STUDIES IN THE GENUS COCCOLOBA, VII. A SYNOPSIS AND KEY TO THE SPECIES IN MEXICO AND CENTRAL AMERICA

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The only complete monograph of the genus *Coccoloba* was prepared by Gustav Lindau and published in Engler's Botanische Jahrbücher 13: 106–229. 1890. Since that time many additional species have been described in the genus as the result of extensive collecting by botanists in Mexico and in the several countries of Central America. Paul Standley revised *Coccoloba* as it occurs in Mexico in his treatment of the trees and shrubs of Mexico published in 1922. More recently Standley with Julian Steyermark treated the species of Guatemala as part of their series of papers on the flora of Guatemala. In addition, lists of species, some with critical notes, will be found in the following papers. Other papers and citations are included in the text.

- ALLEN, P. Preliminary index to the trees of the Golfito-Palmar area, Costa Rica. 37, 1952.
- Smith, J. D. Enumeratio plantarum Guatemalensium 6: 36. 1903.
- STANDLEY, P. C. Flora of the Panama Canal Zone. Contr. U.S. Nat. Herb. 27: 170. 1928.
- Flora of Yucatan. Publ. Field Mus. Bot. 3: 252-253. 1930.
- ——. Flora of the Lancetilla Valley, Honduras. Publ. Field Mus. Bot. 10: 180–181. 1931.
- —. Flora of Costa Rica. Publ. Field Mus. Bot. 182: 413-414. 1937.
- and S. Calderón. Lista preliminar de las plantas de El Salvador. 98. 1925.
- and S. J. RECORD. The forest and flora of British Honduras. Publ. Field Mus. Bot. 12: 125-127, 1936.
- YUNCKER, T. G. A contribution to the flora of Honduras. Publ. Field Mus. Bot. 17: 361, 1938.
- ——. Flora of the Aguan Valley and the coastal regions near La Ceiba, Honduras. Publ. Field Mus. Bot. 9: 286. 1940.

In general, the genus *Coccoloba* has been overdescribed in Mexico and Central America. Of the eighty names which have been applied in published form, only thirty-three species are recognized in this paper. In large part this tendency to excessive description is due to floristic treatments which deal individually with the many small countries of Central America. Many species which were considered endemic in adjacent countries have proved to be identical instead. Several West Indian species are now recognized in the Central American flora and the corresponding Central American name has been reduced to synonymy. Seven species had been described on the basis of sterile branches from adventitious shoots. All of these have now been associated with fertile material and these names placed

in synonymy. Fortunately only one such name had to be retained with a sterile holotype specimen. The failure to recognize the unisexual condition of the plants led to the duplication of specific names and several such species have now been properly associated. Two new species are described and one species has been removed from synonymy and re-established at the species rank.

Lindau in his monograph treated the species from Mexico and Central America in three sections of the genus. While these sections are useful in a preliminary assignment of species within the genus, the sections can not be maintained. When sufficient material is examined, intermediates are

found and the sections grade indistinguishably into one another.

In the previously published studies ¹ of the genus *Coccoloba* in the West Indies I had the advantage of extensive field work and an intimate knowledge of the variation found in the living plant. Much of the information gained in studying the West Indian species has been applied to the current

study.

Many of the experienced field botanists who have described species of Coccoloba in Mexico and Central America have regarded the flowers as being perfect. The extensive group of herbarium specimens I have seen, as well as the living plants I have studied in Mexico and Honduras, clearly indicates, however, that the flowers are unisexual or functionally so. The pistillate flowers are normally borne singly at each nodule of the inflorescence rachis or rarely in clusters of two or three. The stamens of such flowers are rudimentary and included. The staminate flowers with pollen-producing, exserted stamens are borne in clusters of three or more.

Only a few species of Mexico and Central America have heavily coriaceous leaves or leaves much reduced in size. The leaves tend to be more pubescent than those of West Indian species. The variation in size between leaves of normal shoots and/or adventitious shoots is similar in the West Indies and in Central America. The leaves of adventitious shoots are larger, thinner and on longer petioles than those of normal shoots. Short-shoots, or at least shoots of limited growth, occurring laterally on the branches may also produce leaves smaller in size than those of shoots

of normal growth. Pubescence varies with age of the leaf.

An adequate understanding of the species is best obtained from a study of staminate and pistillate flowers, fruits and leaves from both normal and adventitious shoots. I am grateful to the several collectors indicated in the text who made special efforts to get complete material for me. I have also been fortunate to be able to study nearly all the types of the species considered in this paper. I am particularly grateful to the directors and curators of the Botanisches Museum, Berlin; the Jardin Botanique de l'État, Brussels; the Royal Botanic Gardens, Kew; the Chicago Natural History Museum, Chicago; the Botanische Staatssammlung, Munich; and the University Herbarium, University of Michigan, Ann Arbor, for the significant materials sent for this study. Equally valuable but less authen-

¹ Jour. Arnold Arb. 30: 388-424. 1949; 37: 317-339. 1956; 38: 81-106. 1957; 38: 211-242. 1957; 39: 1-48. 1958; 40: 68-93. 1959.

tic specimens were received on loan from the other herbaria designated by the standard abbreviations given in Index Herbariorum.

Distribution of recognized species of Coccoloba in Mexico and Central America

	GREATER ANTILLES	MEXICO	GUATEMALA	BR. HONDURAS	EL SALVADOR	HONDURAS	NICARAGUA	COSTA RICA	PANAMA	SOUTH AMERICA	LESSER ANTILLES
acapulcensis		×	X	×		×		×			
acuminata			X			X	X	×	\times		
barbadensis		X	\times		X						
belizensis			X	X		X	X				
caracasana		X	X		X		X	X	X		
chiapensis		X				X					
cozumelensis		X	X	X			X				
darienensis									X		
diversifolia	X	X	×								
goldmannii		X									
hondurensis		X	X	X		X					
humboldtii		X									
lasseri									X		
lehmannii								X	X	X	
liebmannii		X									
lindeniana		X									
lindaviana						X					
× lundellii				X							
manzanillensis									X		
matudai		X									
montana		X	X	X	X						
nicaraguensis			0.00				X				
novogranatensis			X						×	X	X
obovata								X	×	×	
padiformis								×	×	X	
parimensis									×	X	
reflexiflora		X	X	X		X					
spicata		X		×							
standleyana								X			
swartzii	×			×		X					X
tuerckheimii			X			×	X	X	×		
uvifera	X	X	X	X	X	X	X	X	×	X	X
venosa	X	X	X		X	X	X	X		X	X

The following list contains the names used for species of *Coccoloba* in Mexico and Central America. These names either were used in floras, lists or monographic treatments or apply to taxa based on specimens collected

in this area. The generic name *Coccoloba* has been conserved. *Coccolobis* is regarded as an orthographic variant and all binomials published under this spelling are also known as *Coccoloba*. The many transfers made by Otto Kuntze to the genus *Uvifera* have been omitted. All of the names in this list are discussed in the text under the recognized specific name. Varieties which are treated as distinct from the species are listed below. Varieties not listed are transferred with the species.

Campderia floribunda = Coccoloba venosa

- C. lindeniana = Coccoloba lindeniana
- $C.\ mexicana = Coccoloba venosa$
- C. nematostachya = Coccoloba manzanillensis

Coccoloba acapulcensis Standley

- C. acuminata HBK.
- C. alagoensis major = C. venosa
- C. allenii = C. lehmannii
- C. anisophylla = C. chiapensis
- C. barbadensis Jacquin
- C. belizensis Standley
- $C.\ bracteolosa = C.\ parimensis$
- C. browniana = C. acapulcensis
- C. cardiophylla = C. acapulcensis
- C. caracasana Meisner
- C. changuinolana = C. lehmannii
- C. chiapensis Standley
- C. colonensis = C. reflexiflora
- $C.\ coronata = C.\ spicata$
- C. corozalensis = C. swartzii
- C. cozumelensis Hemsley
- C. darienensis Howard
- C. diversifolia Jacquin
- C. emarginata = Neomillspaughia emarginata (Gross) Blake
- C. escuintlensis = C. montana
- C. excelsa glabra = C. parimensis
- $C.\ excoriata = C.\ venosa$
- $C.\ floribunda = C.\ venosa$
- C. fluviatilis = C. barbadensis
- C. gentlei = C. swartzii
- C. goldmannii Standley
- C. grandifolia Standley = C. liebmannii
- C. guatemalensis = C. tuerckheimii
- C. hirsuta = C. belizensis
- C. hondurensis Lundell
- C. humboldtii Meisner
- C. jurgenseni = C. barbadensis
- $C.\ lancifolia = C.\ diversifolia$
- C. lapathifolia = C. liebmannii
- C. laurifolia = C. diversifolia

Coccoloba lasseri Lundell

- C. latifolia = C. tuerckheimii
- C. lehmannii Lindau
- C. leptostachya = C. barbadensis
- C. liebmanni = C. liebmannii
- C. liebmannii Lindau
- C. lindaviana Howard
- C. lindeniana (Bentham) Lindau
- C. lundellii = C. × lundellii
- C. × lundellii Standley
- C. macrophylla = C. rugosa
 Desfontaines
- C. manzanillensis Beurling
- C. manzinellensis = C. manzanillensis
- $C.\ marginata = C.\ hondurensis$
- $C.\ masoni = C.\ barbadensis$
- C. matudai Lundell
- $C.\ mayana = C.\ barbadensis$
- $C.\ molinae = C.\ venosa$
- C. montana Standley
- $C.\ nematostachya = C.\ manzanillensis$
- C. nicaraguensis Standley & L. Williams
- C. nivea = C. venosa
- C. novogranatensis Lindau
- $C.\ oaxacensis = C.\ barbadensis$
- C. obovata HBK.
- C. orizabae = C. humboldtii
- C. padiformis Meisner
- C. parimensis Bentham
- C. petrophila = C. humboldtii
- C. pubescens = C. liebmannii
- C. roseiflora = C. padiformis
- C. reflexiflora Standley
- C. riparia = C. obovata
- C. sessiliflora = C. barbadensis
- $C.\ schiedeana = C.\ barbadensis$
- C. schippii = C. montana
- C. spicata Lundell
- C. steyermarkii = C. montana
- C. standleyana Allen
- C. strobilulifera = C. acuminata
- C. suborbicularis = $C. \times lundellii$
- C. swartzii Meisner

Coccoloba tuerckheimii Donnell Smith C. umbilicata = C. pyrifolia

Desfontaines

C. uvifera Linnaeus

C. venosa Linnaeus

Coccoloba waittii = C. novogranatensis
C. wercklei = C. acapulcensis
C. yucatana = C. cozumelensis
Uvifera lehmanni = Coccoloba

The following is a synoptic key to the species of Mexico and Central America. To be fully applicable, the key requires both flowers and fruit. It does not apply to sterile material, particularly that of adventitious shoots.

lehmannii

Following the key, the species are listed in alphabetical order with a citation of specimens seen and a discussion of the nomenclature adopted. The countries are considered in order from north to south, with the states, provinces, districts, etc., in each country being listed alphabetically.

KEY TO THE SPECIES

1. Petioles arising from above the base of the ocrea, the diameter of the leaf scar smaller than the distance from the base of the leaf scar to the base of the ocrea.

- 2. Inflorescence paniculate.
 - 3. Inflorescence branches few; leaf base rounded or cordate; fruit spherical, rounded at the base. C. lasseri.
 - 3. Inflorescence many-branched; leaf blade acute at the apex, the base decurrent on the petiole; fruit oval, stalked at the base.

- 2. Inflorescence racemose or spicate.
 - 4. Inflorescence racemose.
 - 5. Leaves narrowly oblong to narrowly elliptic. . . . C. lindaviana.
 - 5. Leaves cordate, elliptic or obovate-elliptic.
 - 6. Leaves cordate, the base strongly cordate, occasionally peltate; flowering and fruiting pedicels 5-15 mm. long; fruit globose, 1 cm. diameter, or abnormally obovoid and 2.5 cm. long; ocreae splitting longitudinally, flaring, the petiole appearing winged at the base; the inflorescence ocrea often appearing spathe-like.

6. Leaves elliptic to obovate-elliptic, flowering and fruiting ped-

icels shorter; ocrea not flaring if split.

- 7. Leaves usually narrowed to a cordate-auriculate base; ocreolae conspicuous, papery, flaring; flowers never reflexed; fruit globose, conspicuously coronate. . . C. novogranatensis.

4. Inflorescence spicate, the fruits essentially sessile.

8. Leaves tan-colored when dry, the petioles usually grayish green; leaf blades acute to obtuse at the apex; fruit globose, obtuse at the apex.

C. spicata.

- 1. Petioles arising from the base of the ocrea, the base of the leaf scar at or close to the base of the ocrea.

- 9. Inflorescence paniculate.
 - 10. Flowering pedicels stout, not exceeding the ocreolae; young stems, ocreae and inflorescence rachis conspicuously puberulent or tomentose to pilose on adventitious shoots, the pubescence golden or chest-nut-colored; the terminal buds large, conspicuously club-shaped, swollen and rounded at the apex, the ocrea of the terminal bud commonly subcalyptrate; fruit globose, not narrowed to a stalk at the base, obtuse or rounded, not coronate, at the apex. C. belizensis.
- 9. Inflorescence racemose or spicate.
 - 11. Inflorescence racemose; the flowers and fruits borne on pedicels which exceed the bracts and the ocreolae.
 - 12. Lianas; leaf blade umbonate between the veins. . . C. parimensis.
 - 12. Trees or shrubs, at most the ends of the branches rarely scrambling.
 - 13. Leaves as broad as or broader than long, orbicular to broadly oblong, apex rounded to emarginate.
 - 14. Fruits 1-2.5 cm. long, obtuse or rounded at the apex, at most very slightly coronate, usually slightly stalked at the base.

 - 15. Leaves usually orbicular, the base of the blade essentially rounded or obtuse. $C. \times lundellii$.
 - 14. Fruits less than 1 cm. long.
 - 16. Fruit strongly coronate at the apex, the base rounded; leaf blades persistently pubescent only along the midrib and primary veins or glabrate.

C. barbadensis hybrid.

16. Fruit elongate, the perianth lobes distinct on the upper 1/3 or 1/2 of the fruit; leaf blades persistently pubescent on the lower surface.

C. goldmannii.

- 13. Leaves noticeably longer than broad.
 - 17. Leaves elliptic-lanceolate in outline, acuminate to long-acuminate at the apex, cuneate or rounded to an obtuse asymmetrical base; petioles 2-6 mm. long.

C. chiapensis.

- 17. Leaves not of this type.
 - 18. Foliar ocreae 3-5 cm. long, membranaceous or

18. Foliar ocreae 1-2 cm. long, coriaceous, or if chartaceous, not silky pubescent.

- 19. Achene surrounded by the expanded perianth lobes, these free nearly to the base.

 - 20. Leaves narrowly oblong or obovate-oblong, the inflorescence of closely associated flower clusters and these not clearly distinct on the rachis and not appearing interrupted.
 - 21. Leaves obovate-oblong. broadest above the middle; midrib and veins usually pubescent below, blades persistently barbate in the axils of the primary veins. C. venosa.
 - 21. Leaves narrowly oblong, broadest at middle; leaves glabrous below.

C. darienensis.

- 19. Achene surrounded by the expanded hypanthium, the perianth lobes coronate or surrounding the upper third of the achene.
 - 22. Fruit conspicuously coronate.
 - 23. Leaves lanceolate-ovate in outline, ocreae glabrous; pedicels in fruit several times as long as the thickness of the inflorescence rachis.

..... C. diversifolia.

- 23. Leaves broader, ovate-oblong to obovate-elliptic in outline, ocreae puberulent; fruiting pedicels not longer than the thickness of the inflorescence rachis.
 - 24. Fruiting pedicels shorter than the ocreolae; leaves usually rounded or with a short, bluntly acute apex, concolorous.

- 24. Fruiting pedicels slightly longer than the ocreolae; leaves usually with a short but sharply acuminate apex, dark or black on the upper surface and lighter below. C. hondurensis.
- 22. Fruit obtuse at the apex, the perianth lobes imbricate over the obtuse apex of the achene.

25. Leaves persistently pubescent below, the margin entire but usually conspicuously crispate to undulate. C. liebmannii. 25. Leaves glabrous, the ocreae or petioles puberulent or glabrous, margin of the blade entire or flat or slightly recurved but not crispate-undulate. 26. Ocreolae conspicuous in flower and fruit, membranaceous and flaring; fruit as broad as or broader than long, rounded to slightly stalked at the base, slightly acute at the apex. 26. Ocreolae small and inconspicuous, appressed and not flaring; fruit longer than broad, rounded or obtuse at the apex and the base. 27. Upper leaf surface with the ultimate venation conspicuuously reticulate when dry, the ocreae and petioles puberulent. C. humboldtii. 27. Upper leaf surface plain between the primary veins, the ultimate venation not evident; ocreae and petioles glabrous. C. padiformis. 11. Inflorescence spicate, the pedicels shorter than the bracts and ocreolae in flower and fruit or, if protruding beyond the ocreolae, the visible portion less than the diameter of the inflorescence axis. 28. Inflorescence rachis swollen at the flower clusters and tapering below them, the flowers appearing at an acute angle to the axis; the lobes of the perianth expanded in fruit and covering at least 28. Inflorescence rachis of uniform thickness and not expanded to each flower cluster, the flowers borne flat or at right angles to the axis. 29. Ocreolae conspicuous in flower and fruit, membranaceous or chartaceous. 30. Leaves narrowly oblong, acute to acuminate at the 30. Leaves broadly oblong to orbicular, often broader than long, the apex rounded or emarginate; the lobes of the perianth expanded in fruit and covering more than 29. Ocreolae small, not conspicuous in flower or fruit; the

hypanthium surrounding the achene in fruit, the perianth lobes imbricate or coronate.

- 31. Leaves rounded or obtuse at the base, acute or obtuse at the apex, the blades turning dark on drying, the petiole almost black when dry; glabrous (in Central America).

Coccoloba acapulcensis Standley, Proc. Biol. Soc. Wash. 33: 66-67. 1920.

Coccoloba cardiophylla Standley, Publ. Field Mus. Bot. 8: 8: 1930. Coccoloba browniana Standley, Trop. Woods 10: 4. 1927. Coccoloba wercklei Standley, Publ. Field Mus. Bot. 4: 304. 1929.

It is unfortunate that the oldest name applicable to this species is based on anomalous material. To the present, Coccoloba acapulcensis has been distinguished by the peltate leaves and the large fruits. The collections cited below, made since the type collection of the species, show clearly that leaves with peltate, cordate or rounded bases may be found on the same shoot. Miranda (Anal. Inst. Biol. México 14: 29. 1943) reports that peltate leaves appear abundantly on all young specimens of C. acapulcensis but that the cordate base is more frequent on older plants. The fruits of this species are larger than is usual in the genus Coccoloba; however, the fruits of the holotype appear to be abnormal, the probable result of an insect attack. Similar abnormal pedicels also occur on the type specimens of the other species which I have examined and which I now consider to be synonymous with C. acapulcensis.

Lundell (Lloydia 2: 83. 1939) placed Coccoloba cardiophylla in the synonymy of C. browniana and reported the affinities of the species to be with C. wercklei, of Costa Rica, and C. acapulcensis, of Guerrero, Mexico. In the original description of C. wercklei Standley suggested that his new species is a relative of the Honduran C. browniana but distinct from it in that C. browniana bears pedicels only 5 mm. long. The series of specimens cited, however, shows the full range of variation in the length of the pedicel between flowering and mature fruiting conditions, as well as the differences

in the pedicel length of the male and female flowers. It is clear to me that all four species must be grouped together under the oldest accepted name, which is *C. acapulcensis*.

México. Guerrero: Acapulco, MacDaniels 249 (f), Haenke 1120 (f), 1125 (F), Palmer 399 (us-type of C. acapulcensis; GH, NY); Tecpán de Galiana, Hinton 14118 (F, GH). YUCATÁN: Chichén Itzá, Bequaert 28 (A, F), C. L. & A. A. Lundell 7471 (DS, F, MICH), 7513 (A, DS, F, MICH); Kancabdzonot, Gaumer & sons 23865 (DS, F, GH), 23905 (F); Quintana Roo, C. L. & A. A. Lundell 7644 (MICH); Ebtún, C. L. & A. A. Lundell 7534 (A, DS, F, MICH); without specific location, Gaumer 24013 (F-type of C. cardiophylla; A, GH). Guatemala. EL Progresso: Barranquilla, Steyermark 46428 (F). Huehuetenango: Between Democracia and canyon of Chamusú, Steyermark 51229 (F); Paso del Boquerón, Stevermark 51152 (F). JUTIAPA: Quebrada above Ovejero, Standley 77647 (F). British Honduras. Orange Walk District: Honey Camp, Lundell 514 (A, DS, F, GH). Honduras. Comayagua; Comayagua, Standley & Chacón 5126 (F), 5383 (F), 5484 (F), 6012 (F); El Banco, Rodriguez 2374 (F, GH); Río Selguapa, Rodriguez 2616 (F, GH); Siguatepeque, Yuncker, Dawson & Youse 6138 (F, GH, MICH). Yoro: Coyoles, Yuncker, Koepper & Wagner 8071 (F, GH, MICH); Olanchito, Record & Kuylen H-54 (US-type of C. browniana; GH, Y). Costa Rica. El Coyolar, Wercklé s.n. (us 865109-type of C. wercklei); San Pedro de San Ramón, Brenes 21872 (F).

Coccoloba acuminata HBK. Nov. Gen. 2: 176. 1817.

Coccoloba acuminata var. pubescens Lindau, Bot. Jahrb. 13: 193. 1890. Coccoloba acuminata var. glabra Lindau, l.c. 194. Coccoloba strobilulifera Meisner, Fl. Bras. 5(1): 25. 1855.

Lindau was correct in concluding that *Coccoloba strobilulifera* Meisner is the same as *C. acuminata*. I have examined the specimens cited by Meisner and Lindau and have also seen this species in the field. On the basis of these observations, I find it impossible to recognize the two varieties that Lindau established on a characteristic of the pubescence. The variation in the amount of pubescence seems to be related to the age and vigor of the plant. Pubescence is present on the young leaves and shoots but is less conspicuous, or the hairs are broken off so that only the clear hair bases remain, on older specimens. Certainly all intermediate stages can be found between the material cited by Lindau as *C. acuminata* var. *pubescens* and that cited as var. *glabra*.

In addition to the material cited below, I have seen collections from Colombia, Venezuela, British Guiana, Brazil, Ecuador and Peru. The type is *Humboldt 1479*, collected along the Río Magdalena, near Mompox, Colombia. Lindau did not select a type for his var. *glabra*, but the type of *C. strobilulifera* Meisner is *Moritz*, without number and without definite locality in Colombia. Lindau places this species in synonymy under his var. *glabra*.

Guatemala. Izabal: Quebradas, Pittier 8592 (GH); between Bananera and Sioux Station, Steyermark 38986 (F, MICH). Honduras. Atlántida: Near Tela, Mitchell 82 (F, GH); near Tela, Standley 54710 (A, F); La Fragua, Standley

55720 (F); vicinity of Tela, Standley 56867 (F); vicinity of San Alejo, Standley 7771 (F); between Tela and Lancetilla, Yuncker 4645 (A, F, GH, MICH). CORTÉS: La Lima, Johansen 45 (A, F); Río Piedras near San Pedro Sula, Molino 3417 (F); La Lima, Standley & Chacón 7556 (F), Williams & Molina 12485 (F). Yoro: Near Progresso, W. D. Hottle 1 (F), Record & Kuylen H-44 (GH), Standley 55013 (A, F); Coyoles, Yuncker, Koepper & Wagner 8034 (F, MICH), 8061 (F, GH, MICH). Department unspecified: Coyol, Carleton 495 (A, GH); Highland Creek, Pto. Sierra, Wilson 84 (F). Nicaragua. Zelaya: La Esperanza, Río Grande, Molina 2109 (F), 2136 (F, GH). Department unspecified: Region of Braggman's Bluff, Englesing 183 (F, Y), 229 (F, Y). Costa Rica. ALAJUELA: Vicinity of Capulin, Rio Grande de Tárcoles, Standley 40189 (F). PUNTARENAS: Canton de Osa, Palmar Norte to Cañablancal, Allen 5226 (GH. MICH). Panamá. CANAL ZONE: Barro Colorado Island, Aviles 74, 976 (F), L.H. & E.Z. Bailey 616 (GH), Bangham 378 (A, F), Starry 223 (F), Wilson 22, 140 (F), Woodworth & Vestal 397 (A, F); Juan Mina, Chagres River, Bartlett & Lasser 16321 (MICH); Gamboa Reach, Maggs II 39 (F); Frijoles, Maxon 4707 (F, GH); Gamboa, Pittier 2608 (F, GH, MO); Upper Chilibre River, Seibert 1510 (MO); Quebrada Bonita, Stevermark & Allen 17194 (MICH, MO). DARIEN: Tucuti, Chepigana, M. E. & R. A. Terry 1381 (A, F. Mo); Yape, Allen 850 (F. GH. Mo); location unspecified, MacBride 2676 (F). Province unspecified: Maume & Gorgone. Wagner s.n. (M); Marraganti. Williams s.n. (NY). Location unspecified: Weddell s.n. (GH, P).

Coccoloba barbadensis Jacquin, Enum. 36, 1760, Obs. Bot. 1: 18. pl. 8. 1764; Howard, Jour. Arnold Arb. 37: 317-339, 1956.

Coccoloba barbadensis var. mexicana Meisner, DC. Prodr. 14: 153. 1856.

Coccoloba schiedeana Lindau, Bot. Jahrb. 13: 187. 1890.

Coccoloba jurgenseni Lindau, Bot. Jahrb. 13: 188. 1890.

Coccoloba leptostachya Bentham, Bot. Sulph. 159. 1856.

Coccoloba oaxacensis Gross, Repert. Sp. Nov. 12: 219, 1913.

Coccoloba mayana Lundell, Bull. Torrey Club 64: 547. 1937.

Coccoloba masoni Lundell, Lloydia 2: 8. 1939.

Coccoloba fluviatilis Lundell, Contr. Univ. Mich. Herb. 7: 8. 1942.

In the second paper of this series (Jour. Arnold Arb. 37: 317–339. 1956). I considered the correct identification and application of the names *Coccoloba swartzii* Meisner and *C. barbadensis* Jacq. The former name had been overlooked by recent workers on the floras of the Antillean Islands and the latter name had been misapplied. I concluded that the material which is properly called *C. swartzii* was first identified by Lindau as *C. barbadensis* and that later he and all recent authors on the West Indian flora used the name *C. diversifolia* Jacq. for the same material.

Coccoloba barbadensis Jacq. was described twice by Jacquin, first in his Enumeratio, and later, supported by an illustration, in his Observationum Botanicarum. A definite location was not given for the species and recent authors have assumed from the name that the island of Barbados was implied. However, in the British Museum (Natural History) there are two sheets which can be referred to the Jacquin description and illustration and these are significant in the correct application of the name. One of

these, from the Miller herbarium, is obviously the material illustrated by Jacquin. Moreover, it bears the Houston catalogue reference which Jacquin cites in the synonymy of his *Coccoloba barbadensis*. Houston collected in Campeche (Yucatán) and his specimen is accurately matched in many of the collections cited below.

In his monograph of the genus *Coccoloba* for De Candolle's Prodromus, Meisner assumed that *C. barbadensis* came from the West Indies and so created a variety, *C. barbadensis* var. *mexicana*, for a Schiede specimen from Mexico. Lindau (Bot. Jahrb. 13: 187. 1890) recognized the variety as a species which he named *Coccoloba schiedeana*, citing in synonymy *C. barbadensis* var. *mexicana* Meisner. Lindau cited additional material, all of which, with the exception of one collection, I have now seen. These are all clearly comparable to the original Jacquin material; thus, *C. barbadensis* Jacq. must henceforth be considered in the flora of Mexico and Central America.

Of the two old specimens in the British Museum (Natural History), one represents a sterile adventitious shoot and the other a vigorous shoot with an old inflorescence from which the fruits have fallen. In all probability, therefore, it will be impossible to describe the fruit which accompanied this original sheet. However, with a knowledge of the variation found in other species of *Coccoloba* in such characteristics as leaf shape, size of petiole, presence or absence of pubescence and length of fruiting pedicels, it is possible to make an accurate comparison with more recent collections. It is clear that *C. barbadensis* has puberulent to tomentose ocreae and inflorescence rachises, although in age these become glabrous. Also, the leaves are coriaceous and the leaf shape, particularly at the base, is variable. As in other species of *Coccoloba*, the plants are dioecious and the pistillate flowers, and later the fruits, are borne on short pedicels which in length barely exceed the ocreolae. The fruit, coronate at the apex, is rounded at the base and not attenuated into a stipe.

The variations with age and environment in these characteristics have caused Coccoloba barbadensis to be described many times. Seven species are assigned to the synonymy of C. barbadensis in this paper alone. Three additional apparently unpublished names have been applied to the specimens in various herbaria. The original variety which Meisner described is also placed in synonymy with the species. Three of these newly recognized synonyms represent only sexual variations, i.e., staminate versus pistillate plants, in the comparisons given by the original authors. Two species were originally distinguished through the failure of the author to recognize the loss of, or to see the residual, pubescence. One species was based on an abnormal fascination of the inflorescence and two others were based on size and texture differences of the leaves. When considered alone or with only the material cited by the original authors, several of the species which I have reduced to synonymy might well represent clones or local populations. When considered with the wealth of material cited below, the differences become of little taxonomic value. It appears desirable to treat Coccoloba barbadensis as a widespread species of central and southern Mexico

and northern Central America, recognizing the considerable variation in leaf size, shape and texture.

Two excellent series of collections by Dr. Robert Dressler made in the states of Veracruz and Guerrero, Mexico, show the variation in leaf-size,

-shape and -pubescence to be found on single plants.

Coccoloba leptostachya Bentham has been a troublesome name. Bentham described this plant, without citing a collection, in reporting on the Botany of the Sulphur Expedition. The locality was given as Libertad in Colombia, and recent collections from Colombia and Panama have been assigned to this species. However, examination of the type material in the Herbarium at the Royal Botanical Gardens at Kew shows clearly that the specimen on which Bentham based the species is a Barclay collection which represents C. barbadensis. Other species from the Sulphur voyage reportedly collected in "Libertad in Colombia" have more recently been recognized as Central American and, in several instances, the collection is believed to have come from Libertad in El Salvador. Coccoloba leptostachya appears to me to be a similar example of the incorrect citation of a locality. The recent collection Carlson 563 (F) from "Finca Santa Emilia west of La Libertad at or near sea level" in El Salvador is a perfect match for the Barclay specimen. No material comparable to the type of C. leptostachya has been seen from Colombia.

In his monograph Lindau distinguishes *Coccoloba jurgenseni* from *C. schiedeana* on the basis of a glabrous inflorescence rachis in the former and a pubescent one in the latter. The distinction is inadequate, especially since the holotype of *C. jurgenseni*, *Jurgensen* 157 (G) shows a slight puberulence within the range of variation expected in this genus.

Coccoloba oaxacensis Gross was reduced to the synynomy of C. schiedeana by Standley in his treatment of the trees and shrubs of Mexico. He reported at the time that he had "seen no material of C. oaxacensis, and it may be a distinct species." I have examined the holotype in the Berlin herbarium but find no reason to maintain C. oaxacensis as a species.

Coccoloba mayana Lundell was based on a staminate flowering specimen collected by Lundell on the bank of the Río San Pedro de Martir above El Paso in the Department of Petén, Guatemala. Lundell reported that the species was found only in wet soils on river banks and around "aguadas." Coccoloba mayana, he states, "is related to Coccoloba schiedeana Lindau, from which it differs in having longer racemes, nodes 1- or 2-flowered, larger flowers, and suborbicular perianth lobes." None of these characteristics is of specific value. At best, C. mayana as conceived by Lundell is an ecological variation, distinct only in having smaller and thinner leaves, but it does not seem to be worth a subspecific category. Coccoloba barbadensis is a variable species and, judging from the collections seen, occurs primarily in drier areas. Plants from other departments in Guatemala show larger leaves of thinner texture and are thus intermediate between the type collection of C. mayana and C. barbadensis.

Coccoloba masoni Lundell was based on a collection by H. L. Mason from Maria Magdalena Island of the Tres Marias Islands off the coast of

Nayarit, Mexico. Lundell recognized the dioecious condition of the flowers, the obovate or oval leaf shape and the pilose pubescence in the axils and on the veins of the leaves as distinguishing characteristics of this species. Two other collections from the same island group, one made earlier and one made later than the Mason specimen, show more clearly the range of variation in leaf-shape and -pubescence and indicate that *C. masoni* and the Mason collection on which it is based are the same as *C. barbadensis*. Only a few recent floras have recognized the dioecious nature of *Coccoloba*. At present it appears that all species are functionally unisexual and the dioecious character is not of specific value in the case of *C. masoni*.

In describing *Coccoloba fluviatilis*, Lundell placed his new species in a group which included *C. jurgenseni* and *C. mayana*, both of which are here included in *C. barbadensis*. Lundell felt that *C. fluviatilis* was distinct because of "large glabrous leaves, subcordate at the base, the stout petioles up to 1.7 cm. long, the glabrous rachis of the inflorescences, and the subsessile fruits." However, all of the size and shape characteristics mentioned by Lundell can be found in many of the single collections cited. The "glabrous" characteristic, however, is an error, for pubescence can be found on the terminal buds and in the axils of the leaves on the holotype, although the plants do become glabrate in the clonal material which Lundell studied.

Seler 1642 from Arroyo de San Carlos, in Mexico, was designated by Gross as the type of an apparently unpublished species named for the large, fasciated inflorescence axis. Many of Gross' new species have been published in obscure papers, so it is possible that this name may be in print. The fasciated inflorescence rachis is relatively common in other species of the genus and has been seen in three additional collections cited below. The Seler collection is clearly identical with the material assigned to this species.

The collection by Edward Palmer which was distributed with the letter "G" in place of a collector's number bears an unpublished name attributed to Rose. This name refers to the sessile flowers, but the collection is not distinct from *C. barbadensis*.

The specimen attributed to Galeotti and numbered 7218 has been cited and annotated by Lindau as C. schiedeana. The material, however, is a mixed collection containing in part C. barbadensis and C. venosa.

México. Campeche: Champotón, Flores 1934 (f); Mundo Nuevo, Karwinsky 733b (le). Chiapas: Escuintla, Matuda 2028 (a, de), f, mich); Javalinero, Palenque, Matuda 3634 (a, f, mich); Malpaso, near Siltepec, Matuda 4517 (mich-type of C. fluviatilis; a, f); Chicomuselo, Matuda 15627 (f); Montecristo, Matuda 15948 (f); Nandolopez, Acapetahua, Matuda 16642 (br, f); Mojarra, Tonalá, Matuda 17139 (f); Mapastepec, Matuda 17517 (f); Monserrate, Purpus 275 (le, us). Colima: Paso del Río, Emrick 168 (f); Manzanillo, Ferris 6209 (de), Palmer "G" (de), Gh, ny); Colima, Palmer 90 (a, c, mich). Guerrero: La Mina near Atoyac, Dressler 1798a, 1798b, 1798c (gh); Vallecitos, Montes de Oca, Hinton 10209 (de), mich), 10221 (de), le, mich); Vallecitos, Llano de Oca, Hinton 11781 (de), le, mich); Sierrita, El Limón,

Galeana, Hinton 14137 (F, GH); Chilpancingo, Kenoyer C-277 (MICH); La Copradilla, Langlassé 134 (B, GH); El Trienta, C.L. & A.A. Lundell 12588 (MICH); Dos Arroyos, Nelson 7029 (GH, NY); Acapulco, Palmer 344 (A, GH), 602 (A, F, GH, MICH). JALISCO: Navidad, McVaugh 11903 (MICH): Tuxpan, Mexia 1051 (A, F, GH). MICHOACÁN: San Naranjillo, Coalcomán, Hinton 13943 (GH); La Placita, Turner 2028 (місн). Nayarit: Acaponeta, Rose 1414 (NY), Rose, Standley & Russell 14399 (NY); Magdalena Island, Tres Marias Islands, Elmore 1B3 (F. MICH), Nelson 4315 (GH), Mason 1806 (F-holotype of C. masoni; A, DS, GH, MICH), Maltby 167 (NY); San Blas, Ferris 5331 (A, DS); Ixitlán, Viereck 1193 (US). OAXACA: Rincón San Antonio, Endlich (B-holotype of C. oaxacensis); Dunes del'Oc. Pacifique, Galeotti 7218, in part (BR, K, P); Pinotepa Nacional, Jurgensen 157 (G-type C. jurgenseni; F-photo & fragment; в, к); Between Llano Grande and Pinotepa, Nelson 2334 (GH); Puerto Angel, Reiche 574 (M): Arroyo de San Carlos, Seler 1642 (B, GH); Almoloya, L. Williams 9906 (F. W). SINALOA: Labradas, Ferris & Mexia 5291 (A. DS). Veracruz: Laguna Encantada, east of San Andrés Tuxtla, Dressler 1804a, 1804b, 1804c (GH), Nelson 452 (A); Tantoyuca, Ervendberg 364 (GH, K, P); Savana de Mata de Don Juan, Karwinsky 734, 735 (LE); Tajín, Papantla, Kelley 65a (GH); Laguna Tamiahua, south of Tampico, LeSueur 100 (F); location unspecified, Liebmann s.n. (B); Mirador, Ross 802 (M); Tierra Blanca. Ross 883 (м); Zacualpan. Purpus 12022 (F, місн); Rancho Camarón, Purpus 13068 (A, F, GH, MICH); Fortin, near Zacualpan, Purpus 2428 (A, F, GH); Papantla, Schiede s.n. (LE-type of C. barbadensis var. mexicana and C. schiedeana by implication; B). State unspecified: location unspecified, Houston s.n. (BM-type of C. barbadensis); Sesse & Mociño 950, 5434 (F).

Guatemala. Escuintla: Naranjo, J. Donnell Smith 2496 (F, GH); San José, Standley 63998 (F); Rio Guacalate, northwest of Escuintla, Standley 89345, 89350 (F, MICH); Rio Michatoya, southeast of Escuintla, Standley 89054, 89060 (F, MICH). HUEHUETENANGO: Ciénaga de Lagartero below Miramar, Steyermark 51488 (A. F). PETÉN: La Libertad, Aquilar 275 (F, MICH. W), 313 (A, MICH), Lundell 3230 (F. GH, MICH), 3212, 3340 (F. MICH); El Paso. Lundell 1498 (MICH-holotype of C. mayana; DS, GH). QUEZALTENANGO: Río Ocosito, J. Donnell Smith 1481 (F. GH). RETALHULEU: Champerico, Standley 66593, 66602, 66631 (F); between Nueva Linda and Champerico, Standley 87699, 87721 (F); Retalhuleu. Standley 88818 (F). SAN MARCOS: Ocos. Stevermark 37780 (F). SANTA Rosa: Guazacapán, Standley 78603 (F); Chiquimulilla, Standley 78785, 79175, 79243 (F); La Sepultura, west of Chiquimulilla, Standley 79378 (F). Suchitepéquez: South of Tiquisate, Stevermark 47807 (F).

Salvador. AHUACHAPÁN: Ahuachapán, Standley & Padilla 2615 (F). Standley 20313 (GH, MICH). LA LIBERTAD: Libertad, Barclay s.n. (K-type of C. leptostachya), Carlson 563 (F). SANTA ANA: Santa Ana. Standley 20404 (GH). Sonsonate: Acajutla. Standley 21895, 21974 (GH).

The following collections are also assigned to Coccoloba barbadensis, but probably represent a hybrid complex. The specimens are all staminate, with sterile, insect-infested fruits on tenuous pedicels twice as long as the ocreolae. The leaves appear to be more coriaceous and the margins are revolute. The leaves are shiny on the upper surface, although this may be an artifact of preservation.

Guatemala. Alta Verapaz: Laguna Sapalá. Stevermark 44899 (F). Petén:

Laguna Petexbatúm, Steyermark 46224 (A, F); Along Río Santa Mónica between Cedral and Ceibal, Steyermark 46040 (F, MICH), 46160 (F).

The series of collections cited below appears to represent a different hybrid population limited to the state of Sinaloa and found only in the coastal areas. The probable parents are Coccoloba barbadensis Jacq. and C. uvifera L., although in general the leaves are smaller than in either of these. Leaf texture, as well as the size and shape of the fruit, indicate a relationship to C. barbadensis. The leaf shape, especially at the base and apex of the blade, and the venation show similarities to C. uvifera. However, in contrast with most of the recognized C. uvifera hybrids from the West Indies and with $C. \times lundellii$ of Central America, C. uvifera seems to be the less dominant parent in this hybrid. Fruits of two types have been found, one essentially globose but strongly coronate and the other more or less oblong and obtusely to slightly coronate at the apex. The first type closely approaches the fruit of C. barbadensis and all fruits opened have fully developed embryos and endosperm. The second type shows the influence of C. uvifera and all fruits examined had either rudimentary seed development or were sterile.

Mexico. Sinaloa: Altata, Rose 1359 (NY); Culiacán, J. Gonzalez Ortega 6583 (DS, GH, M), Palmer 1518 (GH, NY); Elota, J. Gonzalez Ortega 5879 (DS, GH, M); La Concha. Gentry 6804 (F, GH); Mazatlán, Howell 10559 (A), Rose, Standley & Russell 14035 (NY); Villa Union, Rose, Standley & Russell 13953 (NY); locality unspecified, J. Gonzalez Ortega 7203 (F).

Most of these specimens were identified as *Coccoloba goldmanii* or *C. masoni*. The former is a distinct species, but is known from the type and one other collection. It may, in fact, be related here as part of this hybrid population or be one of the parents in place of *C. barbadensis*. *Coccoloba* needs a special study in Sinaloa and southern Chihuahua. *Coccoloba masoni* Lundell is clearly referable to typical *C. barbadensis* Jacq.

Coccoloba belizensis Standley, Trop. Woods 16: 38. 1928.

Coccoloba hirsuta Standley, Publ. Field Mus. Bot. 4: 303. 1929.

Coccoloba belizensis Standley is a clearly defined species and one which is easily recognized. The relatively large, globular terminal buds with tawny to chestnut-brown pubescence are distinctive even on sterile or adventitious shoots. The pubescent inflorescence is branched and consists of racemes arranged as a panicle of nearly equal branches. The leaf size varies considerably in fertile material as well as on sterile shoots which are presumably adventitious. Both staminate and pistillate plants are represented in the collections cited. The mature achene is surrounded by a fleshy perianth which seems to be formed by the equal enlargement of the perianth lobes and the hypanthium.

In the Berlin Herbarium there is a specimen studied by Gross which bears an unpublished herbarium name honoring the collector, Campbell. Much of Gross' work on *Coccoloba* appeared as small notes in miscellaneous

papers. Thus it is possible that this specific name has been published and, if so, it antedates *C. belizensis*.

Coccoloba hirsuta Standley was based on sterile material. The type, Standley 54802, as well as the cotype 52823, was collected in the Lancetilla Valley, near Tela, Honduras. Standley noted the undesirability of basing species on sterile material, but felt that this species was easily recognizable by the "copious long pubescence of the leaves." In their treatment of the genus Coccoloba for the Flora of Guatemala (Fieldiana Bot. 24: 114. 1946) Standley and Steyermark continued to recognize C. hirsuta as a distinct species, referring to, but not citing additional specimens from, Guatemala and thus extending the range. I have seen two collections from the Department of Izabal, Stevermark 38185 and Standley 72945, which are among those which must have been seen by Standley and Steyermark. These authors suggest that C. hirsuta "will be found to have panicled racemes, and to be closely related to C. Tuerckheimii." I am unable to distinguish between material annotated "C. hirsuta" by Standley and Stevermark and cited by Standley and that of occasional sterile specimens which the same authors assigned to C. belizensis. Such collections as C. & W. von Hagen 1344 from the Department of Colón, Honduras, and Lundell 2756 from the Department of Petén, Guatemala, approach C. hirsuta in the amount and type of pubescence. The Von Hagen collection is sterile and was taken from a 75-100-foot tree. This specimen may be an adventitious shoot comparable to the type of C. hirsuta, for the terminal bud is the same in size and shape, but there is less copious pubescence on the stem and much less on the leaves. The Lundell collection grades easily into fertile material which can be clearly defined as C. belizensis and which is found in the same area.

Guatemala. Alta Verapaz: Chirreacté, Standley 91620, 91672 (F); between Sachaj and Sacacac, Steyermark 45157a (F). Izabal: between Bananera and La Presa in Montaña del Mico, Steyermark 38185, 38186 (F); Escoba, Standley 72945 (F). Petén: La Libertad, Lundell 3463 (F, MICH); Monte Santa Teresa, Lundell 2736 (F), 2756 (MICH). British Honduras. Corozal District: San Roque, Gentle 554 (F); Corozal, Orange Walk Rd., Gentle 4967 (F. MICH); Corozal, Pachacan Rd., Lundell 4784 (A, F, MICH). EL CAYO DISTRICT: San Agustin, Lundell 6812 (F, GH, MICH). ORANGE WALK DISTRICT: Honey Camp, Lundell 637 (DS, F, GH, MICH, US). STANN CREEK DISTRICT: Carib Reserve, Gentle 3088 (MICH); Mullins River, Gentle 3365, 3369 (A. MICH); Silk Grass Creek Reserve, Gentle 2982 (MICH); Stann Creek, Gentle 2964 (A. MICH); Stann Creek Valley, Stevenson 7 (us-holotype; A, F, Y). Toledo District: Jenkins Creek, Gentle 4080 (A. MICH). District unspecified: Belize, Campbell 117 (B); Crique Negra, Stevenson 104 (F, Y); All Pines, Schipp 794 (A, F, GH, MICH); Tower Hill Estate, Karling 14 (F, GH). Honduras. ATLANTIDA: Lancetilla Valley near Tela, Howard, Briggs, et al. 451 (A), Standley 52823 (F), 53555 (A, F), 54802 (F-type of C. hirsuta; A); San Alejo, Standley 7971 (F); San Juan near Tela, Yuncker 4817 (A, F, MICH); Tela, Standley 53402 (A, F). Colón: Guarunta, C. & W. von Hagen 1344 (F). Nicaragua. Eastern Nicaragua. Shank 93 (Y).

Coccoloba caracasana Meisner, DC. Prod. 14: 157. 1856.

Coccoloba caracasana forma glabra Lindau, Bot. Jahrb. 13: 211. 1890.

This species was formerly considered to have orbicular leaves, but the large number of specimens examined indicates that a broadly oblong leaf is more characteristic than a strictly orbicular one. Considerable variation in leaf size and shape is found in the species. Leaves of adventitious shoots may have nearly ovate blades up to 34 cm. long and 28 cm. wide on petioles to 4 cm. long. The straw-colored ocreolae are membranaceous, with several occurring at each nodule because of the presence of numerous flowers, several of which are frequently aborted. In fruit the lobes of the perianth expand to cover more than the upper half of the achene.

The forma *glabra* which Lindau described is scarcely worthy of recognition since the density and persistence of the pubescence varies in single collections and on single plants.

In addition to the specimens cited below, the species is known from Venezuela and Colombia and possibly farther south along the Andes. The type has been cited both as *Humboldt 732* and as *Bonpland 732*. One collection cites only Caracas, Venezuela, as the locality, while another bears a label referring to the "valley of Araguensibus."

México. Chiapas: Las Garzas, Acapetagua, Matuda 2677 (A, DS, F, MICH), 2806 (A, місн); Mapastepec, Matuda 17516 (F); Tapachula, Matuda 17704 (F). Guatemala. Escuintla: Iztapa, J. R. Johnston 1171 (F); San José, Standley 64232 (f, MICH), 64019, 64190 (f). JUTIAPA: Between Trapiche Vargas & Asunción Mita, Steyermark 31792 (F). RETALHULEU: Between Nueva Linda and Champerico, Standley 87673 (F). SANTA Rosa: Santa Rosa, Ørsted 668 (м); Capulin, Standley 79592 (F); Los Cerritos region, Capulin, Standley 79607, 79563 (F. MICH). SUCHITEPÉQUEZ: Tiquisate, Steyermark 47700 (F). El Salvador. La Paz: Zacatecoluca, Calderon 305 (GH). La Unión: Laguna de Maquigüe, Standley 20977 (GH). SAN MIGUEL: San Miguel, Standley 21139 (GH); Laguna Jaguay, San Miguel, Fassett 28813 (A); Laguna de Olomega, Standley 20990 (GH). SAN SALVADOR: San Salvador, Renson 139 (NY), Standley 23611 (F, GH). SAN VICENTE: San Vicente, Standley 21261 (F, GH), Standley & Padilla 3702 (F). Santa Ana: Hacienda la Barra, Carlson 1031 (F). Sonsonate: San Antonio del Monte, Standley 22171 (GH). Nicaragua. CHINANDEGA: Chichigalpa, Standley 11187, 11334 (f). CHONTALES: Juigalpa, Standley 9302, 9305 (f). GRANADA: Granada, Baker 2435 (A, MICH). LEÓN: La Paz, Baker 2272 (GH). Locality unspecified: C. Wright s.n. (GH); Ørsted 670, 671 (C). Costa Rica. GUANACASTE: between Bebedero and Taboga, Brenes 12562 (F); Filadelfia, Echeverria 295 (F); Nicoya, Tonduz 13799 (F, G, GH), 13974 (G, GH); Isla de Chira, Valerio 1467 (F); Santa Ana de Nicoya, León 989 (F). Province unspecified: Los Loros, Brenes 22056 (F). Locality unspecified: Hoffmann 292 (B), Warscewicz s.n. (B). Panamá. CANAL ZONE: Ancón, Pittier 2730 (US); Gorgas Memorial Laboratory grounds, White 106 (F, GH, MO); Río Agua Salud near Frijoles, Piper 5848 (GH); Victoria Fill near Miraflores Locks, Allen 1701 (F, GH, MO, NY). CHIRIQUÍ: Progreso, Cooper & Slater 270 (F). Los Santos: La Jagua, Bartlett & Lasser 16382 (MICH). PANAMÁ: Sabanas Road, Gillespie P-34, P-34a (DS); Chepo, Kluge 25 (F, NY).

Coccoloba chiapensis Standley, Proc. Biol. Soc. Wash. 33: 67. 1920.

Coccoloba anisophylla Standley, Publ. Field Mus. Bot. 4: 303. 1929.

Coccoloba anisophylla was based on sterile material, but Standley reported that "the form of the leaves is quite different from that of any other Central American species." On studying the material cited by Standley and being unable to distinguish C. chiapensis from C. anisophylla, I have referred the latter to the synonymy of C. chiapensis. This species is distinct in having leaves which are oblong to elliptic, broadest near the middle, tapering to an acuminate apex and narrowing to an abruptly obtuse and asymmetrical base. Only staminate flowers are known for this species and additional material is needed. Sterile specimens may resemble C. novogranatensis but can be distinguished by the basal origin of the petiole and by the pubescence.

México. Chiapas: Finca Irlanda, Purpus 7699 (us-holotype of C. chiapensis; B, GH, NY); location unspecified, Purpus 7599 (GH, NY). Honduras. Atlántida: Lancetilla Valley near Tela, Standley 53260 (F-holotype of C. anisophylla; A), 53364, 54840 (A, F).

Coccoloba cozumelensis Hemsley, Biol. Am. Centr. 4: 108. 1887.

Coccoloba yucatana Lindau, Bot. Jahrb. 13: 190. 1890.

Coccoloba cozumelensis is readily recognized but difficult to define and separate in a key. The species seems amply distinct on the basis of the pale tan color of the leaves which often dry a lighter yellow-brown on the lower surface, and the sessile fruits which are obtuse at the apex with the perianth lobes not at all coronate. Also, the petioles are puberulent and along the midrib and veins on the lower leaf surface there is a characteristic crispate pubescence.

Some specimens of *Coccoloba cozumelensis* grade into the Central American phase of *C. swartzii* and it is possible that a hybrid complex exists in coastal areas where these species occur together. Since I have insufficient material to resolve this problem, the key characteristics used here apply to plants represented by the distinctive holotypes of each.

Two recent collections from the state of Chiapas are referred here. One collection, Margery C. Carlson 2071, made at Tuxtla Gutiérrez. is annotated as a new species by Standley and Williams. The name used refers to the tenuous spike. This collection, in flowering condition, is intermediate between typical material of C. cozumelensis and specimens referred to C. spicata, but other than the larger leaves of Carlson 2071. I find no reason for recognizing the collection as a new species. The second collection, Dressler 1408, from El Real, Chiapas, is intermediate between typical C. cozumelensis and the Carlson collection.

Standley placed Coccoloba yucatana in the synonymy of C. cozumelensis. I have re-examined authentic material of this and confirm his decision.

México. Campeche: Tuxpeña, Lundell 853 (A, DS, F, GH, MICH). CHIAPAS:

Tuxtla Gutiérrez, Carlson 2071 (F, NY); El Real, east of Ocosingo, Dressler 1408 (GH). Quintana Roo: Cozumel, Gaumer 18 (B-holotype of C. yucatana; GH, K); Cobá, C.L. & A.A. Lundell 7804 (A, DS, F, M, MICH), 7830 (A, DS, F, MICH). Tabasco: Reforma, Balancán, Matuda 3173 (A, MICH). British Honduras. Belize District: Maskall, Gentle 1068 (A, F, GH, MICH), 1349 (A, F, MICH). Corozal District: San Antonio, Bartlett 13031 (A, F, MICH), Lundell 4815 (A, F, MICH); Corozal, Gentle 524 (F, MICH). El Cayo District: Little Mountain Pine Ridge, Bartlett 13060a (MICH); Mountain Pine Ridge, San Agustín. Lundell 6648 (DS, F, GH, MICH). Orange Walk District: Honey Camp, Meyer 50 (F). Guatemala. Izabal: Río Dulce. Wilson 387 (F). Petén: Carmelita. Egler 42-249 (F); La Libertad, Lundell 3570 (F. GH, MICH).

Coccoloba darienensis, sp. nov.

Arbor, 12 m., ramulis teretibus, glabris; ocreis chartaceis, oblique truncatis, 1 cm. longis, glandulis (?) resinosis, adpressis; petiolis ad basem ocreis gerentibus, teretibus, supra canaliculatis, glabris, 7–11 mm. longis; laminis anguste oblongis vel lanceolati-oblongis, apice acutis vel breviter acuminatis, basi acutis, 10.5×3.5 vel 14.5×5 cm. longislatisque glabris, tenuiter coriaceis, nerviis primariis 9 vel 10, arcuato-adscendentibus; inflorescentibus racemosis, 8–14 cm. longis, floribus crebris, nodulis confluentibus, pedunculis 1 cm. longis, rachis striatis, puberulentibus; floribus ignotis, bracteis ovatis vel oblongis, apice obtusis, 1 mm. longis, puberulentibus vel breviter pilosis, ocreolis membranaceis, raro bracteolisque puberulentibus vel apice ciliatis; pedicellis fructiferis 1 mm. longis, glabris; fructu ovoideo basi rotundato, 5–6 mm. longo, 5 mm. diametro, obtuse trigono, hypanthio non manifesto, lobis perianthii ad basem distinctibus, late ovatis. imbricatis, acheniis nitidis, nigris.

Panamá. Darien: Pinogana, P. H. Allen 934 (GH-type: F. MO).

This collection had been identified as *Coccoloba acuminata*, which is certainly a related species. The strongly divided fruiting perianth would allow this species to be placed in Lindau's section *Campderia*. *Coccoloba darienensis* is distinct from *C. acuminata* on the many-flowered inflorescence in which the flowers are confluent, not clustered, and the axis is terete but striate or grooved and not swollen below each nodule. Furthermore, *C. darienensis* differs in the evident fruiting pedicels, while *C. acuminata* can be regarded as having only spicate inflorescences without evident pedicels in fruit.

Coccoloba diversifolia Jacquin, Enum. Pl. 19. 1760.

Coccoloba laurifolia Lundell, Bull. Torrey Club 66: 594. 1939, and authors. possibly Jacquin, Hort. Schoenbr. 3: 9, t. 267, 1798. Coccoloba laucifolia Lundell, Bull. Torrey Club 66: 593, 1939.

I have previously discussed the proper application of the epithet *Coccoloba diversifolia* Jacq. (Jour. Arnold Arb. 30: 421–424. 1949). All recent publications, however, have used *C. laurifolia* Jacq. for material more prop-

erly called *C. diversifolia*. *Coccoloba laurifolia*, based on material from Caracas, Venezuela, was described and illustrated by Jacquin, but I have been unable to find any collections from northern South America which exactly duplicate the characteristics which he illustrated. It is probable that *C. laurifolia* is the same as *C. diversifolia*, described by Jacquin twenty-eight years earlier. Oddly enough, no specimens of this which could be attributed to Jacquin have been seen in European herbaria, although a few specimens collected from cultivated plants and labelled "*C. laurifolia* Jacq." are present in the herbaria at Berlin, Leningrad and Geneva. However, all of these are true *C. diversifolia* and fail to compare favorably with the original illustration of *C. laurifolia* Jacq.

Lundell compares *Coccoloba lancifolia* with the original description of *C. laurifolia*, reporting that his new species differs in its small, lanceolate and pointed leaves. *Coccoloba diversifolia*, as its name implies, is a variable species in respect to leaf shape, but in all the characteristics which I can observe, it is the same as *C. lancifolia*. In their treatment of the genus for Guatemala (Fieldiana Bot. 24: 114. 1946), Standley and Steyermark placed *C. lancifolia* Lundell in synonymy of *C. laurifolia*, but without comment. I concur with their decision, but call the species *C. diversifolia* Jacq. The small leaf size and the pointed apex can be found in many populations of *C. diversifolia*, especially in Cuba, the Bahamas and the Florida Keys.

This is the first time that this common West Indian species has been recognized in Central America and Mexico.

México. Quintana Roo: Lago San José, Frère Arsène s.n. (B). San Luis Potosí: Tamazunchale, Edwards 921 (F). Guatemala. Alta Verapaz: Cerro Cinajá, Steyermark 45669 (A, F, MICH). Izabal: Bay of Santo Tomás, Steyermark 39232 (F), 39351 (F, MICH), 39357, 39363 (F).

British Honduras. Corozal District: Location unspecified, Gentle 231 (F, MICH, NY); Consejo, Lundell 4945 (F, MICH). District unspecified: Jacinto Hills, Schipp 1200 (MICH-holotype of C. lancifolia; A, GH, W).

Coccoloba emarginata Jacquin, Enum. Syst. Pl. 37. 1760.

This species was described by Jacquin in 1760 and illustrated in his Observationum Botanicarum in 1764 (tab. 9). It is based on a specimen from the herbarium of Mygind but no locality is given. The species was compared with the Hispaniolan Coccoloba leoganensis Jacq., which I have recognized (Jour. Arnold Arb. 39: 28–30. 1958), but which is better known in that flora as C. rotundifolia Meisn., a later homonym. Lindau was unable to place the Jacquin species and so listed it as of uncertain identity.

The situation here is similar to that of Coccoloba barbadensis. The specimen which Jacquin described must have come from the Yucatán Peninsula of Mexico. The illustration, although of a sterile plant, is an excellent one and is obviously the same as Neomillspaughia emarginata (Gross) Blake (Bull. Torrey Club 48: 84. 1921), the basionym of which is Podopterus emarginatus Gross (Repert. Sp. Nov. 12: 218. 1913). Gross' species is

based on Seler 5600 from Yucatán, Mexico. Since the combination has already been made, I can only add Coccoloba emarginata Jacquin to the synonymy of Neomillspaughia emarginata (Gross) Blake and thereby dispose of a troublesome and misplaced ancient epithet in the genus Coccoloba.

Coccoloba goldmanii Standley, Contr. U.S. Nat. Herb. 23: 245. 1922.

This distinctive species from the drier areas of northern Mexico has not been recollected in the past sixty years. Cited below are the Goldman collection made in 1898 and the Hartman collection made in 1891. The latter was misidentified as *Coccoloba orizabae*. *Coccoloba goldmanii* is recognized by the nearly orbicular leaves which are persistent short pubescent below and which possess a conspicuous network of veins on the lower surface. The flowers are unknown. The ellipsoidal fruits are not coronate and the lobes of the fruiting perianth cover the upper half of the achene, the hypanthium the lower half.

México. Сніниания: Apajcachi, Hartman 535 (GH). Sinaloa: Valley of Río Fuerte, Goldman 245 (us-holotype; GH).

Coccoloba hondurensis Lundell, Bull. Torrey Club 66: 591. 1939.

Coccoloba marginata J. Donnell Smith, Enum. Plant. Guat. 6: 36. 1903, not Benth.

In describing this species, Lundell states, "the specimens show considerable variation, especially in leaf shape, inflorescence, and fruits but all appear to be referable to a single species. . . . Collections of *C. hondurensis* have been referred to *C. Schiedeana* Lindau, *C. marginata* Benth., *C. barbadensis* Jacq., and *C. leptostachya* Benth. I have not been able to associate the species with any of these."

It is unfortunate that Lundell did not state how he distinguished C. hondurensis from the other species he lists. Standley and Steyermark (Fieldiana Bot. 24: 116. 1946) refer C. hondurensis to the synonymy of C. schiedeana Lindau in their treatment of the genus for Guatemala. I regard C. schiedeana Lindau as identical to C. barbadensis Jacq. I hesitate to follow Standley and Steyermark in reducing C. hondurensis, for there is a problem here which I cannot solve, even with abundant herbarium material. I prefer to keep C. hondurensis as a distinct species and to call this problem to the attention of field workers for further study. Material cited below as C. hondurensis is easily recognized, but difficult to define or to separate in a key. For the present, C. hondurensis can be recognized when dry by the dark brown or black upper leaf surface which contrasts with the lighter-colored lower surface. The inflorescences are usually twice as long as the subtending leaves. The fruiting pedicels are slightly more tenuous and seem relatively longer than those of C. barbadensis and the apex of the fruit, while coronate, is more obtuse than is general in C. barbadensis. Usually such distinctions are not valid in this difficult genus and I am maintaining this as a distinct species for temporary convenience only.

Further study should be rewarding, for C. hondurensis may prove to be either a variety of C. barbadensis or of hybrid origin.

México. Oaxaca: Tehuantepec, L. Williams 9906 (y). Veracruz: Fortuno, Coatzacoalcos River, L. Williams 8701 (y). Guatemala. Alta Verapaz: Río Sebol, near Carrizal, Steyermark 45785 (f). Izabal: Quiriguá, Standley 23867, 23988, 24547, 24601 (gh), 72249 (f); Puerto Barrios, Standley 72143 (f); Salomón Creek, south of Bananera, Steyermark 38934 (f). Petén: Río Cancuén, Steyermark 45925 (a, f); Río Machaquilla, north of El Cambio, Steyermark 45928 (f).

Honduras. Atlántida: Vicinity of Tela, Bangham 212 (A); Chickering 233 (F, MICH), Howard, Briggs et al. 452, 503, 504, 505, 506, 507 (A), Salvoza 810 (A), Standley 53716, 54476, 54481, 54752, 56598, 56659 (A, F); La Ceiba, Yuncker, Koepper & Wagner 8295 (F, GH). Colón: Cuyamel, Carleton 598 (US). Santa Bárbara: San Pedro Sula, J. Donnell Smith 5433 (A, F, GH, M). Dept. unspecified: Puerto Sierra, Wilson 74 (NY), 562 (F, GH, NY).

British Honduras. Belize District: Quamina Creek, Manatee, Gentle 3437 (A, MICH); Cornhouse Creek, Manatee River, Bartlett 11275 (F, MICH); Sibun River, Bartlett 11361 (GH, MICH); Northern River, Gentle 897 (A, F, MICH). El Cavo District: Little Cocquericot, Belize River, Lundell 3995 (MICH), 3996 (MICH-holotype; F), 3997 (GH, MICH). STANN CREEK DISTRICT: Sarawee Pine Ridge, Gentle 2699 (A, F, MICH), 2748 (A, F, MICH); Mullins River Road, Gentle 2731A (A, F, MICH); Carib Reserve, Gentle 2734 (A, F, MICH), s.n. (A, MICH, WIS); Stann Creek Valley, Gentle 2733 (A, F, MICH), 2735 (A, F, MICH, WIS), 2737, 2738 (A, F, MICH), s.n. (MICH); Middlesex, Gentle 2820, 2874, 2878, 2887 (A, MICH), 3011, 3018 (A, F, MICH); Silk Grass Creek Reserve, Gentle 2989 (A, MICH); Big Eddy Ridge, Gentle 3348 (A, MICH); Mt. Cow Vayyel, Gentle 3538 (A, MICH); Silk Grass Creek Reserve, Record BH-20 (Y); Middlesex, Schipp 453 (A, F, GH, MICH). Toledo District: Swasey Branch, Monkey River, Gentle 3716, 3584 (A, MICH). District unspecified: Manatee Lagoon, Peck 255 (GH).

Coccoloba humboldtii Meisner, DC. Prodr. 14: 163. 1856.

Coccoloba orizabae Lindau, Bot. Jahrb. 13: 189. 1890.

Coccoloba humboldtii var. longipedicellata Gross, Repert. Sp. Nov. 12: 219. 1913.

Coccoloba petrophila Brandegee, Univ. Calif. Publ. Bot. 10: 404. 1924.

Meisner cited two collections in the original description of this species, *Humboldt 4484*, which is in the Willdenow Herbarium as No. 7705, and *Berlandier 105*, collected near Tampico. Although the Humboldt specimen in the Willdenow herbarium at Berlin bears no specific locality beyond "Mexico," this should be selected as the lectotype. A second specimen collected by Humboldt is in the Paris herbarium and bears the number 4484, with the locality given as "Vera Cruz." Unhappily, this specimen was identified and annotated by Lindau as *Coccoloba nutans*, an entirely different species.

Coccoloba orizabae Lindau was distinguished by Lindau in a key to the species on the shape of the leaf blade, especially the narrowed base and the

acuminate apex. The type of this species was Bourgeau 2822 from Orizaba, Veracruz.

Gross distinguished his new variety Coccoloba humboldtii var. longipedicellata by the longer pedicels and the inflorescence rachis as long as the leaves. Gross failed to appreciate the dioecious character of the species and based his variety on a staminate plant, in contrast to the holotype, which is a pistillate plant. The variety is clearly included within the range of variation of the Humboldt type collection and, as more recent collections demonstrate, should be included within the species.

Coccoloba petrophila was described by Brandegee in a report on Purpus collections from Mexico. Purpus 8872 from Camerón, Veracruz, was selected as the type. No discussion was given of the distinctions or affinities of the species. Another collection, Purpus 8736, made at the same time and location, was not seen, or at least not cited, by Brandegee. Subsequently Purpus collected additional material assigned to this species from near Los Conejos (16425, 16430) and Rancho Remudadero (10967). The last number was suggested to be a wide-leaved variety in Brandegee's herbarium notes. These Purpus collections, together with Seler 4482, show the extremes of variation to be expected in C. humboldtii, as well as the intermediate forms which made a continuous series from former concepts of C. humboldtii to C. petrophila and C. orizabae. Several of the Purpus collections also show thin-textured immature leaves of varying sizes and shapes. It is in such specimens as Purpus 16425 that transitions to the thin-textured acuminate-tipped leaves of C. orizabae can be found.

In his treatment of the trees and shrubs of Mexico, Standley places both *Coccoloba orizabae* and *C. humboldtii* in a division of his key headed "rachis of the inflorescence glabrous." In all of the material cited below, the young inflorescence rachis is subtomentose, but at maturity is puberulent or glabrate. The same is true of the ocreae. The original descriptions of the three species and the variety fail to mention pubescence.

México. San Luis Potosí: Las Canoas, Pringle 5111 (A, GH). Veracruz; Tampico, Berlandier 105 (A, B, LE, P), 201 (LE), Palmer 322 (GH, NY); Veracruz, Galeotti 109 (BR), Juzepczuk 1116 (F, LE), Gorrin s.n. (LE); Colipa, Karwinsky s.n. (LE); Laguna Tamiahua, LeSueur 100 (GH), 101 (F); Orizaba, Bourgeau 2822 (B-holotype of C. orizabae; P); Pánuco River near Ebano, LeSueur 102 (F, GH); Pacho, Liebmann s.n. (LE); Coatzacoalcos, Orcutt 3162 (DS, F, GH); Pueblo Viejo, Palmer 443 (F, G, GH, NY); Camerón, Purpus 8736 (GH, NY, US), 8872 (GH-isotype of C. petrophila); Rancho Remudadero, Purpus 10967 (B, F); Zacualpan, Purpus 12022, in part (DS); Los Conejos, Purpus 16425 (A, F, LE), 16430 (A, F); Puerto de Alvarado, Seler 4482 (B-holotype of C. humboldtii var. longipedicellata; GH); Mocambo, Troll 59 (M); Alvarado, Schubert & Rojas 1844a (A); location unspecified, Humboldt 4484 (B-Herb. Willd. 7705, lectotype; P).

Coccoloba lasseri Lundell, Contr. Univ. Mich. Herb. 6: 10. 1941.

This species is regarded as endemic to Panama and is perhaps not distinct from Coccoloba tuerckheimii Donn. Sm. For the present, C. lasseri

may be recognized by the paniculate inflorescence of few branches, the leaves with short, stout petioles and the blades which, while narrowed below the middle, are truncate or abruptly rounded at the base. Finally, the fruits known for *C. lasseri* are rounded at the base. In contrast, *C. tuerckheimii* has a paniculate inflorescence of many more branches, leaves with longer, tenuous petioles and blades cuneate at the base with fruits narrowed to a short stipe at the base.

Panamá. Coclé: Aguadulce, Pittier 4989 (F); Penonomé, Williams 357 (NY). Herrera: Chitré, Allen 1111 (F, GH, MO); Mangle Bejuco, Steyermark, Allen & Dodge, s.n. (F). Panamá: Bejuco, Allen 2542 (A, F); Panamá Nat. Highway, Las Lajas Bridge, Bartlett & Lasser 16638 (MICH); Río Pacora, Bartlett & Lasser 16946 (MICH-holotype); Balboa to Chamé, Dodge, Hunter, Steyermark & Allen 16732 (MO); Punta Paitilla, Standley 26265 (A). Province unspecified: Duchassaing s.n. (P).

Coccoloba liebmannii Lindau, Bot. Jahrb. 13: 189. 1890.

Coccoloba lapathifolia Standley, Contr. U.S. Nat. Herb. 23: 245. 1922.

This species is quickly and easily recognized by the persistent pubescence on the lower leaf surface. Most of the leaves show a tendency toward an undulate or wavy margin to the blade, while in some specimens this tendency is so exaggerated that the marginal folds overlap in the dried specimens. The fruit is globose and the perianth lobes are imbricate in fruit. The achene is not coronate.

Standley distinguished his new species, *Coccoloba lapathifolia*, from *C. liebmannii* on the basis of a "glabrous or very minutely puberulent" inflorescence rachis, in contrast to one densely short-pilose. Examination of the material cited below, however, including both types, indicates quite clearly that *C. lapathifolia* is the same as *C. liebmannii* and should be placed in synonymy.

México. Colima: Manzanillo, Ferris 6061 (A, DS, F), Palmer 965 (GH, NY); between Galera and Pochutla, Liebmann s.n. (c-holotype of C. liebmannii; B). Guerrero: Acapulco, Palmer 206 (Us-holotype of C. lapathifolia; GH); Placeres, Hinton 9101 (NY). Oaxaca: Distrito de Tamiltepec, Conzatti 4406½ (GH); Llano Grande & Pinotepa, Nelson 2341 (GH); Cerro de Picacho, Purpus 7735 (GH, NY); Tequisistlán, Seler 1719 (B).

Coccoloba lehmannii Lindau, Bot. Jahrb. 20 (Beibl. 49): 7. 1895.

Uvifera lehmanni Lindau, in footnote, l.c.
Coccoloba lehmanni Lindau, Repert. Sp. Nov. 1: 156. 1905.
Coccoloba changuinolana Standley, Publ. Field Mus. Bot. 8: 9. 1930.
Coccoloba williamsii Standley, Publ. Field Mus. Bot. 11: 148–149. 1936.
Coccoloba allenii Lundell, Contr. Univ. Mich. Herb. 6: 8. 1941.

Lindau described this species in two papers. In the earlier publication the specific name is spelled "lehmannii" and in the later one, "lehmanni." Two collections (Lehmann 6109 and 7560) were cited in the first publication, but in the second description only Lehmann 7560 was cited. In both

descriptions this new species is compared with *Coccoloba gracilis* of the section *Campderia*. Lindau's two descriptions of *Lehmann 7560* are comparable; thus one may assume that Lindau overlooked the first publication which described both of these collections. It seems desirable to select *Lehmann 7560* in the Berlin Botanic Garden Herbarium as the lectotype.

Coccoloba changuinolana was based on three collections from Panama with Dunlap 499 being selected as the type. An examination of these specimens shows Standley's original description to be in error on the important character of "perianthii tubo accrescente inclusus." The perianth lobes, not the perianth tube, increase in size to surround the mature achene, and the species as represented by the collections cited by Standley belongs to the section Campderia. Although Standley stated that the new species was related to C. schiedeana, I can find no basis for comparison between the two. However, C. changuinolana is comparable in all characteristics with C. lehmannii, from Columbia, and is assigned in synonymy to that species.

I have seen only the type collection, *Llewellyn Williams 4803*, of the several specimens that Standley cited in his original description of *C. williamsii*. This Peruvian species must also be placed in the synonymy of *C. lehmannii*. *Williams 4803* is in fruiting condition and the longer fruiting pedicels are in contrast to the shorter pedicels found on the flowering specimens of the Lehmann collection which is the type of the species. Additional collections which I have seen are intermediate. Standley indicated a relationship of *C. williamsii* with *C. caracasana*, both species being assigned to the section Campderia, but these are clearly distinct in the leaf shape and nature as well as in the abundant pubescence.

Still a third species, *Coccoloba allenii* Lundell is assigned to synonymy here. Lundell correctly noted the alliance of *C. allenii* with *C. williamsii*, but distinguished *C. allenii* on the basis of a furfuraceous-lepidote indument and large apiculate spathaceous ochreolae. Additional specimens collected by Allen in Panama show many intermediate conditions in both characteristics.

Coccoloba lehmannii is currently known to occur in Columbia (type), Panamá, Peru, Costa Rica and Venezuela.

Costa Rica. La Palma, Suxaola Valley, Dunlap 467 (F, Y). Panamá. Bocas Del Toro: Daytonia farm, Region of Almirante, Proctor Cooper 421 (F, Y); Changuinola Valley, Dunlap 499 (F-type of C. changuinolana; B, Y). Coclé: El Valle, Allen 2181 (MICH-type of C. alleni; A, F), Allen & Alston 1857 (F, GH, MO).

Coccoloba lindaviana, sp. nov.

Frutex, 8 m., ramulis teretibus, leviter striatis, glabris; ocreis coriaceis, dense strigosis vel glabratis, 9–12 mm. longis; petiolis supra basem ocrearum gerentibus, 8–11 mm. longis, glabris; laminis oblongis, anguste oblongis vel oblongi-ellipticis, apice acutis vel breviter acuminatis, basi rotundatis, vel truncatis, 15×4.5 vel 22×8.5 cm. longislatisque, cori-

aceis, glabris, nerviis primariis 11–15, adscendentibus; inflorescentiis terminalibus, racemosis 12–15 cm. longis, rachis glabris, bracteis triangularibus, minutis, minusque 0.5 mm. longis, glabris, ocreolis membranaceis, glabris vel ciliatis ad marginem, bracteis aequaliter; floribus ignotis; pedicellis fructiferis 1.5–2 mm. longis, glabris; fructu ovato, 8 mm. longo, 6 mm. diametro, ad apicem obtuse coronato; acheniis castaneis, levibus, nitidis.

Honduras. Yoro: Aguan river valley, vicinity of Coyoles, Yuncker, Koepper & Wagner 8032 (GH-holotype; F); Cortés, canyon of Rio Piedras, 3 km. from San Pedro Sula, Molina 3430 (F); El Encanto in Montana La Cumbre, Molina 3577 (F); Montana de Rio Piedras, Molina 3555 (F).

The Molina collections bear an unpublished name attributed to Standley and L. Williams. I agree with them that a new taxon is represented here, even though this species is currently known only from old and fruiting specimens. *Coccoloba lindaviana* is, therefore, distinct on the basis of the leaf shape, the position of the leaves, which are borne above the base of the ocreae, and by the oval fruit which is slightly coronate at the apex. It is also similar to *C. hondurensis*, differing in the venation of the leaves and the position of the petiole base. All of the fruits I have examined had fully-formed seeds. Nevertheless, there is a possibility of a hybrid origin of this species.

The species is named in honor of Gustav Lindau who published a monograph of the genus *Coccoloba* in 1890.

Coccoloba lindeniana (Bentham) Lindau, Bot. Jahrb. 13: 82. 1890.

Campderia lindeniana Bentham, in Benth. & Hook. Gen. Pl. 3: 103. 1880.

This species is known only from the type collection made by J. Linden (1602) in Tabasco, near Teapa, Mexico, in May, 1840. An altitude of 300 m. is given on the collector's label. Specimens have been seen in the herbaria at Geneva, Leningrad and Paris, as well as a fragment in the Berlin herbarium.

Coccoloba lindeniana seems distinctive among Mexican and Central American species in the very pubescent leaves and inflorescence axis and the pubescence of the bracts and ocreolae. It may prove to be nothing more than the pubescent form of C. acuminata which Lindau described as C. acuminata var. pubescens. Coccoloba acuminata is widely distributed through Central America and adequately represented in herbaria, although only a few collections are available from Guatemala. The pubescent phase, which I do not recognize as a distinct taxon, is found throughout the range of the species. The abundance and persistence of the pubescence varies.

The inflorescence of *Coccoloba acuminata* is characteristically interrupted, with the axis swollen below each flower cluster. The clusters therefore appear at an acute angle to the inflorescence axis. In *C. lindeniana*

the axis is not swollen and the flower clusters appear to be produced flat on the axis.

The final position of Coccoloba lindeniana will await the collection of more material from Mexico. It is to be hoped that some of this will be in fruiting condition.

Coccoloba X lundellii Standley (pro sp.)

Coccoloba lundellii Standley, Publ. Field Mus. Bot. 8: 138. 1930. Coccoloba suborbicularis Lundell, Lloydia 2: 84. 1939.

In the original description of Coccoloba lundellii Standley stated. "Evidently a relative of the widespread C. schiedeana Lindau, but differing conspicuously in its very broad leaves, somewhat suggestive of those of the common sea grape, C. uvifera."

A few years later Lundell described Coccoloba suborbicularis and reported that "among the species of the Yucatan Peninsula, C. suborbicularis

is unique in having the leaf conspicuously unequal at the base."

The type of Coccoloba lundellii bears a few fruits, two of which were opened and found to be sterile. The type specimen of C. suborbicularis bears a few staminate flowers. Both holotypes show many of the characteristics of C. uvifera. The few fruits, the clustered flowers, the puberulence and the asymmetrical leaf base are characteristics of C. uvifera. The broad. orbicular leaves are dominant on all specimens seen, but a few smaller oblong leaves, with a strong development of secondary veins when dry, are suggestive of some other influence.

Several hybrids of Coccoloba uvifera and neighboring species have been found or suggested in the flora of the West Indies and it appears that a parallel situation is present here. It is not clear from the material on hand whether the second parent is C. hondurensis, which may, in turn, be a variation of C. barbadensis, or C. reflexistora. Both species are known from the area of the hybrid.

British Honduras. Orange Walk District: Honey Camp, coastal region, Lundell 649 (F-holotype; DS, GH). STANN CREEK DISTRICT: Stann Creek Railway, Gentle 2687 (MICH-holotype of C. suborbicularis; A, F); Stann Creek Valley. Gentle 2716 (A, MICH); Middlesex, Gentle 2877 (A, MICH), 2890 (A, MICH).

(To be concluded)



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STUDIES IN THE GENUS COCCOLOBA, VII. A SYNOPSIS AND KEY TO THE SPECIES IN MEXICO AND CENTRAL AMERICA *

RICHARD A. HOWARD

Coccoloba macrophylla Sessé & Mociño, Fl. Mex. ed. 2. 96. 1894.

Although *Coccoloba macrophylla* appears to be published as a new epithet in the "Flora Mexicana," the name is a later homonym of *C. macrophylla* Desf. ex Hook. (see Jour. Arnold Arb. 38: 225–227. 1957), a synonym of *C. rugosa* Desf. There are no specimens cited by number in the work of Sessé and Mociño and all of their collections I have seen which bear the name are to be referred to *C. rugosa*. *Coccoloba rugosa* is endemic to Puerto Rico and the species is attributed to Mexico in error.

Coccoloba manzanillensis Beurling, Prim. Fl. Portobello in Kongl. Vetensk. Akad. Handl. 142. 1854; Lindau, Bot. Jahrb. 13: 209. 1890.

Campderia nematostachya Grisebach, Bonplandia 6: 4. 1858. Coccoloba nematostachya Lindau, Bot. Jahrb. 13: 208. 1890.

The original description of *Coccoloba manzanillensis* cited *Billberg 234* as the type collection and Lindau reported seeing specimens from the Berlin herbarium and from Stockholm. The fragment at Berlin which Lindau annotated is *Billberg 230*, although the Stockholm specimen, presumably the origin of the fragment, is correctly numbered *Billberg 234*. The collection was made on the island of Manzanilla near the port which Lindau called Puerto Belo, known on modern maps as Porto Bello.

The name of this species was originally spelled "manzinellensis" by Beurling, but the spelling was changed to "manzanillensis" by Lindau. While the island where Billberg collected the type specimen is not on modern maps, Beurling's intention in describing the species is obvious. "Manzanillo," or "little apple" in Spanish, is commonly applied to the widespread and infamous strand plant *Hippomane manchineel* and although Lindau failed to comment on his correction of an orthographic error or to cite the original spelling, it seems desirable to allow this correction to stand.

^{*} Continued from vol. XL, p. 203.

Campderia nematostachya Griseb., transferred to Coccoloba by Lindau, is based on an unnumbered Andersson specimen from Panama. A specimen from the Meisner herbarium, now at the New York Botanical Garden, appears to be identical with the Göttingen specimen and part of the Andersson collection. A label bears Grisebach's handwriting, but unfortunately it carries the legend, "Coccoloba fagifolia Guadeloupe? coll. Duchassaing." The label is obviously incorrect.

Lindau recognized both *Coccoloba nematostachya* and *C. manzanillensis*. He distinguished them by placing *C. manzanillensis* in a group of species having glabrous leaves, while associating *C. nematostachya* with species having persistent pubescence. However, examination of the specimens cited shows the distinction which Lindau established to be untenable, since it is based on the age of the specimen. *Coccoloba nematostachya*, therefore, must be considered to be the same as *C. manzanillensis*. A long foliar ocrea distinguishes this species which is further characterized by having long, almost silky, hairs.

The Shattuck specimen cited carries a plant of Oryctanthus cordifolius as a parasite.

Bailey 42 is the first mature specimen with fruit.

Panamá. Canal Zone: Barro Colorado Island, L.H. & E.Z Bailey 42 (f), Shattuck 425 (f); between Gatún and Lion Hill. Pittier 2570 (ny). Colón: Porto Bello, Billberg 230 (b). Darién: La Palma, Pittier 6599 (gh). Panamá: Pacora, Allen 3450 (a, brux, f, mo). Province unspecified: location unspecified, Andersson s.n. (goet-type of C. nematostachya; b, ny), Billberg 234 (f-photo; s).

Coccoloba matudai Lundell, Contr. Univ. Mich. Herb. 7: 8. 1942.

Further study of populations in the field may prove this species to be a hybrid, possibly of *Coccoloba belizensis* and *C. montana*. However, the collections assigned here show an even greater range of leaf size, shape and texture than is normally found in either species. Lundell described both staminate and pistillate flowers, the former apparently from *Matuda 2002* and the latter from *Matuda 4315*. No fruits were formed. The species at present is recognizable only through the character of the branched inflorescence.

México. Сніараs: Finca Olvido, Mapastepec, Matuda 2002 (A, MICH, NY, US); Saxchanal, Sierra Madre, Matuda 4315 (місн-holotype; A); Cascada, Siltepec, Matuda 5144 (F, GH).

Coccoloba montana Standley, Jour. Wash. Acad. 13: 368. 1923.

Coccoloba escuintlensis Lundell, Phytologia 1: 213. 1937. Coccoloba schippii Lundell, Bull. Torrey Club. 66: 594. 1939. Coccoloba steyermarkii Standley, Publ. Field Mus. Bot. 22: 138. 1940.

It is unfortunate that the oldest name to be applied to this taxon is based on a sterile, fast-growing shoot. In describing *Coccoloba montana* Standley suggested that the "leaves of this *Coccoloba* are so distinct from

those of other Central American species that it seems desirable to give it a name for purposes of reference."

In the Flora of Guatemala (Fieldiana Bot. 24: 115. 1946) Standley and Steyermark suggested that the material represented is from "C. escuintlensis or perhaps of one of the other species listed." The specimens cited below include sterile shoots, as well as fertile specimens, but unfortunately no collections of both sterile, fast-growing shoots and fertile branches have been made from a single plant. Nevertheless, it appears certain that only one species is represented here. A pubescence in the axils of the veins and along the midrib appears in some of the specimens cited, but the leaves are usually glabrous when mature.

Coccoloba schippii was described by Lundell and the suggested relationship was with C. guyanensis Meisner. This was apparently made on the basis of the sessile flowers which were in bud, appearing in a "spicate" inflorescence. In their key to the Guatemalan species, Standley and Steyermark distinguished C. schippii on the characters of sessile flowers, conspicuous nerves and short racemes, but the type of C. schippii is obviously a branch with an immature inflorescence. Comparable inflorescence branches can be found on many of the other specimens cited. I believe the mature inflorescence of C. schippii as defined by Lundell would be elongated and the flowers would be borne on longer pedicels. Coccoloba schippii, with C. escuintlensis, seems properly referred to the synonymy of C. montana.

In describing *Coccoloba steyermarkii* Standley noted "the species is remarkable for its narrow leaves, more elongate and narrower than those of any other Central American species except *C. acuminata* HBK., to which it is not closely related. It is similar to *C. escuintlensis* Lundell [*C. montana*], of the Pacific slope of Guatemala and of Chiapas, but that has broader leaves, almost concolorous and with much fewer nerves." I have examined sufficient material of *C. montana* to be certain that the type specimen of *C. steyermarkii* can safely be included in *C. montana*. The few specimens which have been assigned to *C. steyermarkii* differ at most in a slightly more coriaceous texture to the leaves and less venation. In all other characteristics I have been able to compare, these same specimens agree well with material here considered as *C. montana*.

Coccoloba montana appears to be similar to C. padiformis which was described from South America and is represented by recent collections from Panama and Costa Rica. In all specimens seen the apex of the leaf is acute or acuminate, while C. padiformis has a rounded or obtuse leaf apex.

México. Chiapas: Escuintla, Matuda 413 (Mich-holotype of C. escuintlensis; A, F, GH); Acacoyagua, Matuda 17410 (F); Esperanza, Escuintla, Matuda 4143, 4145 (A, F, GH, MICH), 17466, s.n. (F). British Honduras. Toledo District: at the British Honduras-Guatemala boundary, Schipp S-687 (F-holotype of C. schippii).

Guatemala. Escuintla: Río Guacalate, Standley 60190, 89302 (f); between Río Jute and Río Pantaléon, Standley 63464 (f, Mich), 63488 (f); Las Lajas, Standley 64787 (f). Izabal: Puerto Barrios, Standley 25075 (us). Quezalte-

NANGO: Colomba, Skutch 2022 (A, F); Finca "Pireneos" below Santa María de Jesús, Standley 68207 (F); between Finca "Pirineos" and Patzulín, Standley 86954 (F), 86964 (MICH); between Santa María de Jesús and Calahuaché, Steyermark 33677 (F); Calahuaché, Steyermark 35473 (F); Río Dulce, west of Livingston, Steyermark 39533 (F-type of C. steyermarkii), 39404 (F). RETALHULEU: between Retalhuleu and Nueva Linda, Standley 87219 (F, US), 87291, 88516 (F); Ajaxá, east of Santa Cruz Muluá, Standley 88220, 88232 (F); vicinity of Retalhuleu, Standley 88604, 88807 (F, MICH); between Asintal and Colomba, Standley 87876 (F). SAN MARCOS: Río Mopá, below Rodeo, Standley 68770 (F); Finca Vergel, near Rodeo, Standley 68949, 68952 (F); Finca El Porvenir, Steyermark 37601 (F, MICH), 52336 (F). SUCHITEPÉQUEZ: Pueblo Nuevo, Standley 66936 (F).

El Salvador. Ahuachapán: Sierra de Apaneca, region of Finca Colima, Standley 20061 (us-holotype of C. montana; GH). La Libertad: near Comasagua between Finca Germania and Finca San Antonio, Carlson 238 (F).

Coccoloba nicaraguensis Standley & L. Williams, Ceiba 3: 198. 1952.

This species is based on material which is inadequate for an accurate analysis. All the specimens available to me were collected in the mountains at an altitude of 1050-1350 m. west of Jinotega, Department of Jinotega, Nicaragua. The four numbers cited in the original description are Standley 9768, 10194, 10233 and 10409, the last of which is the holotype in the herbarium of the Chicago Natural History Museum. A fifth number, Standley 10318, was also referred to this species by the original authors by annotation, but was not cited in their paper. The type, Standley 10409, and one other, Standley 9768, bear young developing leaves which have turned black on drying. Another collection, Standley 10233, bears both mature leaves as well as young blackish leaves comparable to the type. The other sheets are of mature branches. Only the type sheet bears flowers and this specimen has four immature inflorescences. On the basis of the sterile specimens with mature foliage, the material would be referred unhesitatingly to Coccoloba diversifolia, for it is strictly comparable to material described by Lundell as C. lancifolia and later referred by Standley and Stevermark to C. laurifolia, a species which is here called C. diversifolia. However, as indicated in the original description, the young inflorescence axis is minutely puberulent when seen under a microscope. In this characteristic the species is similar to C. cozumelensis. Stevermark 45669, from Cerro Chinajá, Department of Alta Verapaz, Guatemala, referred to C. diversifolia (C. laurifolia Standley & Stevermark), is an accurate match except for a glabrous inflorescence rachis.

Coccoloba novogranatensis Lindau, Bot. Jahrb. 13: 192. 1890.

Coccoloba caribaea Urban, Symb. Ant. 5: 337. 1907. Coccoloba waittii Johnston, Sargentia 8: 122. 1949.

The typification of this species has been discussed in an earlier paper where the lectotype was designated as *Triana 978* (P), Bogotá, Colombia (Jour. Arnold Arb. 40: 85–87. 1959). For over sixty years no collections

have been assigned to *Coccoloba novogranatensis*. This is a wide-ranging species found at lower elevations and along the seacoast. The sole exception is *R. S. Williams 945*, a collection of very young material from an altitude of 2800 feet in Panama. Additional material from this area may prove this to be *C. obovata*, for in both species the leaves are attached above the base of the ocrea. In *C. novogranatensis* the leaf blades are broadest above the middle, while those of *C. obovata* are broadest below the middle. Leaves of adventitious shoots are nearly indistinguishable. The species are clearly distinct, however, in the stages with mature flowers or fruit. The Steyermark collection from Guatemala, also sterile, is referred here, again with some question.

Johnston does not make any specific comparison in describing *Coccoloba* waittii, noting only that "it is a well-marked species." Although all the specimens I have seen from Panama are from the Pacific side of the Isthmus, *C. novogranatensis* is to be expected to be on the Atlantic coast, as well.

This species is known from the Lesser Antilles, Trinidad, Venezuela, Colombia and Peru, in addition to the specimens cited below from Guatemala and Panama.

Guatemala. Petén: Between Cerro Ceibal and Ceibal, Steyermark 46178 (f). Panamá. Herrera: Pesé. Allen 802 (f, gh, mo, ny). Panamá: Perlas Islands, Pedro Gonzalez, Allen 2602 (mo); San José Island, Erlandson 377 (gh), 550 (gh, ny), 216 (gh); Harlow 41 (gh); Johnston 213 (gh, mo), 230 (gh-type of C. waittii; mo), 975, 1306 (gh). Darién: Cana, Williams 945 (ny, us).

Coccoloba obovata HBK. Nov. Gen. 2: 176. 1817.

Coccoloba coriacea Willdenow ex Lindau, Bot. Jahrb. 13: 194. 1890, not Sagra. Coccoloba goudotiana Weddell, Ann. Sci. Nat. Bot. III. 13: 260. 1849. Coccoloba riparia Lundell, Contr. Univ. Mich. Herb. 6: 11. 1951.

Coccoloba obovata HBK. was based on a Humboldt specimen collected in flower in June, 1805, at Honda in Colombia. Although the specimen in the Willdenow Herbarium has been considered authentic, I wish to designate a sheet in the herbarium at Paris as the lectotype since the latter sheet is more complete, in better condition and bears a label with more adequate data than does the specimen in Berlin.

The name *Coccoloba coriacea*, attributed to Willdenow by Lindau (not *C. coriacea* Sagra), was not published by Willdenow but occurs on the label of the lectotype as the first two words of a long polynomial written in one line. On the sheet which Lindau saw in the Willdenow herbarium the label is smaller and the name "*Coccoloba coriacea*" appears as one complete line, the two words being underlined. It is unfortunate that Lindau chose to pay any attention to this binomial which has no standing.

Lundell described *Coccoloba riparia* from Panama but did not discuss the species or indicate affinities or differences. *Coccoloba riparia* as represented by the type specimen is clearly the same as *C. obovata*.

The majority of the specimens cited below from Central America had been identified either as Coccoloba marginata or C. leptostachya. I con-

sider the former species to be the same as C. nitida and C. guianensis from Trinidad and northeastern South America. The latter species, C. lepto-

stachya, is referred to the synonymy of C. barbadensis.

Coccoloba obovata is known from Costa Rica, Panama and Colombia. The type is Humboldt s.n. from Honda, province of Tolima, Colombia. The type of Coccoloba goudotiana is Goudot s.n. from San Luis in Colombia.

Costa Rica. Peninsula Osa near Puerto Jimenez. Brenes 12218 (F); Cufodontis 91 (F); San Rafael de San Ramón, Brenes 22020 (F, NY); Santo Domingo de Golfo Dulce, Tonduz 7122 (F, GH, US), 9934 (BR, LE, M).

Panamá. Canal Zone: Barro Colorado Island, Aviles 998 (F), Salvoza 984 (A), Shattuck 1063 (F), Starry 298 (F); F. L. Island, Bangham 593 (A, F); Salamanca Hydrographic Station, Dodge, Steyermark & Allen 16983 (BR, DS, G, K, MO), 16983a (BR, K, MICH, MO); Woodson, Allen & Seibert 1572 (A, F, MO); northwestern part of Canal Zone, Johnston 1519 (MO); between Tumba Vieja & Salamanca, Stevermark & Allen 16758 (BR. MO). CHIRIQUÍ: Cerro Galera Chorcha, Gualaca, Allen 5020 (A, MO); San Félix, Allen 3655 (A, BR, MO); between San Félix and Cerro Flor, Allen 1917 (F, GH, MO); Progreso, Cooper & Slater 270 (US); San Bartolomé, Woodson & Schery 947 (F. MO); between Río Chiriqui and Remedios, Woodson, Allen & Seibert 1182 (A. F. MO). Coclé: El Valle, Allen 2229 (MICH-holotype of C. riparia).

Coccoloba padiformis Meisner, DC. Prodr. 14: 166. 1856.

Coccoloba roseiflora Standley & L. Williams in Allen, Preliminary Index to the Trees of the Golfito-Palmar area, 37. 1952; Rain Forests of Golfo Dulce, 177. 1956.

Coccoloba padiformis Meisner is very similar to C. densifrons Martius and perhaps is not distinct. At the present time the distinguishing characteristics of C. densifrons are the larger leaves, broadest above the middle, and the longer inflorescence rachis. Lindau did not include C. densifrons in his key; hence it is difficult to determine his basis of separation.

Coccoloba candolleana Meisner is likewise similar, if not identical, and further material is needed for study before drawing the final limits of any of these species. Certainly the specimens of "Goudot 4" cited by Lindau in extending the range of C. candolleana from Bahia, Brazil, to Colombia are better referred to C. padiformis. The type of C. candolleana, Blanchet 1818, has a nearly orbicular and umbonate leaf blade. If this is true of the species and not just a growth form, C. candolleana can be maintained as a distinct species.

Coccoloba roseiflora, credited to Standley and L. Williams by Allen in the latter's book, "The Rain Forests of Golfo Dulce" is not validly published, since it lacks a description in Latin. The holotype in the herbarium of the Escuela Agricola Panamericana at Tegucigalpa cannot be sent on loan, but I have seen duplicates of the two collections cited by Allen and on the basis of these, refer the species to C. padiformis. Allen 5964 consists of branches with young leaves indicating a completely deciduous

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plant. Mature foliage of this species is represented by Allen 5944 and the Tonduz collection from the same area of Costa Rica.

The species is currently known from Costa Rica, Panama, Venezuela and Colombia. The type is *Moritz 377*, collected near Caracas in Venezuela.

Costa Rica. Puntarenas: Palmar Norte de Osa, Allen 5944 (F-isotype of C. roseiflora), 5964 (F); Santo Domingo de Golfo Dulce, Tonduz 7119 (A, F, GH), 7120 (A, F, GH).

Panamá. Canal Zone: South of Fort Sherman, Johnston 1737, 1814 (MO); Quebrada Ancha, Steyermark & Allen 17101 (MICH, MO); Río Indio de Gatun, Pittier 2785 (GH).

Coccoloba parimensis Bentham in Hooker, Lond. Jour. Bot. 4: 626. 1845.

Coccoloba parimensis var. schomburgkii Meisner, Fl. Bras. 5(1): 35. 1855.

Coccoloba excelsa var. glabra Lindau, Bot. Jahrb. 13: 171. 1890.

Coccoloba bracteolosa Meisner, Fl. Bras. 5(1): 30. 1855.

Coccoloba paraensis Meisner, Fl. Bras., 5(1): 38. 1855.

The habit of this plant has accounted in part for the confusion surrounding its description in botanical literature. With regard to the collections studied here, the specimens have been described as a liana, a slender climber, a small tree, a tree, or a tree with scrambling branches. As for the varying leaf aspects which have been described, many of which are cited below, there is no question in my mind that they can be associated with the growth habits of the plant. Other species in northern South America also show the habit of a woody, tree-like plant with scrambling branches. The branches are often so thin and tenuous as to be liana-like in character. Collections made from older plants or those growing in isolated situations show a tree-like habit. Collections from the ends of branches or from plants growing in thickets are likely to be considered liana-like.

Most of the specimens I have seen are in fruiting condition. One specimen, Maxon & Harvey 6700 from Panama, is in flower and has been cited by Lundell as Coccoloba bracteolosa Meisn. (Contr. Univ. Mich. Herb. 6: 9. 1941). The type specimen of C. bracteolosa was a staminate flowering specimen and all specimens I have seen referred to this species have likewise been in flowering condition. The same is true for C. parimensis. Coccoloba paraensis, however, was based on fruiting material and

only fruiting material has been referred to this species since.

The numerous specimens from Barro Colorado island were all collected near the laboratory and are either sterile or in fruit. Nevertheless, the series is elaborate and complete, showing the variation in leaf shape, size and texture between the flowering material called *Coccoloba bracteolosa* and the fruiting material called *C. paraensis*. The thin-textured leaves associated with the flowering condition indicate a tendency towards deciduousness in this species. The mature foliage associated with the fruiting specimens is coriaceous and the leaf blades are umbonate or bullate.

Although this evidence is convincing from the specimens on hand, Cocco-

loba bracteolosa was based on specimens from Bahia and Alagoas on the east coast of Brazil. It is possible that further collections from that area will show that *C. bracteolosa* is better assigned to the synonymy of *C. ochreolata*. The latter species is distinctive in the shape of the fruit.

Coccoloba parimensis was based on a Schomburgk collection, without number, from Rio Parime. Lindau assigned this species to the synonymy of C. excelsa. I cannot agree completely with this conclusion and am recognizing these as distinct species to call attention to the problem. Field study and mass collections from one plant are needed. For the present, C. excelsa is distinct in being more pubescent on the lower leaf surface and on the inflorescence axis. Coccoloba excelsa also appears to have larger hairs which break off and leave clear hair bases or black-colored hair bases, either of which frequently appear as punctations. Coccoloba parimensis leaves, in contrast, are only puberulent with minute hairs. When Lindau assigned C. parimensis to the synonymy of C. excelsa he recognized a glabrous state which he called C. excelsa var. glabra. Lindau also recognized C. paraensis and distinguished between this species and C. excelsa on a key character of pubescence being present in C. excelsa and absent in C. paraensis. Lindau's C. excelsa var. glabra, therefore, becomes an anomaly in his key.

Meisner divided Bentham's Coccoloba parimensis, recognizing two varieties. Coccoloba parimensis var. schomburgkii contained the type and is assigned here to C. parimensis. Meisner's second variety, C. parimensis var. hostmanni, is better referred to C. excelsa.

Coccoloba paraensis Meisner was based on an unnumbered Martius specimen from Iquapèmirim in the Province of Pará and a Spruce collection, also without number, from Barra in the province of Rio Negro. The latter collection has been distributed with labels written "Coccoloba /2/" and printed "In vicinibus Barra, Prov. Rio Negro, coll. R. Spruce, Dec.—Mart. 1850—51." The Spruce specimens appear in many herbaria and all are unidentified. No type was designated by Meisner but the Field Museum has distributed photographs of the Martius collection from the Munich herbarium and indicated this as the lectotype.

I have seen material of this species from Brazil, British Guiana, Colombia, Peru and Panama.

Panamá. Canal Zone: Barro Colorado Island, Aviles 15 (f), L.H. & E.Z. Bailey 219 (f), 654 (gh), Bangham 447 (A, f), Salvoza 904 (A), Shattuck 1123 (f), Standley 41099 (A), Wetmore & Woodworth 859 (A). Panamá: Juan Díaz region, near Tapia river, Maxon & Harvey 6700 (f).

Coccoloba pubescens Linnaeus, Syst. Nat. ed. 10. 1007. 1759.

This is a West Indian species which I have seen, studied in the field, collected many times and discussed in a previous paper (Jour. Arnold Arb. 38: 229–231. 1957). Lindau described the species (Bot. Jahrb. 13: 202. 1890), citing, in addition to West Indian collections, a Schiede specimen from "herb. Petrop." credited to Mexico without specific location

and a specimen from "Guyana batava" which Meisner also cited. I have not seen Kegel 1339 which Meisner cited from Dutch Guiana, nor was it present in the Prodromus Herbarium at Geneva.

Coccoloba pubescens was also credited to the Mexican flora by Standley in his "Trees and Shrubs of Mexico" (page 245), although he uses a later homonym, C. grandifolia Jacq., for the species. No recent collections are cited by Standley and none is available to me. This species is conspicuous wherever it occurs and it is difficult to believe that it would be overlooked or not be collected in a flora where sterile material has been the basis of many species.

I have on loan three sheets credited to Schiede from Mexico and identified as *Coccoloba pubescens*. Two of these sheets, one from the Berlin herbarium and one from Paris, were not cited by Lindau and do not bear his annotation label. These sheets bear a number "60" in the same script as the generic name, although the specific name and the collector and locality of "Mexico" are in a different hand and possibly may be different from each other. The sheet from the herbarium at Leningrad bears Lindau's annotation label, as well as a label indicating that the specimen was from Fischer's herbarium and was collected at "la Cuesta grande de Chiconquraos." There is no indication of the collector (i.e., Schiede), and "Mexico" has been added in a different script.

Schiede's travels in Mexico have been described in Linnaea, volumes four and five, in 1829 and 1830. There are several references to *Coccoloba*. One is referred to as a seacoast plant known as "uva" and this is probably *C. uvifera*. The other two refer to plants collected between Río de Tecoluta and Río de Nantla and at Cambre del Obispo. Neither of these locations fits the data cited above for *Schiede 60*. Lindau refers to three unnumbered Schiede collections, but all are cited by him as having come from "Mexico" without further locality.

All three specimens called "C. pubescens" consist of a single leaf and a short piece of branch with a terminal bud. The leaves are large (30 \times 28 cm. and 38 \times 32 cm.) and the branch stout (10 mm. diameter), suggesting an adventitious shoot or one of vigorous growth. The leaves are suggestive of Coccoloba pubescens and the pubescence distribution and hair type can be matched in recent West Indian collections. However, the terminal bud is not that of the West Indian C. pubescens but is that of the Mexican C. liebmannii Lindau. Only one collection of C. liebmannii (Ferris 6061 from the vicinity of Manzanillo, Colima, Mexico) is available showing the large leaves of vigorous and adventitious shoots. In the three examples of Ferris 6061 cited elsewhere in this paper, the specimen consists of a fertile branch in fruit with small leaves (average 9 \times 3.5 cm.) and a single detached larger leaf (23 \times 13 cm). No stem section is available for these larger leaves. The pubescence is similar to that of the Schiede specimens; the terminal bud is the same, though the leaves are smaller.

The Fischer herbarium, particularly in reference to *Coccoloba* specimens, is primarily of fragments from cultivated plants; adventitious shoots and associated leaves are common. It seems likely that the Schiede specimen

cited by Lindau is from a plant cultivated in a greenhouse and that the country of origin given on the label is faulty. However, if the data with the specimen are correct, it is probable that this specimen should be identified as C. liebmannii and the record of C. pubescens be removed from the Mexican flora. Additional field study of C. liebmannii is needed to determine variation in size and shape of the leaves and the terminal buds of vigorous and adventitious shoots.

Coccoloba reflexiflora Standley, Publ. Field Mus. Bot. 4: 203. 1929. Coccoloba colonensis Lundell, Contr. Univ. Mich. Herb. 6: 9. 1941.

This species is readily distinguished by the basically obovate-oblong leaves, broadest above the middle, which are borne on pale grayish petioles which, in turn, are borne above the bases of the ocreae. The margin of the leaf is invariably revolute and the upper surface is darker than the lower surface upon drying.

The inflorescence is rarely longer than the leaves and the staminate flowers appear to be reflexed, a character on which Standley based the specific name. However, the fruiting pedicels are at right angles to the inflorescence axis and are 1-1.5 mm. long, exceeding the ocreolae. The fruits are smaller than those of other Central American species and the perianth lobes are imbricate, not coronate, over the obtuse apex of the achene.

Coccoloba colonensis was based by Lundell on sterile material. He suggested an affinity with C. lundellii, which I have concluded is a hybrid of C. uvifera and an unknown parent, possibly C. reflexistora. The type of C. colonensis is from an adventitious shoot. In the characteristics of the ocreae and the point of attachment of the petiole, as well as in the color and venation of the leaf blade, the specimen is clearly identical with comparable vegetable adventitious shoots of C. reflexiflora.

México. Campeche: Villahermosa, Lundell 1139 (f., MICH). Yucatan: Chichén Itzá, Steere 1600 (F. MICH). Guatemala. Petén: Between Uaxactun & San Clemente, Bartlett 12815 (F. MICH); Carmelita, Egler 42-244 (F). British Honduras. Belize District: Northern River, Gentle 990 (A, F, LE, MICH); Maskall, Gentle 1223 (A. F. GH, MICH), 1274 (A. DS, F. GH, MICH), O'Neill 8557 (A, F, MICH); Sibun Road, southwest of Belize, O'Neill 8570 (Mich). Corocal DISTRICT: San Antonio, Schipp S-614 (F. GH). ORANGE WALK DISTRICT: Honey Camp, Lundell 488 (A, F), Meyer 45 (F); Hillbank, Winzerling I-17 (Y). STANN CREEK DISTRICT: Silk Grass Creek Reserve, Gentle 2959 (A, MICH). TOLEDO District: Monkey River, Gentle 4150 (A. MICH). District unspecified: Tower Hill, Karling 15 (F-holotype; US); Manatee Lagoon, Peck 92 (GH). Honduras. Colon: Guarunta, Wispernini Camp, C. & W. von Hagen (Ny-isotype of C. colonensis).

Coccoloba spicata Lundell, Bull. Torrey Club 66: 594. 1939.

"Coccoloba coronata Jacquin?." Millspaugh, Publ. Field Mus. Bot. 1: 294. 1896.

Lundell compares this species with Coccoloba mayana Lundell which I have placed in synonymy with C. barbadensis Jacq. The specimens cited below, with one exception, are those also cited by Lundell in the original publication.

Coccoloba spicata was based on staminate flowering material. Only one fruiting collection is known. The species appears distinct in the sessile flowers and densely flowered inflorescence. In fruit the pedicels are scarcely developed and, if present, are less than one-fourth the length of the ocreolae. In contrast to C. barbadensis, the apex of the fruit is obtuse to rounded and not at all coronate. The perianth lobes are orbicular and represent the upper third of the fruiting perianth. In sterile condition it is almost impossible to distinguish C. spicata from C. barbadensis.

México. Quintana Roo: Coba, Lundell 7813 (A, F, Mich). Yucatán: Chichén Itzá, Bequaert 103 (A, F); Valladolid, Flores 1935 (F); Kancabdzonot, Gaumer & sons 23894 (A, F); Izabal, Gaumer 819 (F, GH); Location unspecified, Gaumer 23976 (F, GH, Mich), Steggerda 1B (F); Chichén Itzá, Sacred Cenote, C.A. & A.A. Lundell 7325 (Mich-holotype; A, F). British Honduras. Corozal District: Santa Rita, Lundell 4951 (A, F, GH, MICH). Orange Walk District: Honey Camp, Lundell 560 (DS, F, GH).

Coccoloba standleyana Allen, The Rain Forests of Golfo Dulce 177, 409. 1956.

The holotype of this species, *Allen 6645*, is in the herbarium of the Escuela Agricola Panamericana, Tegucigalpa, Honduras. Since the school does not send specimens on loan, I have been unable to study the material; duplicates are not available in other institutions.

Coccoloba standleyana is based on sterile material collected in the Esquinas forests of Costa Rica, at an elevation of 200 feet. Allen suggests that the species is "probably related to C. hirsuta Standl. and C. belizensis Standl. but amply distinct in the much smaller ocreae and other characters." I regard C. hirsuta as the same as C. belizensis and I suspect that Coccoloba standleyana will ultimately be assigned to the synonymy of C. belizensis.

Coccoloba swartzii Meisner, DC. Prodr. 14: 159. 1856.

Coccoloba corozalensis Lundell, Bull. Torrey Club 66: 588. 1939. Coccoloba gentlei Lundell, Bull. Torrey Club 66: 591. 1939.

Coccoloba swartzii has not been recognized previously in the flora of Central America, although it is a common element in the vegetation of the West Indies, occurring from Cuba and Jamaica to Curaçao and Aruba and having a great variation in leaf size and shape on all the islands of the Lesser Antilles. The collections cited can be compared favorably with many other collections from the West Indies, especially those populations occurring in the Virgin Islands, the Leeward Islands and the French islands of Guadeloupe and Martinique.

I am not satisfied that the Central American specimens have characteristics of sufficient value to create even a geographical variety. Only the

slightly more tenuous inflorescence axis, with its fewer flowers, appears to differ from the West Indian representatives of the species.

The type of *Coccoloba gentlei* Lundell is *Percy Gentle 56*. The meager material appears to be from a vigorous shoot, perhaps even an adventitious shoot. If considered as the latter, the leaves are comparable to collections I have made on St. Kitts and Montserrat (*R.A. & E.S. Howard 11882*, 11867, 11938). In describing the species Lundell put undue emphasis on the branched inflorescence which in reality is a spike with one anomalous branch developing from the base. This is not an unusual condition either in the genus, or in the West Indian specimens of *C. swartzii*. Standley and Steyermark (Fieldiana Bot. 24: 108. 1946) place this species in a section of their key with other species having much-branched panicles.

Coccoloba corozalensis Lundell is clearly the same as C. swartzii.

British Honduras. Belize District: Belize-Sibun Road, Gentle 56 (Michholotype of C. gentlei); Pine Ridge, Maskall, Gentle 1113 (A, F, GH, MICH). COROZAL DISTRICT: Xiabe, Lundell 4908 (Mich-type of C. corozalensis; A, GH). Orange Walk District: Honey Camp, Lundell 347 (DS, F). Toledo District: Monkey Ridge, Gentle 3651, 3656 (A, Mich). District unspecified: Cornhouse Creek, Bartlett 11281 (Mich, NY); Mullins River at Stann Creek Road, Gentle 3359, 3368 (A, MICH). Honduras. Point Triumfo, Puerto Sierra, Wilson 33 (NY).

Coccoloba tuerckheimii Donnell Smith, Bot. Gaz. 37: 213. 1904.

Coccoloba guatemalensis hort. ex Lindau, Bot. Jahrb. 13: 226. 1890. Coccoloba latifolia Goyena, Flora Nicarag. 2: 707. 1911, not Lam.

According to the collectors' labels, several botanists have believed *Coccoloba tuerckheimii* to be similar to, if not identical with, *C. latifolia* Lamarck from Trinidad and northern South America, although John Donnell Smith made no comparison of these two species in his original description. In a footnote to his monograph of the genus, Lindau assigned cultivated material carrying the unpublished horticultural name *Coccoloba guatemalensis* to *C. latifolia*. I have seen this material which has been attributed to Guatemala and believe it is more correctly referred to the present species than to *C. latifolia*.

Coccoloba latifolia is similar to C. tuerckheimii in having stout, generally hollow stems, petioles borne slightly above the base of the ocrea, and a paniculate inflorescence. The leaf base is generally rounded or cordate, while the blades are bullate between the veins. In contrast, C. tuerckheimii has solid stems with leaf blades tapering to a cuneate base and appearing to be flat. The fruits of C. tuerckheimii appear to be larger and more stalked than those of C. latifolia.

Guatemala. Alta Verapaz: Finca Santa Inés, Record & Kuylen G-92 (Y); Tucurú, Standley 70724 (F); between Campur and Socoyó, Standley 91708 (F); Cubilgüitz, Steyermark 44674 (F), Tuerckheim 8493 (F-isotype; GH); Cerro, Chinaja, Steyermark 45568 (F). Izabal: Río Dulce, Livingston, Steyermark 39552 (F).

Honduras. Atlántida: Lancetilla Valley near Tela, Standley 55812 (A, F);

La Ceiba, Yuncker, Koepper & Wagner 8603 (F, GH, MICH); Tiquitapa, Howard, Briggs, et al. 560 (A). Yoro: Progreso, Hottle 92 (F); Subirana, C. & W. von Hagen 1058 (F). Nicaragua. Chontales: La Libertad, Standley 9064 (F). Costa Rica. Alajuela: San Carlos, Suere, A. Smith H-1694 (F, MICH). Panamá. Bocas del Toro: Changuinola Valley, Island of Potrero, Dunlap 181 (F, Y). Colón: Dos Bocas, Río Fato Valley, Pittier 4197 (F). Cultivated. Kalbreyer s.n. as C. guatemalensis (B).

Coccoloba umbilicata Sessé & Mociño, Fl. Mex. ed. 2. 96. 1894.

No specimens are cited in the original description in which the species is attributed to Mexico. I have seen the Madrid specimens on loan to the Field Museum, and the sheets labelled "C. umbilicata" are all to be referred to Coccoloba pyrifolia Desf., a species limited to Puerto Rico.

Coccoloba uvifera Linnaeus, Syst. Nat. ed. 10. 1007. 1759.

Polygonum uvifera Linnaeus, Sp. Pl. 365. 1753.

A common strand plant known to all botanical collectors and, as a consequence, one which is poorly represented in herbaria. Presumably the species has a wider distribution in Mexico and Central America than is indicated by the collections cited below.

México. Campeche: Lerma, Seler 4019 (A, F); Champotón, Steere 1968 (f., mich). Sinaloa: Mazatlán, J. Gonzalez Ortega 7203 (brux). Tamaulipas: Moron, LeSueur 103 (f); Tampico, Palmer 477 (f). Yucatán: Chichancanab, Gaumer 1897 (F); Sisal, Gaumer 23235 (F); Cozumel Island, Goldman 673 (F), Millspaugh 1590 (F); Progreso, Goldman 603 (F); C.L. & A.A. Lundell 8060 (MICH); Location unspecified, Gaumer 638 (F), Millspaugh 6 (F). Guatemala: Izabal: Bay of Santo Tomás, Stevermark 39248 (F, MICH). British Honduras. Belize District: Turneffe Island, Egler 42-42 (F); Belize. Gentle 27 (A, F, MICH). COROZAL DISTRICT: Corozal, Lundell 4927 (F. MICH). STANN CREEK DISTRICT: Stann Creek, Gentle 3119 (MICH), 3120 (MICH), 3131 (A. MICH), 3123 (MICH). District unspecified: All Pines, Schipp 796 (A, F. MICH). El Salvador. LA LIBERTAD: La Libertad, M.C. Carlson 575 (F). SAN SALVADOR: San Salvador, Calderón 2624 (F). Honduras. ATLÁNTIDA: Tela, Chickering 51 (MICH), Standley 53056 (A, F), Yuncker 4655 (A, F, MICH); Ceiba, Yuncker, Koepper & Wagner 8235 (F. MICH). COMAYAGUA: Comayagua, Standley & Chacon 5486 (F). Department unspecified: Puerto Sierra, P. Wilson 23 (F). SWAN ISLANDS: Nelson 22 (GH). Nicaragua. Zelaya: Bahia de Bluefields, Río Escondito, A. Molina 1281 (F). Costa Rica. Alajuela: San Roque de Barbe, León 10 (F). Limón: Limón. Costa de Portete. Quirós 508 (F); Talamanca, Puerto Viejo, Tonduz 9423 (BRUX). PUNTARENAS: Los Loros and Tivives. Brenes 22661 (F). Panamá. Bocas del Toro: Almirante, G. Proctor Cooper 558 (F, Y); Changuinola Valley, Cooper & Slater 82 (Y); Chiriqui Lagoon. Von Wedel 2826 (MO). Province unspecified: Isthmus of Chagres, Fendler 287 (LE, MO).

Coccoloba venosa Linnaeus, Syst. Nat. ed. 10. 1007. 1759.

Campderia floribunda Bentham, Bot. Sulphur 159. tab. 52. 1846.

Campderia mexicana Meisner, DC. Prodr. 14: 171. 1856.

Coccoloba alagoensis Weddell var. major Meisner, DC. Prodr. 14: 163: 1856.

Coccoloba floribunda Lindau, Bot. Jahrb. 13: 217. 1890. Coccoloba molinae Standley & L. Williams, Ceiba 3: 198. 1952.

The synonymy given for *Coccoloba venosa* is new, *C. floribunda* and *C. molinae* and *Campderia mexicana* being reduced here for the first time. An examination of the type specimens alone would make this decision a questionable one, except for *C. molinae* which is clearly the typical West Indian expression of *C. venosa*. Standley and Williams described *C. molinae* in 1952 but were incorrect in believing that their new species was unlike any material then known from southern Central America. In his Flora Nicaragüense (2: 707. 1911), M. Ramírez Goyena recognized *Coccoloba nivea* from Nicaragua and gave the same common name reported for *C. molinae*. *Coccoloba nivea* Jacq. is a synonym of *Coccoloba venosa* L. The specimens which Standley and Williams cite for *C. molinae* are obviously variable, since two phases of coriaceous leaves are shown even in the two specimens of the type number which I have seen. *Coccoloba molinae* is undoubtedly the same as *C. venosa* L.

Coccoloba floribunda described by Bentham was based on material collected on the voyage of the Sulphur. The type came from Tiger Island in the Gulf of Fonseca, Honduras. Campderia mexicana was based on Andrieux 115, a specimen from Tehuantepec, Oaxaca, Mexico, and since there is no difference between these, Lindau placed Campderia mexicana in

synonymy. Recent collections from the same area are also cited.

Coccoloba floribunda as defined by Lindau and as generally recognized in current floras is strikingly different from C. venosa as generally recognized in the West Indies. In drier areas the leaves are thick and almost rigidly coriaceous. The leaf apex is obtuse, rounded or even truncate and the base slightly narrowed but rounded or obtuse. Bentham described the leaf base as emarginate to slightly peltate, although the type specimen and the illustration fail to show the latter condition. The leaves are much smaller and the inflorescence generally shorter and thicker than C. venosa. At greater altitudes and in wetter areas, according to the data on the specimens studied, the differences are less obvious between C. floribunda and C. venosa. The leaves become thinner, longer, the apex pointed, the inflorescence axis longer and more tenuous in comparison.

A full range of variation between the extremes has been found in the specimens cited below to indicate a variable population over the geographic range of the species. I have been unable to find any stable characteristics which would allow the segregation of the smaller, coriaceous-leaved form as a geographic variety. Lindau separated *C. floribunda* from *C. venosa* (his *C. excoriata*) in a key to the species (Bot. Jahrb. 13: 130. 1890) by placing *C. floribunda* in a group in which the leaves are more or less pubescent below or at least barbellate in the vein axils, while *C. venosa* reportedly had glabrous leaves. Comparable pubescence along the midrib and in the axils of the veins is found in the West Indian specimens, so Lindau's distinction does not hold.

Additional study of this species in the field is needed to establish leaf shape, size and texture variations on single plants in Central America, espe-

cially since none of the collections I have seen represents adventitious or fast-growing shoots. In their treatment of *Coccoloba floribunda* for the Flora of Guatemala (Fieldiana Bot. 24: 113. 1946), Standley and Steyermark described the species as "a densely branched shrub or tree, sometimes 9 meters high, with a broad spreading crown, the low trunk often gnarled and twisted, sometimes a meter in diameter." This description fits well many of the plants seen in the Antilles. Variations in leaf texture from membranaceous and chartaceous to coriaceous have also been encountered in *C. venosa* in the Lesser Antilles, although a reduction in leaf size or an adjustment of shape comparable to that found in many of the specimens cited has not been encountered.

Among the specimens cited is *Standley 74249* from Guatemala, represented by two sheets from two different locations.

Coccoloba venosa is under cultivation in Cuba and has been reported from Jamaica in old literature, but no specimens referable to the island have been seen. It is common in Hispaniola, Puerto Rico and the Virgin Islands south through the Lesser Antilles to Trinidad. I have also seen two collections from Venezuela.

México. Chiapas: Belem, Mapastepec, Matuda 16741 (f, gh); Tapachula, Fisher 35437 (f, ny); Huixtle, Matuda 16795 (f); Las Garzas, Acapetagua, Matuda 2683 (a, f, mich); Mojarra, Tonala, Matuda 17125 (f). Colima: Manzanillo, Ferris 6057 (ds), 6245 (a, ds). Guerrero: Acapulco, MacDaniels 199 (f, mich). Jalisco: Mazatlán, Liebmann s.n. (b). Oaxaca: Salina Cruz, Deam 121 (gh, mich), L. I. Williams 9708 (f, mich); Tehuantepec, Zuccarini s.n. (m). Province unspecified: Haenke 1608 (f); Sessé & Mociño 5432, 5435 (f).

Guatemala. Chiquimula: Quebrada Shusho above Chiquimula, Standley 74249 (F). Guatemala: Location unspecified, Aguilar 550 (F). Jutiapa: Jutiapa, Standley 75193 (F, MICH). Retalhuleu: Champerico, Bernoulli & Cario 2663 (LE), Standley 66507 (A, F), 87547 (F, MICH). Santa Rosa: between Chiquimulilla & El Ahumado, Standley 79541 (F). Zacapa: Zacapa, Standley 74249 (F); 74379 (F, MICH); Río Motagua west of Teculután, Steyermark 29195, 42167 (F). Department unspecified: Location unspecified, Friedrichsthal s.n. (MICH-type of C. alagoensis var. major; F).

El Salvador. La Libertad: La Libertad, Standley 23231 (GH, US), Calderón 2399 (F). La Unión: La Unión, Grant 722 (A, F), Standley 20644 (GH). SAN MIGUEL: Laguna de Olomega, Standley 21015 (GH); San Miguel, Standley 21133 (GH). SAN SALVADOR: Hacienda Santo Tomás, Carlson 1124 (F). SANTA ANA: Metapán, Standley & Padilla 3297 (F). Sonsonate: Acajutla, Calderón 1662 (GH, US); Izalco, Standley 21861 (GH, US). Department unspecified: location unspecified, Choussy 2054 (US).

Honduras. Valle: San Lorenzo, Rodriguez 3299 (f); Isla Tigre, near Amapala, Standley 20728 (gh, us); El Tigre volcano above Amapala, West 3534 (gh); Jícaro Galán, Williams & Molina 15002 (f); Nacaome, Williams & Molina 16721 (f).

Nicaragua. Chinandega: Corinto, Standley 11545 (f). Chontales: Juigalpa, Standley 9220 (f). Granada: Granada, Baker 203 (ds, gh), Lévy 1352 (f). Managua: Managua, Garnier 320 (w); Sierras de Managua, Grant 1097 (A, f).

ZELAYA: Río Grande, Molina 2291 (F, GH); Toumarin, Río Grande, Molina 2436 (F-isotype; GH); El Recreo on Río Mico, Standley 19600 (F). Department unspecified: Asseradores Island, Baker 81 (DS, GH); Location unspecified, Lévy 1103 (B), Wright s.n. (GH, NY).

Costa Rica. Guanacaste: Libano, Standley & Valerio 44900 (f). Nicoya: Nicoya, Tonduz 13779 (f, gh, mich). Puntarenas: Los Loros, Brenes 22470 (f); between Los Loros & Tivives, Brenes 22680 (f); Caldera, Echeverria 4155 (f); Isla de Chira, Orozco 233 (f); Valerio 1466 (f).