n = 14$, one was $2n = 15$, and one was pentaploid, $2n = 35$. The specimen of the last is: Arboretum plots, *Bowden*, June 12, 1956.

Potentilla arbuscula D. Don var. **albicans** (Rehd. et Wilson) Hand.-Mazz.

Cultivated collections in Arboretum plots; hexaploid, $2n = 42$. Alpenglow Gardens, Michaud & Co., New Westminster, B.C., *Rhodes 2808*; Hillier & Sons, Winchester, England, received as *P. davurica beesii*, *Bowden*, June 25 and July 13, 1956; Hillier & Sons, received as *P. sulphurescens vilmoriniana*, *Bowden*, June 14 and 15, 1956.

The plant from Alpenglow Gardens had bright-yellow flowers; the other two accessions had pale-yellow flowers. All the specimens had both surfaces of the leaves densely covered with a white shining silky indumentum as mentioned by Fletcher (1950).

Potentilla arbuscula D. Don var.

Cultivated collections; octoploid, $2n = 56$. Arboretum plots (received as *Potentilla*, *Purdom 841*, from the Arnold Arboretum in 1921), *N. Taylor*, June 13, 1946, *Rhodes 1577*, and *Rhodes & Mills 2313*.

The plants of diploid, triploid and octoploid *P. arbuscula* had white flowers. The flowers of dried herbarium specimens tend to turn yellowish with age. One would expect tetraploid plants to occur in this complex. It remains for future biosystematic studies to clarify the taxonomy of these plants, particularly the relationship of white and yellow flower-colors, and whether or not the glabrous plants that I have listed under *P. davurica*

Nestl. are specifically distinct from the more pubescent plants listed under *P. arbuscula* D. Don.

Potentilla × rehderiana Hand.-Mazz.

These plants were said to be hybrids between *P. parvifolia* and *P. glabra* var. *mandshurica*. Our accessions were diploid, $2n = 14$.

Cultivated specimens in the Dominion Arboretum plots: Two accessions from the Montreal Botanical Garden, MTJB *837*, *Bowden*, June 19, 1956, and MTJB *5485*, *Rhodes 4355*; from the Arnold Arboretum, *Bowden*, June 21, 1956. The last specimen shows the characteristics of *P. parvifolia* very strongly.

Potentilla × friedrichsenii Späth

Handel-Mazzetti (1939) stated that this name was applied to hybrids of *P. fruticosa* × *P. glabra*. Our three accessions were diploid, $2n = 14$. The diploid number suggests that if this taxon is a hybrid between these two species, then the *P. fruticosa* parent was a diploid plant, not the tetraploid from Sweden or England. I do not know the chromosome-number of *P. fruticosa* in the area from the European USSR to the Pacific coast of Asia but possibly there may be diploids there. As already shown, the North American plants of *P. fruticosa* are diploid.

Cultivated specimens in the Dominion Arboretum plots: from Basel Botanical Garden, Basel, Switzerland, *Rhodes*, June 16, 1950; from University of St. Andrews, Scotland, received as *P. fruticosa veitchii*, *Rhodes*, June 16, 1950; from Hillier & Sons, received as *P. friedrichsenii leucantha*, *Bowden*, June 12, 1956.

Miscellaneous Collections

These last accessions were received under various names. I was not able to refer any of the specimens with certainty to the taxa listed above. These undetermined specimens were all diploid, $2n = 14$. Some of the plants may be hybrids.

Specimens preserved from Dominion Arboretum plots: the Montreal Botanical Garden, MTJB *1821*, received as *P. fruticosa* 'Friesengold', *Bowden*, June 21, 1956; Alpenglow Gardens, New Westminster, B.C., received as *P. fruticosa pyrenaica*, *Rhodes 2809*; The Montreal Botanical Garden, MTJB *1136*, received as *P. fruticosa*, *Bowden*, June 11, 1956; Manitoba Hardy Plant Nursery, Dropmore, Man., received as *P. davurica*, *Bowden*, June 19, 1956; Hillier & Sons, received as *P. davurica* from France, *Bowden*, June 11, 1956; Hillier & Sons, received as *Potentilla* 'Katherine Dykes', *Rhodes & Vrugtman 9138*; Hillier & Sons, received as *P. davurica* 'Nyewoods form', *Bowden*, June 11, 1956; Hillier & Sons, received as *P. davurica* 'Lady Daresbury's form', *Rhodes & Vrugtman 9137* and *Bowden*, June 11, 1956.

SUMMARY

Plants of *Potentilla fruticosa* L., *sensu stricto*, from Teesdale, England, and Öland, Sweden, are tetraploid ($2n = 28$); North American populations of "*P. fruticosa*" are diploid ($2n = 14$). *Potentilla parvifolia* and

P. davurica (*glabra*) from Eastern Asia are diploid. ***Potentilla arbuscula*** from Eastern Asia is a polyploid complex; diploids, one triploid ($2n = 21$), hexaploids ($2n = 42$) and one octoploid ($2n = 56$) are so far known. The cytological data should be helpful when a thorough biosystematic study is made of the shrubby potentillas.

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THE DIRECTOR'S REPORT

The Arnold Arboretum During the Fiscal Year Ended June 30, 1957

This year marks the eighty-fifth anniversary of the establishment of the Arnold Arboretum. To commemorate this event, special exhibits and open houses have focused attention on the outstanding living collections of trees and shrubs in the Arboretum's plantings both in Jamaica Plain and Weston, as well as on the research collections in Jamaica Plain and Cambridge, while news stories, magazine articles and other types of publicity have dealt with the contributions of the staff members of this organization since its founding in 1872. From its inception, the Arnold Arboretum has played an important role in the introduction of plants new to American gardens from distant parts of the globe. In order to single out some of the plants which members of the Arboretum staff have introduced into cultivation in America, Mr. Heman Howard, the assistant horticulturist, prepared special wooden labels painted yellow to be attached to the proper plants. A survey of the records was made to locate those plants or their descendants now growing in the Arboretum which had been introduced into American horticulture for the first time at Jamaica Plain; about 1800 yellow tags were required to label those plants in immediate view from the roads and paths. Such plants proved to be of immense interest to the many visitors of the past season. They saw that some of the most common and the most sought-after varieties were first introduced into American gardens by the Arnold Arboretum.

The Staff:

At the fiftieth anniversary banquet of the Botanical Society of America the president of the Society presented Certificates of Merit to fifty distinguished botanists for their contributions to their fields. Two staff members of the Arnold Arboretum, Irving Widmer Bailey and Karl Sax, were among those so honored. Their citations were:

> "Irving Widmer Bailey, Plant anatomist and inspiring teacher, for his outstanding contributions on the structure of the cell wall and the histology of the cambium, and for his application of anatomy and morphology to problems of evolution of angiosperms."
>
> "Karl Sax, for his classical studies on the chromosomes of wheat, his continued interest in the chromosomes of ornamental woody plants and his extensive contributions about the effect of irradiation on chromosome breakage and chromosome structure."

The presentations were made at the University of Connecticut during the annual meeting of the American Institute of Biological Sciences.

Two staff members, Drs. Sax and Howard, were invited to serve as American Institute of Biological Sciences lecturers to stimulate interest in a biological career among students in smaller liberal arts colleges. This program places outstanding scientists, teachers and lecturers on the campus of the college for several days. The speaker has the opportunity of meeting with students, staff and the public formally in lectures and informally about the campus and in the dining halls. Dr. Sax was able to visit the College of Wooster, in Ohio, and Dickinson College at Carlisle, Pennsylvania, for this program during the year. The association has proved to be stimulating and the program is being continued.

The demand for Arboretum staff members as speakers exceeds our abilities to fill all requests. During the year staff members attended conferences or gave lectures in seventeen states and in Canada. Dr. Sax took part in symposia on "Biological Effects of Ionizing Radiation" at Storrs, Connecticut, on "Population" at the University of Minnesota, on the hazards of ionizing radiation at the Canadian Atomic Energy Commission meetings at Chalk River, Canada, and on Forest Tree Physiology at the Harvard Forest. Dr. Howard talked to many horticultural organizations and other groups on the Arnold Arboretum, emergency survival problems, his research in plant taxonomy and on the vegetation of the West Indies. On one trip he met with garden clubs and botany departments of universities in Tennessee, Georgia, Louisiana and Texas. Dr. Wyman attended horticultural meetings in Delaware and Michigan and spoke at the Williamsburg symposium and at the Longwood Gardens. Mr. Coggeshall represented the Arboretum at the Propagators Convention in Cleveland and nearly all of the staff attended the annual meetings of the American Institute of Biological Sciences at Storrs, Connecticut.

During the year Dr. Sax was elected an honorary member of the Japanese Genetics Society and his appointment as consultant in biology to the Oak Ridge National Laboratories was renewed.

One annual appointment was made to the staff for work on the Flora of the Southeastern States and three for work on the herbarium integration and general curatorial duties. Dr. Charles W. James joined our staff after an appointment at the University of Tennessee and Dr. Frances M. Jarrett came to the Arboretum at the completion of her graduate work at Cambridge University, Cambridge, England. Dr. Jarrett is a specialist in the flora of the Malaysian area. Mrs. Jeanne Germaine Weber, who has been working on the flora of Europe at the Botanical Garden in Geneva, Switzerland, will assist in the herbarium integration. Dr. Howard F. L. Rock completed his graduate work at Duke University and, having specialized in the Compositae, has been working on the reorganization of that large family of flowering plants. With the exception of that of Miss Jarrett, these appointments were made jointly with the Gray Herbarium.

Horticulture:

One of the functions of the Arnold Arboretum is the growing of plants hardy in the vicinity of West Roxbury. Regardless of staff efforts, the ultimate success of the trees and shrubs planted in Jamaica Plain seems to be controlled by the weather. In past years, hurricanes, summer heat or flooding, late frosts, ice storms or other vagaries of the climate have had their effect on the growth of the plants in our collection. This past winter was marked by a period of unusually cold weather. A four-night period of sub-zero weather climaxed by a low temperature of twelve degrees below zero was recorded at the greenhouses on January 15 and lower temperatures were probably experienced elsewhere on the grounds. At Weston the temperature dropped to thirty degrees below zero on the same day. Many of the plants considered marginally hardy were killed outright, killed to the ground or severely injured during this cold weather. These have been listed and the injuries discussed in two issues of ARNOLDIA during recent months. Some of the recent introductions, particularly among the rhododendrons growing in the nurseries at Weston, died during the winter. The spring flowering of many genera and species was also affected by the cold weather, for flower-buds formed last summer were killed during the period of low temperatures, except where snow accumulation or other forms of fortuitous or deliberate protection were present. With the exception of the *Forsythia* 'Beatrix Farrand,' most selections of *Forsythia* were in poor flower. The flowering cherries and the early azaleas were likewise disappointing in bloom, with the protective effect of snow-line strongly marked. In contrast, or perhaps in reality, other groups such as the lilacs, the crab apples, the Ghent and flame azaleas and the rhododendrons seemed to have extremely profuse bloom. Specimens of some trees, such as *Cladrastis lutea*, carried unusually heavy bloom, while others, as the dove tree (*Davidia involucrata*), failed to produce a single flower.

The Park Department of the City of Boston, through the cooperation of Commissioner Frank Kelley and his assistants, Mr. O'Keefe and Mr. Byrne, continued its work of rehabilitation on the grounds of the Arboretum. During the year sections of the roads and sidewalks were patched, benches painted and repaired and, with the assistance of the Arboretum staff, all of the cobblestone gutters except those in the Peter's Hill tract, have now been dug out and cleaned. The appearance of the paths and roads has been materially improved by this work.

The Arboretum staff has under way work on the collections and the grounds which adds to the appearance of the Arnold Arboretum plants and plantings. Twenty-five large truckloads of well-screened and composted leaf mould were distributed around the shrubs. The spent hops which have been used as a mulch for a number of years are no longer available and the use of ground cocoa shells has been started on an experimental basis. Early reports of this material as a mulch have been published in ARNOLDIA. Test plots using various applications of the cocoa shell have been established on the grounds of the Case Estates in Weston. While the cocoa shell will not burn, as did some other mulches tried at the Arboretum, there are certain disadvantages to the new mulch which must be evaluated before final acceptance of this material.

A section of native woodland adjacent to our collection of dwarf conifers was cleared during the winter and work has begun on transplanting some of the smaller plants in this collection. It is hoped to extend the collection toward the road, thus giving individual plants more room and displaying them to greater advantage.

Over twenty varieties of narcissus and daffodils have been planted along Bussey Brook near the rhododendron collection to establish a naturalized display a few years hence. Some of the collection bloomed well this spring. The bed of *Calluna* nearby was reduced in size. For a number of years we have attempted to maintain and replace where needed a large number of named varieties, many of which have died in cold winters, even with protection. It now seems desirable to limit our plantings to the cultivars which have proved hardy.

Several additional vistas have been opened up at the top of Bussey Hill and ground-covers have been established there. The ground-covers selected for this much-visited spot were those of the larger collection in Weston which have been most attractive to visitors.

Some work was done by the Park Department in partial repair of the retaining wall along Bussey Brook behind the rhododendron collection. On the steep slopes of Hemlock Hill near the rhododendron collection additional hurricane debris and damaged trees were removed. A new planting of rhododendron species has been started in this cleared area. If the present test planting of forty specimens thrives, as is expected, additional areas will be cleared and developed into a new and attractive display for the Arboretum.

A saran-cloth house 104 × 16 feet was erected near the greenhouse to replace the badly broken lath shade structure which had been used for many years. This is a temporary expedient until the threatened eminent domain procedures against the greenhouse area are clarified.

Planting in the Jamaica Plain collections has been difficult due to the continued dry weather of late spring and early summer. In all, three hundred specimens of twenty-two species and varieties of evergreens and one hundred thirty-five deciduous species have been added to our collections during the fall and spring plantings. These are either new plants or replacements for defective specimens. All have required continuous watering and care.

Approximately one hundred seventy-five species and varieties have been introduced from foreign countries during the year. These plants apparently are not available from commercial sources or other gardens in this country. After testing and observation at Weston they will be planted in Jamaica Plain.

Dr. Wyman, the horticulturist, in cooperation with the U. S. Department of Agriculture and other arboreta, arranged for the introduction of twenty-six kinds of evergreens and twenty-nine varieties of deciduous plants which are normally prohibited entry into this country. These plants will be grown at Glen Dale, Maryland, for the quarantine period and then released when judged free of insect and disease pests. The Arnold Arboretum, which manages this program, has been responsible for assisting other gardens in introducing about one hundred varieties of plants in this program during the year.

Requests for plant materials from the living collections of the Arboretum included pollen for breeding programs and reference collections, samples of leaves and stems for chemical analysis, soil samples from roots of specific trees for chemical and antibiotic tests, herbarium specimens and propagating material. During the past fiscal year two hundred forty-nine shipments of propagating materials were sent out, representing eight hundred sixty species and varieties. The majority of these went to arboreta and botanic gardens within the United States and Canada. However, requests received from twelve countries in Europe, Asia, Africa and Australia were filled. Only thirty-seven shipments of one hundred fifty-two species and varieties were of seeds. This indicates the increasing demand for material for vegetative propagation in the horticultural interest.

Eight plants were grown in quantity and distributed to thirty-three cooperating commercial growers in North America for eventual distribution through sale to the general public. These new or selected species, hybrids or clones, considered by the staff to be of significant horticultural value, were *Acer capillipes*, *Acer rufinerve*, *Carpinus japonica*, *Lonicera amoena rosea*, *Malus* 'Henrietta Crosby', *Malus* 'Henry F. du Pont', *Malus* 'Mary Potter' and *Syringa* × *swegiflexa*.

During the past year the Arnold Arboretum received one hundred ninety-one shipments, representing six hundred ninety species and varieties, as seeds, propagating material or plants. These were included in the 1102 species and varieties handled by the propagation department during the year. Not all of the seeds proved viable, nor did all the propagating material for rooting, budding and grafting prove useful.

The development of proper techniques in propagating and handling the rare and unusual plants in the living collections is important to the extended acceptance and use of these plants. Many of the most interesting plants introduced by the Arboretum have never had wide use because of difficulties in propagating or transplanting the species. Much of the experimental work in the greenhouses by the propagator and other staff members concerns various aspects of this basic problem. Some of the work which has been done in the last year concerned species of *Abies*, *Acer*, *Davidia*, *Fagus*, *Picea*, *Pinus*, *Tilia* and *Stewartia* and varieties of *Syringa vulgaris*.

Experimental work was tried to overcome the double dormancy of seeds of *Davidia involucrata* by exposing the seeds to warm temperatures followed by cold temperatures prior to planting. Seeds were collected from the ripe fruits, mixed with moistened sand and peat and placed in polyethylene bags. The bags were then stored at greenhouse temperature, from 60 to 85 degrees, for six months and then kept in a refrigerator for three months at 40 to 42 degrees. When planted immediately afterward, a germination of from 65 to 70 percent was obtained within three weeks.

Selected varieties of *Syringa vulgaris* were tested to compare the effect of different hormone concentrations on rooting and the resulting rates of growth between these rooted cuttings and grafted plants. Results indicated that if the softwood cuttings are taken early in May and treated with Hormodin No. 3 for maximum rooting, such plants will produce growth equal to that of scions grafted during the year.

Attempts were also made to graft varieties of *Syringa vulgaris* in the fall, storing such grafts through the winter to obtain more rapid growth during the following spring. Such experiments were not successful. The grafts callused normally in one month in sawdust and were stored in plastic bags in a refrigerator. Abnormal or no growth was obtained the following year.

Various species of *Tilia* were propagated from softwood cuttings taken in August. Again good rooting was obtained, but unexplained difficulty was encountered in overwintering such rooted plants. Previously, the same difficulty was experienced when *Stewartia* cuttings taken in August were rooted. Experiments of the past years have shown that cuttings of the latter plant taken in June and treated with Hormodin No. 3 rooted well. When these were potted and stored in a cold pit for the winter, normal recovery and growth was experienced the following year.

Normally, the lack of space in the greenhouse and nursery area necessitates the transplanting of young plants from two to five times before they are large enough for permanent planting in the Arboretum. Many plants survive such treatment, but certain others suffer extremely heavy losses in the course of the many transplantings. In the last few years we have attempted to reduce these losses by the use of metal containers which can be moved about without disturbing the root systems while the plants increase in size. Thus young seedlings of *Davidia*, rooted cuttings of *Stewartia* and grafted plants of *Abies*, *Fagus*, *Picea* and *Pinus* have been handled with a minimum of loss and the elimination of an average of three transplanting operations.

The Case Estates:

Shortly after the Arboretum was given the property known as the Case Estates in Weston, the town felt the need for additional land for new school buildings. In 1946 a tract of forty-two acres was sold to the town of Weston from the Case Estates for a modest sum. As the town has grown, however, the need for additional school buildings and adjacent playground space has increased. During the past year a study committee, termed the School Site Committee, returned a recommendation that the future growth of the school population be met by a decentralized school building program. The committee's report containing the negative vote of a single member was supported by the selectmen and other town officials. Nevertheless, at a town meeting held in the fall the committee's report was not accepted and the town meeting voted to take by eminent domain the land of the Case Estates north and west of a 500-foot line parallel to Wellesley Street. Although the town officials have taken no further action during the past fiscal year, a School Building Committee and a firm of surveyors have given consideration to building three additional schools on land to be taken from the Case Estates. Such action could involve seventy or more acres of the one hundred forty-five acres now in the Case Estates, leaving less than half of the land originally given to the Arboretum for horticultural purposes in Weston. The director has indicated to the selectmen of the town that the Arboretum does not wish to lose this land and that such a loss will seriously restrict future development of the Arnold Arboretum. Nevertheless, much time has been spent with appraisers and surveyors during the past year and considerable staff planning has been necessary to determine what plants can be moved and what others should be propagated if the land-taking proceedings are carried out.

The collections at the Case Estates such as the ground-cover demonstration plots, the small-tree demonstration area and the shrub and perennial gardens are being visited by an ever-increasing number of people. Garden clubs have requested special trips and tours of these plots and plantings. A new pruning demonstration tract has been established this year and will show results next spring. Comparison tests on the use of cocoa shell as a mulch are also being conducted at Weston. Repairs were completed on the Chandler house which was turned over to the Arboretum last year and which is now occupied by the Director of the Arnold Arboretum.

Education Program:

During the third year of the informal education program for adults conducted at the Arnold Arboretum, the spring and fall field classes with Dr. Wyman and the propagation classes with Mr. Coggeshall were continued and were well attended. Again this year the applications for the classes in plant propagation exceeded the physical limits of the greenhouse and some people had to be disappointed. Dr. Wood offered a class in identification of cultivated plants and Dr. Howard taught two new classes in economic botany entitled "Botany in Boston I and II." The former dealt with the commercial utilization of plant materials in industry and greenhouses in the Boston area and the second concerned the use of plant materials as foods in various Boston restaurants. During the spring the staff combined to present a series of seminars on cultivated plants which were open to the public as one of the regularly scheduled classes. At each seminar Dr. Howard discussed the history and botanical classification of the group, Dr. Wyman the horticultural utilization and values, Dr. Sax the genetics and breeding programs, Mr. Williams the diseases and maintenance and Mr. Coggeshall the methods of propagation. Each seminar was scheduled to be held when the plant group under discussion was in flower on the grounds. When the weather permitted, visits were made to the collections of lilacs, magnolias and forsythias, crab-apples, cherries and rhododendrons before the seminar discussion. The interest of the class members was high in this concentrated presentation of information regarding restricted groups of ornamental plants. During the three years of the education program which has been conducted at the Arboretum, four hundred and eighty-eight people have attended one or more courses.

All staff members were needed to assist when the Arboretum cooperated with the Massachusetts Horticultural Society in presenting their annual Field Day in Jamaica Plain. Eight buses were filled for the two-hour trip around the grounds; other visitors followed in their own cars. A staff member served as a guide in each bus and attempted to answer the many questions which were asked. In addition to this regularly scheduled event, many garden clubs now hold meetings at the Arboretum where staff members conduct the groups through the grounds. Special tours have been arranged for children's groups, older people and the handicapped.

Exhibits and displays:

The Arboretum display at the Massachusetts Horticultural Society's Spring Flower Show held in Mechanics Building emphasized the eighty-fifth anniversary of the Arnold Arboretum by featuring a planting of ornamental trees and shrubs introduced by the Arboretum staff. The featured plants numbered about forty of the over 5000 species and varieties for which the Arboretum receives credit. These ranged from a red-leaved variety of the Japanese barberry, introduced in 1879, to the dawn redwood, *Metasequoia*, introduced as seed in 1948. Plants developed at the Arboretum or selected from progeny grown for testing included *Forsythia* 'Beatrix Farrand' and *Prunus* 'Hally Jolivette' developed by Dr. Sax, the crab-apple 'Dorothea' and the bush-honeysuckle 'Arnold Red'. The exhibit received a first prize from the Massachusetts Horticultural Society and was awarded the gold medal of the Pennsylvania Horticultural Society for "an exhibit of special merit which stimulates an interest in horticulture." The latter is one of the two top awards offered at this show.

A Christmas show was held at the Administration Building in Jamaica Plain and featured plant material used in Christmas decorations, such as tree ornaments, wreath-making materials and broad-leaved evergreens used in floral arrangements. Mrs. Donald Wyman created several wreaths and arrangements showing the steps in preparation of such decorations which proved to be a feature of the exhibit. This was held from December 4 to 21, 1956 and was enthusiastically attended.

A selection of fifteen plants from the Larz Anderson Collection of Japanese Dwarf trees was sent to Detroit for display in the March Spring Flower Show in that city. These proved to be an interesting feature of the Michigan show and received a great deal of comment.

Open houses were held on May 12 at the Case Estates in Weston, on May 19 at Jamaica Plain and on June 10 in Cambridge. Staff members, identified by badges, were on the grounds and in the buildings at each location to answer questions or explain work in progress. The interest expressed by the many visitors proved stimulating to all.

Library:

The librarian, Mrs. Lazella Schwarten, and her staff continued the work on the integration of the Arnold and Gray libraries and the reconditioning of books in addition to the regular service of an active library. During the preceding year the integration of the periodicals had been completed; work continued this year on the other categories, so that the total task is now over half finished. Additional stacks were constructed for volumes dealing with the horticultural subjects in Jamaica Plain and a further reorganization is under way on the latter collection.

During the year two hundred and twenty-nine bound volumes were added to the library, bringing the total of bound volumes to 49,738. Two hundred and fifty pamphlets were received and added to the collection, which now contains 16,218 items. Among the various catalogues maintained, 580 cards were added to the general card file and 4000 to the Gray Herbarium Index.

The requests for interlibrary loans from outside organizations continues to mount and, of necessity, certain procedures have been incorporated into our operations. Except in very special cases, books over one hundred years old or those currently available on the commercial market are not sent on loan. Even within these limits, the librarian may restrict the privilege of a loan depending on the condition, value and local need for the book. Wherever possible, microfilm, photocopy or a typed description of the material needed is suggested as a substitute for a loan. Nevertheless, ninety-five books were sent out during the year on interlibrary loan. The use of the library by staff and students increased measurably during the year as work in other parts of the Arboretum increased.

Herbarium:

The work concerned with the integration of the two major collections housed in the Harvard University Herbarium in Cambridge involved most of the efforts of the herbarium staff again this year. The plans for progress in this essential task have been discussed in previous reports. During the past year it was possible to appoint additional taxonomists to the staff to assist with this work. Special funds were made available by the Harvard Corporation for this project. Such funds have been used to employ full-time workers as well as some part-time help. During the year the operation of placing in sequence all genera of the various families in the collections was completed. At this time the family sequence is complete and all of the genera are in proper order. Actual integration at the specific level has progressed so that one hundred sixty families or about one-half of the herbarium is in final arrangement. During the course of this work, which is under the direction of Dr. Kobuski, annotations are made according to the latest monographs available, geographical arrangements are coordinated, repairs to specimens are made where possible and types and other authentic specimens are indicated and placed in special folders. The completed portions of the herbarium stand as a model for future work.

The fruit and seed collections received special care during the year and this collection is now uniformly boxed, adequately spaced, and completely rearranged. The sequence used follows that of the herbarium.

Curatorial work on the herbarium of cultivated plants at Jamaica Plain was limited, but the task of checking the coverage continued. Additional collections of cultivated plants from the United States and Europe were inserted.

During the past year 6,874 specimens were mounted and inserted in the herbarium, bringing the total accession count to 694,681 specimens in the Arnold Arboretum.

The herbarium received 17,157 specimens during the year. About 10,900 of these were in exchange, 5,900 were from collectors subsidized by the Arboretum and the remainder as gifts or for identification. The largest number of these came again this year from Malaysia. Of the total 5,400 represented the flora of the New World, 1,900 that of Europe and the remainder that of Asia, Africa and Australia. The largest and most important Asiatic collections were received from Canberra, Australia; the Rijksherbarium, Leiden, the Netherlands; the Royal Botanic Garden at Kew, England; and the Herbarium Bogoriense, in Indonesia. The materials received by subsidy were largely photographs of type-specimens in European herbaria made by the New York Botanical Garden.

During the year the Arnold Arboretum sent out 878 specimens to American institutions and 665 to foreign institutions in a regular continuation of exchange. In addition, a special shipment of 2613 specimens was sent to the Forestry Department at Lae, New Guinea, representing a complete set of the plants collected by L. J. Brass on the Fourth Archbold Expedition. Three hundred and eighty-six specimens of this same collection were sent to specialists for identification.

Again the facilities of the herbarium were made available to many visitors and additional materials were sent on loan or services rendered in response to requests by mail or phone. During the year 10,421 herbarium specimens were sent out from the combined herbaria on loan to qualified scholars. These represented seventy-eight separate loans to forty-five different institutions and averaged over one hundred thirty specimens per loan. Fifty of the loans were to twenty-eight American institutions, while twenty-eight loans went to seventeen different foreign herbaria. The size of these loans is indicative of the wealth of material in the Harvard herbaria and the need for these same materials for comprehensive research programs. In addition to these requests, the staff, where possible, answered questions concerning identifications, distributions or technical problems which could be handled more reasonably by our staff than by the shipment of specimens.

Most of the research interests of the staff continue at present as mentioned in the previous annual report.

Comparative Morphology:

Professor I. W. Bailey, Professor of Plant Anatomy, *emeritus*, has continued to serve as curator of the wood and pollen-slide collections. Professor Bailey's services materially assist the herbarium staff and assure the maintenance of the collections in good condition. A small number of accessions of wood samples and slides were added to the collection during the year and the requests for specimens from these collections continued at a normal rate.

Professor Bailey completed several papers on wood anatomy and the use of anatomical characters in other aspects of botanical study. His recent interests have turned to the anatomical structure of the stem in the Cactaceae.

Cytogenetics:

Dr. Karl Sax, his assistants and students have reported the following contributions in the field of cytogenetics:

The cytogenetic work with *Malus sargentii* continues and now shows that this species is both facultatively apomictic and tetraploid. *Malus sargentii* var. *rosea*, however, is a triploid. When the species is crossed with diploids the sexual progeny are usually triploids. When the variety is crossed with diploids the progeny range from near diploid to approximately tetraploid. In most of the crosses made, facultative apomixis is inherited as a dominant trait.

New hybrids of *Malus*, *Forsythia*, and *Magnolia* species are being propagated for further testing. Induced polyploidy and the induction of mutations by ionizing radiation continue to be used in an attempt to create new ornamental plants.

The work on dwarfing techniques for fruit and ornamental trees and shrubs now shows that knots tied in the stems of apple seedlings curtail growth but do not cause earlier flowering as they do in the case of vegetatively propagated clonal varieties. Further experiments with bark inversions have shown that following bark removal the freshly exposed wood can be induced to form new bark by covering the exposed surface with either polyethylene film or with a non-toxic grease such as lanolin. These techniques should be of value in treating injured trees.

Instruction:

Three staff members offered four regularly scheduled classes within the college and the graduate schools during the year. Dr. Johnston taught his course in the "Phylogeny and Classification of the Flowering Plants" and Dr. Sax gave "Plant Cytology with special reference to Genetics and Taxonomy." Dr. Howard offered two new courses. "Plant Materials" was offered as Landscape Architecture 7–1a in the fall semester and was taught at the Arboretum. During the spring semester a second course, "Principles and Problems of Horticultural Taxonomy," open to undergraduates in the college, was offered through the Department of Biology. The latter course included lectures in Cambridge as well as field and laboratory work on the grounds of the Arboretum in Jamaica Plain as the spring season progressed.

Mr. Tchang Bok Lee, a UNKRA Fellow from Korea, completed the requirements for the degree of Master of Arts under the direction of Dr. Howard and was awarded the degree at the mid-year commencement. Mr. Lee undertook a research program of hybridizing Korean and North American oaks and returned to Korea with seeds of these hybrids for trial. Mr. Lee also spent considerable time reviewing recent forestry literature and checking collections and distributions of trees and shrubs from Korea in the herbaria of the Arnold Arboretum and the Gray Herbarium. Mr. Claud Brown continued his graduate research on pine hybrids with Dr. Sax.

Regularly scheduled seminars on problems of plant taxonomy and plant geography were held in the Harvard University Herbarium during the year. Arboretum staff members took part in these non-credit programs open to undergraduate and graduate students.

Travel and Exploration:

Staff members of the Arboretum did not personally engage in any extensive program of field work during the past year. Small grants from special funds were made to support the work of collectors in foreign countries and to obtain material of value to the work of the Arboretum staff or specimens desired for our collections. Such grants enabled us to obtain seeds of additional ornamental woody plants from Japan, Scotland and Sweden. Herbarium specimens of authentically identified cultivated woody shrubs were obtained from several European gardens by extending nominal financial support.

Miss Lily Perry was granted a leave of absence during the spring to study at several European herbaria. This work was made possible by a grant several years ago to Dr. E. D. Merrill, which was known as the E. D. Merrill Discretionary Fund. It was Dr. Merrill's request that the residue of this fund at the time of his death be made available for Dr. Perry's use and that she use it to further the studies they had begun cooperatively on the flora of New Guinea. Miss Perry has been able to study at the British Museum, Natural History Department and the Royal Botanic Gardens at Kew. Later she will spend some time at Leiden and Utrecht in Holland.

Gifts and Grants:

In this period of continuing inflation there is a great need for gifts for the general operation of the Arnold Arboretum. Happily, the Friends of the Arnold Arboretum have increased in number and in many cases the gifts have also increased in size. During the past fiscal year the Trustees of the Arnold Arboretum, the President and Fellows of Harvard College, increased the book value of the Arboretum endowment funds entrusted to their care. This resulted in an increase in the restricted and unrestricted income from endowment and, in part, met the general increase in wages as well as the increased cost of supplies and materials of the past year. A bequest from the estate of Mrs. Clement Houghton was also added to the endowment.

Gifts for cultural purposes from the Friends of the Arnold Arboretum during the year were used to employ summer labor for care of the living collections on the grounds of the Arboretum at Jamaica Plain and Weston. These funds were also used to supply an assistant in the field of cytogenetics to work with Dr. Sax and an assistant in the greenhouse to help the propagator, Mr. Coggeshall.

The staff has been encouraged to apply to government agencies, private foundations and industry for grants to support research where applicable. A renewed grant from the Atomic Energy Commission was awarded to Dr. Sax for his work on the conduction of materials through the plant and for work on chromosome breakage patterns. Dr. Howard received an award from the National Science Foundation for two years to support morphological work on the vascular pattern of petioles in flowering plants. In both of these cases the awards enabled the recipients to employ technicians to do work which, if carried on otherwise, would have had to be supported by unrestricted funds from the Arboretum endowment. The necessity for such applications and grants will probably increase in the future. Currently only one Arboretum staff member has a research assistant paid from Arboretum funds.

Mr. George Cooley has renewed his support through gifts for taxonomic work under the joint direction of Dr. Rollins, Director of the Gray Herbarium, and Dr. Howard. This special fund has been used to further work on the wild and cultivated vegetation of the southeastern United States leading towards a generic flora of that area.

Publications:

During the past fiscal year the usual twelve numbers of ARNOLDIA were published with Dr. Wyman as editor and four issues of the JOURNAL OF THE ARNOLD ARBORETUM with Dr. Kobuski as editor. There were no special publications during the year.

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Staff of the Arnold Arboretum
1956–1957

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DONALD WYMAN, Ph.D., Horticulturist.

* Appointed jointly with the Gray Herbarium.

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