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

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

Ekman recognized the general nature of the adventitious shoot in the genus Coccoloba and indicated in his field notes the variations from plant to plant and on single plants. Schmidt, in contrast, did not know the plants in the field and failed to appreciate Ekman's comments. As was indicated in an earlier study of the genus Coccoloba in Cuba (Jour. Arnold
Schmidt's failure to recognize adventitious shoots, the dioecious condition in the inflorescence and the nature of the pubescence led him to describe the two sexes of a single species under different names and to assign the adventitious shoots or the parent plants to different species, varieties or forms. Over a period of several years I have had the opportunity of spending several months collecting in the Dominican Republic and in Haiti. During these collecting trips considerable emphasis was given to a field study of populations of the species of Coccoloba. I have made careful collections of young plants, mature plants, adventitious shoots and normal growth, as well as sun and shade foliage, to represent the range of leaf variation both on individual plants and in populations. Not all of the species reported from the island, or in fact, collected by Ekman, could be studied in the field. I believe, however, that the material which I have examined has made the conclusions drawn in this paper more reliable than the previously existing work.

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

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

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

1 I am indebted to the trustees of the American Philosophical Society for a grant from the Penrose Fund which made one of these trips possible. I am also indebted to Mr. George Hamor of Hull's Cove, Maine, formerly of Barahona in the Dominican Republic, for his hospitality and assistance in the course of my field work. My appreciation is also gratefully expressed for the kindnesses and the co-operation given by many officials of the Dominican Republic; by the various officials of Compañía Grenada of the United Fruit Company; by Dr. José de Js. Jiménez and Dr. M. Canela in services of value to this study. I am also grateful to the directors and curators of the herbaria cited in this paper for the long-term use of materials entrusted to their care when various aspects of this problem took extended time.
few species requires the use of complete material, including flowers and fruits. The majority of the species recognized are variable in vegetative characters, as an examination of the species descriptions will verify. The key given is applicable for all of the material which I have examined in fruiting condition and for most of the material when in flower. The key is not applicable in all cases to either sterile mature shoots or adventitious shoots. Abnormal variations on mature and adventitious shoots, such as fasciations, pathological anomalies and contortions have not been included in the key. Such specimens are common in herbaria and have been annotated, but are relatively infrequent in the field.

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

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

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

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

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

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

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

**Key to the Species of Coccoloba in Hispaniola**

A. Perianth lobes exceeding the hypanthium in length, dominant in fruit; ocreolae increasing in size from flowering to fruiting condition; leaves chartaceous to membranaceous, rarely subcoriaceous.

B. Leaves oblong-lanceolate to elliptic, longer than broad, apex acuminate.

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

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

C. leoganensis.

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

C. subcordata.

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

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

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

C. fawcettii.

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

F. Leaves oblong or elliptic.

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

C. flavescens.

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

C. hotteana.

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

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

C. incrassata.

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

C. juertesii.

DD. Leaves not spine-tipped.

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

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

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

C. picardae.

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

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

L. Leaves longer than broad; fruit ovoid.

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

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

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

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

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

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

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

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

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

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

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

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

RR. Leaves dull when dry.

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

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

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

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

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

V. Leaves drying black; petioles arising from above the base of the ocreae; branchlets ferruginously pubescent. .......... C. nodosa.
VV. Leaves not turning black on drying; petioles arising from the base of the ocreae; branchlets pale puberulent. \(\ldots\) \(C. \textit{buchii}\).

UU. Branchlets terete, the nodes not conspicuously swollen.

W. Perianth lobes and achene corona in fruit.

X. Inflorescence rachis 1–2.5 cm. long. \(\ldots\) \(C. \textit{buchii}\).

XX. Inflorescence rachis 10–20 cm. long. \(\ldots\) \(C. \textit{costata}\).

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

Y. Leaves 6 \(\times\) 8 to 13 \(\times\) 18 cm. long and broad or larger; venation not conspicuous; fruit obpyriform, 1.2–2 cm. long. \(\ldots\) \(C. \textit{uvijera}\).

VVV. Leaves 1.1 \(\times\) 1.2 to 2.5 \(\times\) 2.5 cm. long and broad; fruit 3-4 mm. long.

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

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

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

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

b. Fruit coronate. \(\ldots\) \(C. \textit{buchii}\).

bb. Fruit not coronate, perianth lobes imbricate.

c. Leaves ovate, broadest below the middle, cordate at the base. \(\ldots\) \(C. \textit{krugii}\).

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

d. Leaves rounded-truncate to emarginate at the apex. \(\ldots\) \(C. \textit{picardae}\).

dd. Leaves normally apiculate to acuminate, rarely rounded but never subtruncate or emarginate at the apex. \(\ldots\) \(C. \textit{pauciflora}\).

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

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

f. Fruit sub-cornate at the apex; ocreae, petioles and rachises puberulent when young, the hairs generally persisting; leaves of normal shoots generally 7 \(\times\) 5 cm. long and broad or larger; blades dark green when fresh and golden to dark brown when dry. \(\ldots\) \(C. \textit{costata}\).

ff. Fruit not coronate at the apex; ocreae, petioles and rachises glabrous; leaves of normal shoots generally...
4 × 3 cm. long and broad or smaller; leaf blades pale greenish-tan in color when fresh or dry. C. krugii.

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

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

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

h. All parts glabrous. C. diversifolia.

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


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

**Distribution:** Endemic to Haiti.

**Haiti. Depart du Sud:** Massif de la Hotte, Les Roseaux, Nan-Patates, Ekman H-10693 (slectotype, US); Les Roseaux between Nan-Patates and Alnette, Ek-
It is not clear to me whether Schmidt or Ekman compiled the original description of *Coccoloba albicans*. Although the species was published by Schmidt, he gives credit to Ekman for the taxon as a new entity. Various herbarium sheets bear labels indicating as author either Ekman or Ekman and Schmidt. In any case, leaves from fast-growing shoots and those from shoots of normal growth have been combined in the description, with a resulting lack of clarity. The description above distinguishes between the branches which are mature and those which are terminal shoots or adventitious branches. Among the specimens cited are both flowering and sterile adventitious shoots.

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

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

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


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

Local name: Papelite (H).

Distribution: Endemic to Hispaniola.


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

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

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

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

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

Coccoloba buchii is similar in general appearance to C. praecox of Cuba, especially in sterile condition. The two species can be distinguished on the basis of the more tumid nodes, the longer inflorescences, the larger leaves and petioles of C. praecox.
Coccoloba krugii is also similar to *C. buchii*, but the former can be distinguished by the more cordate-ovate leaves, the angular rachis of the inflorescence and the angular fruits.


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

**Distribution:** Endemic to Hispaniola.

**Dominican Republic.** Prov. Trujillo: Llano Costero, Cuenca at La Ceiba, Ekman H-13344 (b-type, s); Llano Costero, El Manielito, Ekman H-14281 (s); Bayaguana at Loma Managua, Ekman H-11108 (s).

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

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


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

**Distribution:** Cuba, Hispaniola, Puerto Rico.

Puerto Plata: La Rosa, Eggers 1762 (b-type of C. verruculosa, k, m, nbv); Sosúa, Ekman H-14459 (s); Puerto Plata, Eggers 2731 (b-type of C. eggersiana, gh, m), Ekman H-14401 (A, s). Prov. Trujillo: Villa Altangracia, Ekman H-11231 (s).

Haiti. Dept. du Nord Ouest: Bombardopolis, EC & GM Leonard 13509 (ny, us). Dept. du Nord: Massif du Nord, Le Borgne, edge of Estere Savate, Ekman H-4855 (b-type of C. samuelssonii, s, us); Massif du Nord, Gros Morne, Morne Bonpère, Ekman H-4944 (s, us), H-8523 (b-type of C. helwigii, s); Massif du Nord, Hinche, Bois Charles, Ekman H-6077 (s, us); Massif du Nord, Bayeux, Morne Brigand, Ekman H-2855 (b, s, us); Massif du Nord, St. Louis du Nord, Morne Baron, Ekman H-4684 (s); Massif du Nord, St. Louis du Nord, between Baron and Rio Jean-Claire, Ekman H-3904 (s). Dept de l'Ouest: Massif des Matheux, l'Arche, Lully to Caye-Nicolas, Ekman H-9287 (a, s, us); Massif des Cahos, Las Caobas, Belladère, Ekman H-5589 (b, s); Ile de la Gonave, Ekman H-8721 (s).

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

The following series of specimens from near Puerto Plata and from the Province of Samaná are referred to Coccoloba costata, but with some question: Prov. Puerto Plata: Sosúa, coral reef at Forma, Ekman H-14460 (s, us). Prov. Samaná: San Lorenzo Bay, Abbott 2237 (b, gh, NY, us); 2245 (us); Samaná, Laguna, Ekman H-15096 (s, us); Los Haitises, Cueva de Cal, Ekman H-15573 (s); Samaná, Laguna, Loma Zaramaguna, Ekman H-15249; Los Haitises, Cayo de los Cueros, Ekman H-15516 (s).

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

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

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

Dominican Republic. Prov. Puerto Plata: Puerto Plata, cliffs facing the sea
at Arroyo Francés, Ekman H-14402 (A, 8).

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


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

Common names: Mainisse (H), raisin marron (H), resinier (H), uvacimarrona, uvero (DR), uvilla (DR), zamon maron (H).

Distribution: Florida, Bahamas, Greater and Lesser Antilles.

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

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


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

**Distribution:** Endemic to the Dominican Republic. Known only from the type collection.
Dominican Republic. Prov. Barahona: Mare-à-chat, Ekman H-6948 (B-type, s).

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

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

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

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

Shrub, often with many trunks, to small tree with single trunk reaching 15 feet in height; bark gray, the youngest branches tan, slightly puberulent, geniculate, the nodes commonly swollen; ocreae membranaceous except at the base, to 3 mm. long, the base cartilaginous, ring-like, the petioles arising from this ring-like base, often appearing terminal due to geniculation of the stem; leaves of normal shoots with petioles 2–5 mm. long, puberulent to glabrous, the blades elliptic, ovate-elliptic or lanceolate-elliptic, 1.6 × 1.2, 3.6 × 1.8, 4.0 × 1.6, to 5.6 × 2.2 cm. long and broad, rigid, flat or slightly umbonate, the apex acute, mucronate, the cartilaginous mucro to 1 mm. long, sharp and stiff, the base rounded to slightly cordate, the margin entire; venation not evident in fresh condition, only slightly evident when dry, the veins 10–20 pairs, equally developed; leaves of adventitious shoots similar in shape, 6.0 × 3.2 to 7.8 × 3.1 cm. long and wide; inflorescence terminal, 2–2.5 cm. long, the rachis glabrous, the bracts to 1 mm. long, slightly erose at the apex, the ocreolae less than 1 mm. long, the flowering pedicels short, those of the staminate flowers less than 1 mm. long, deciduous or rarely persisting and elongating slightly; staminate flowers borne singly at each locus, the hypanthium short, about 0.5 mm. long, the lobes 5 or 6, ovate, 2–3 mm. long, 1.5–2.5
mm. wide, the filaments 1–1.5 mm. long, the pistil rudiment to 2 mm. long; female flowers not seen; fruiting inflorescence stout, 1–4 cm. long, often strongly angled, the peduncles decurrent on the axis; fruit bright red, 4–5 mm. diameter, 6–9 mm. long, broadest at the middle, the apex rounded, the base slightly pedicellate, the perianth segments free to the middle, imbricate over the achene, strongly lined but the vascular bundles not evident.

Distribution: Endemic to Hispaniola.


This is a distinctive species apparently restricted to the dry areas at low elevation. Three leaf forms were seen in the field. The normal leaves were found on the much-branched and geniculate branches. Much smaller leaves were seen occasionally on fasciated lateral branches which are borne on wand-like shoots; see _Ekman H-3499_. Slightly larger than normal leaves are found on shoots of less compact habit, having longer internodes and these are considered to be adventitious shoots. All three habits and leaf sizes are commonly found on one plant. The leaves are rigid even when fresh and the short but sharp mucro is very much in evidence when collecting this species. The leaves when fresh have the characteristic grayish-green color dominant in arid regions of the West Indies. The fruits of _C. flavesens_ are distinctive in shape and in the nature of the perianth in fruit. The fine striations on the lobes of the fruiting perianth seem to be characteristic of this species. Much larger fruits are associated with _Ekman 989_. These appear to be teratological and gall-infested. The few fruits opened were devoid of seed.

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


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

**Distribution:** Endemic to Hispaniola.


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

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

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

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


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

**Distribution:** Endemic to Haiti.


The type collection of this species represented by herbarium specimens from Berlin, Stockholm and the U.S. National Museum comprises nine plant fragments. Normally Erik Ekman collected material of good quality and a single specimen fills an herbarium sheet. It would be interesting to know what happened to this material. The nine specimens of plant material represent sterile mature growth, possible adventitious growth, staminate, flower-bearing branches, pistillate flower-bearing branches and fruiting twigs. One fruit is attached to an inflorescence which appears to be from a staminate plant. Additional fruits in the packet on this sheet are hollow and sterile. The type specimen from the Berlin herbarium consists of three fragments, one pistillate flowering axis, one fruiting axis and one sterile branchlet. In the packet on this sheet are three fruits on which both Schmidt and I have based our descriptions. If the fruit belongs with the specimen, its characteristics are of value in recognizing this species, but I question the authenticity of this fruit.
Coccoloba hotteana appears to be a distinct species. At the present it is known only from a coral reef west of Anse-à-Veau and from Ile Grande Cayemitte. Additional material is much desired. The species can be recognized by the shape and venation of the leaf, the apiculate apex to the leaves and the pubescence on the ocreae and inflorescence rachis.

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

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

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


This hybrid is represented by collections of Ekman and Eyerdam numbered separately but made when these men were travelling together, on the same date and obviously from the same plant. This material in some respects resembles hybrids of Coccoloba uvifera and C. costata recognized from the vicinity of Puerto Plata and some specimens (e.g., Eggers 1762, the type of C. verruculosa) assigned to C. costata as a species. It seems distinct from these and appears to be derived from the parentage of C. uvifera and C. hotteana, both of which occur on Ile Grande Cayemitte. The leaf shape, particularly the nature of the leaf apex and the venation, appears to be derived from C. hotteana. The texture of the leaf, the nature of the inflorescence and the shape of the sterile fruits are those of C. uvifera. The inflorescences are old in the specimens cited above and a few fruits have been retained in packets. The flowering pedicels are borne, 3–5 at each node, on the inflorescence rachis, a character usually associated with staminate plants. As has been pointed out (Jour. Arnold Arb.
staminate plants of *Coccoloba uvijera* often form fruits which are of full size and normal shape but hollow or with aborted seeds or embryos. The fruits associated with the cited specimens resemble those of *C. uvijera*, not *C. hotteana*. They are obovoid, to 1.5 cm. long and 1 cm. in diameter. The fruits are strongly narrowed at the base and rounded at the apex with imbricated perianth lobes. The achene is dark brown and smooth but hollow or with a very small seed and is obviously infertile.

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


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

**Distribution**: Endemic to Hispaniola.


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

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


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

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

Dominican Republic. Prov. Monte Cristi: El Morro, Ekman 13143 (s), R.A. & E.S. Howard 12532 (gh), 12534 (gh), Jiménez 1356 (A).

Haiti. Dept. Du Nord Ouest: Isle Tortue, Morne Barranca, Ekman 4314 (B-type of C. borgesentii, s, us); Port au Paix, Vallée des Trois Rivières, Ekman 3588 (B-type of C. borgesentii forma ovato-lanceolata, s, us); Port au Paix, E.C. & G.M. Leonard 15252 (A, gh, s, us).

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

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


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

**Distribution:** Puerto Rico, Virgin Islands, Hispaniola.

Dominican Republic. Prov. Monte Cristi: Los Siete Hermanos, Howard 12524 (GH), 12525 (GH), 12526 (GH), 12527 (GH), 12528 (GH), 12529 (GH); Ekman H-13164 (s, US).


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

Ekman first discovered one population in 1925 on Île de la Tortue and suggested in his field notes that it was a new species related to *Coccoloba uvifera*. A few days later he encountered it again along the sea coast west of Saline Michel near Port de Paix and indicated in his field notes that while sterile it was not the same as the Tortue plant and that it was “not *C. uvifera*, by no means.” Schmidt annotated these specimens as *C. verruculosa* Lindau; Leonard, who collected in the same areas, also found the plant and used the same species identification. In 1929 Ekman visited Monte Grande in the Los Siete Hermanos island group off Monte Cristi and collected the plant there. In his field notes he identified the plant as *C. verruculosa* again, but comments, “I am beginning to feel suspicious about this. It is altogether too widely distributed and common to have escaped notice of the old collectors; e.g., Jacquin. How about
In a brief published report of this last island trip, Ekman refers to the occurrence of "Coccoloba scandens" on Monte Grande. *Coccoloba scandens* is published without description and, in any case, is a later homonym of *Coccoloba scandens* Benth., also a nomen nudum. The epithet "scandens" however was particularly appropriate, for several of the plants seen on Monte Grande had scrambling branches. As was true with populations of this hybrid in Puerto Rico and the Virgin Islands, there is a considerable range of variation between plants, accentuated in some cases by the normal variation between adventitious and juvenile shoots and those of more mature plants.

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


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

**Local names:** Uvero (DR), uvilla (DR).

**Distribution:** Endemic to Hispaniola.


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

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

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

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

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

Perhaps the most unusual feature of Coccoloba leoganensis is the size of the leaves produced by lateral and adventitious shoots. Root sprouts and lateral stem sprouts were found on a number of trees near Bani in the Dominican Republic. This was the largest stand of C. leoganensis seen and here the species was the dominant tree in the dry thorn-shrub region at kilometer 80. The sprouts produced near the base of the trunk and on the trunk of these trees were short, compacted and contorted, in contrast to the normal elongate, fast-growing trunk sprouts of other species. In addition, the leaves are exceedingly small, ranging in size from 4 × 4 mm. to 12 × 15 mm. on petioles 2–3 mm. long. The leaves of these sprouts were generally orbicular and rounded at the apex, although some were ovate and obtuse at the apex. These sprouts all resembled C. subcordata. Careful attention was required to determine that these were parts of the plant of C. leoganensis. Even now, in dealing with the herbarium specimens, it has been necessary to recheck field notebooks to make certain that this point had been determined in the field and that the labels were not in error. Several of Leonard's collections (12071, 11820 and 14603) posed the same problem, although they had leaves grading to a larger size. In all of these collections, the petioles arise from the base of the ocreae, as in C. leoganensis, and not from the apex of of the ocreae, as in C. subcordata. Coccoloba subcordata has an entirely distinct habit in the field and has short inflorescences, but in sterile herbarium specimens that two may well be confused. This is the only species of Coccoloba so far encountered in which the leaves of the sprout shoots are smaller instead of larger than the leaves of mature branches.
Coccoloba leonardii Howard, Jour. Arnold Arb. 30: 419. 1949.

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

Distribution: Haiti and Cuba.


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


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


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

**Distribution:** Endemic to the Dominican Republic.

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

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

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


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

**Distribution:** Endemic to Hispaniola.

**Dominican Republic. Prov. Barahona:** El Aguacate to crest on road to

Haiti. Dept. du Nord Ouest: Massif du Nord, Port de Paix, Haut Piton, Ekman H-3697 (b, s, us); Bassin Bleu, Morne Haut Piton, E.C. & G.M. Leonard 15043 (a, gh, us), 15046 (m, ny, us), 15064 (us). Dept. du Nord: Massif du Nord, Bayeux, Morne Brigand, Ekman H-2855 (s, us). Dept. de l’Artibonite: Ennery, Puilboreau Pass, Leonard 9145 (b, gh, ny, us-type of C. fulgens); Massif du Nord, Gros Morne, Morne Belance, Buch 811 (type of C. mornicola), Ekman H-4910 (s). Dept. du Sud: Massif de la Hotte, Nouvelle Touraine, Ekman H-1657 (a, s). Dept. de l’Ouest: Massif de la Selle, Morne Tranchant near Godet, Ekman H-1953 (s); Massif de la Selle, Petionville, Ekman H-1657 (us); Massif des Matheux, Grand-Bois, Cornillon, Ekman H-5686 (s, us); Massif de la Hotte, Petit Goave, road to Morne Calumette, Ekman H-7304 (s); Fond Verettes, Leonard 5347 (b-type of C. neurophylla, us).

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

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

Leaf variation is considerable, both within a population and on the same plant, as to size, texture and apex. The shape of the leaf apex is related either to the development of the midrib or to its failure to develop at the apex. Three conditions are found on different plants, or on the same tree on one branch, or on different branches: (1) the midrib can be uniformly developed to the apex, in which case the tip of the blade is acuminate; (2) the midrib may apparently fail to develop at the apex of the blade, in which case this area is vascularized by the upper pair of primary veins; or (3) a remnant of the midrib may be present or absent. In this situation the apex of the leaf is obtuse or rounded.
In the third condition observed, the midrib fails to develop to the tip of the blade and one of the upper pair of primary veins dominates the other. In this case the leaf apex is asymmetrical. Examples of the three types of leaf apices on one plant are found in the collections of Ekman H-2853, H-1657 and Howard 12586, the latter collected especially for this purpose.

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

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

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

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

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

**Distribution:** Endemic to Hispaniola.

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

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

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


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

**Coccoloba rubescens** L. Sp. Pl. ed. 2. 523. 1762.
Coccolobis pubescens Sandwith, Jour. Bot. 78: 98. 1940.
Coccolobis antiguenis Sandwith, Jour. Bot. 78: 98. 1940.

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

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


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

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


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

**Distribution:** Endemic to Hispaniola.

**Dominican Republic.** Prov. Samaná: Los Haitises, Boca del Infierno, *Ekman H-15392* (s); Samaná, slopes of Pan de Azúcar, *Ekman H-15175* (a, b-type, s, us), *H-15095* (s); Samaná, Laguna, Los Bañaderos Prietos, *Ekman H-15125* (s).

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


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

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

**Distribution:** Endemic to Hispaniola.


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

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

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

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


*Coccoloba swartzii* var. (?) portoricensis Meisner, DC. Prodr. 14: 160. 1856.
*Coccoloba diversijolia* Lindau, Symb. Antill. 1: 223. 1899, and most recent authors, not Jacquin.

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

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


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

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

Polygono·num uvifera L. Sp. Pl. 365. 1753.

Guaiabara uvifera House, Amer. Midl. Nat. 8: 64. 1922.

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

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


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


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


Haiti. Dept. du Sud: Miragoane, Eyerdam 397 (GH, NY, US); Anse à Veau, Picarda s.n. (GH).

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

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

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

While the suggested hybrid origin of Coccoloba antiguenensis Sandwith from Antigua has been rejected and that species referred to the synonymy of C. pubescens, there is no doubt in my mind as to the valid nature and the origin of the present hybrid. The hybrid nature of this collection is obvious in the field and equally so in the specimens cited.
The other hybrid plants and populations involving *Coccoloba uvifera* considered in this paper are *C. costata × C. uvifera*, *C. hotteana × C. uvifera* and *C. krugii × C. uvifera*.

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

*Uvifera arbor americana*, fructu aromatico punctatus, Plak. Alm. 394, t. 237, fig. 4. 1696, as to leaf only.


**Gnaiabara venosa** House, Amer. Midi. Nat. 8: 64. 1922, as Gualbara.

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

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


**Haiti**. **Dept. du Nord Ouest**: Ile de la Tortue, La Vallée, Ekman H-9758 (s, us). **Dept. du Nord**: Massif du Nord, Port Margot, Bayeux, Ekman H-2699 (s, us). Without specific location: Sesse & Mocino 952 (f), 5431 (f).
Shrub or small tree to 21 feet tall; branches terete, the nodes not swollen, glabrate; ocreae membranaceous, 4–6 mm. long, puberulent to tomentose or glabrate; leaves of normal shoots with petioles 4–7 mm. long arising from the bases of the ocreae, the blades ovate, elliptic, obovate or rarely ovate-lanceolate, 5 × 2.5, 8 × 4, 10 × 7 to 11 × 10 cm. long and wide on mature shoots, coriaceous, umbonate between the veins, shining above when young but dull on both surfaces when mature, the apex acute to abruptly short acuminate or truncate, the base narrowed to obtuse, usually slightly oblique, the primary veins 4–6 pairs, arcuate, impressed above, conspicuous below, the lower surface more or less dotted with stomatal excretions; adventitious shoots with ocreae to 2 cm. long; leaves with petioles 2.5 cm. long, the blades broadly ovate to elliptic, 15 × 14 to 20 × 17 cm. long and broad, the apex of these leaves rounded to obtusely short mucronate, the bases rounded to subcordate; inflorescences terminal, 3–10 cm. long, the rachis pubescent or with resinous excretions, the bracts ovate, to 0.5 mm. long, the ocreoleae membranaceous, 1 mm. long, the flowering pedicels 1 mm. long, increasing in length either in fruit or after staminate flowers have fallen to 3 mm.; staminate flowers 2–3 per locus, the pistillate flowers borne singly at each locus; hypanthium to 1 mm. long, the perianth lobes 1–1.5 mm. long and broad, the fertile stamens united at the base for 1 mm., the free portions 0.5–1 mm. long, the sterile stamens less than 1 mm. long, the functional pistil to 2 mm. long; fruit ovoid, slightly contracted at the base, rounded but only slightly coronate at the apex, 7–9 mm. long, 4–5 mm. in diameter.

**Distribution:** Cuba and Hispaniola.


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

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

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

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

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DOI: https://doi.org/10.5962/bhl.part.19109
Permalink: https://www.biodiversitylibrary.org/partpdf/19109

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