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

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*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.



*Campteria 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.** CHIAPAS: Finca Olvido, Mapastepec, *Matuda 2002* (A, MICH, NY, US); Saxchanal, Sierra Madre, *Matuda 4315* (MICH-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 Steyermark 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*. *Steyermark* 45669, from Cerro Chinajá, Department of Alta Verapaz, Guatemala, referred to *C. diversifolia* (*C. laurifolia* Standley & Steyermark), 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. leptostachya*, 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, *Steyermark & Allen 16758* (BR, MO). CHIRIQUÍ: Cerro Galera Chorchá, 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 Chiriquí 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 Golfo-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 Agrícola 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



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 Prodrromus 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 Chiconqueraos." 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 × 28 cm. and 38 × 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 × 3.5 cm.) and a single detached larger leaf (23 × 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. reflexiflora*. 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). YUCATÁN: 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.** COLÓN: Guarunta, Wisperini 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 Agrícola 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* (MICH-holotype 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 Triunfo, 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), *Millsbaugh* 1590 (F); Progreso, *Goldman* 603 (F); C.L. & A.A. *Lundell* 8060 (MICH); Location unspecified, *Gaumer* 638 (F), *Millsbaugh* 6 (F). **Guatemala:** IZABAL: Bay of Santo Tomás, *Steyermark* 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 & Chacón* 5486 (F). Department unspecified: Puerto Sierra, *P. Wilson* 23 (F). SWAN ISLANDS: *Nelson* 22 (GH). **Nicaragua.** ZELAYA: Bahía 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); Chiriquí Lagoon, *Von Wedel* 2826 (MO). Province unspecified: Isthmus of Chagres, *Fendler* 287 (LE, MO).

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

*Campteria floribunda* Bentham, Bot. Sulphur 159. tab. 52. 1846.

*Campteria 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, Tonalá, *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, *Rodríguez 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).