

# A REVIEW OF THE GENUS RHIZOPHORA

with special reference to the Pacific species

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## Introduction

The species of the Atlantic *Rhizophora* have formerly been considered as belonging to one species, *R. mangle* L. In 1818 G. F. W. Meyer (11) described a second species, *R. racemosa*, from British Guiana. On working up the Rhizophoras of British Guiana Leechman (10) added a third species, *R. harrisonii* in 1908, and distinguished all these three species. Through the works of Salvoza (13), Savory (14), Keay (9), Stearn (15), and Jonker (8), it has become clear that these three species occur on the West African and East American shores as well as in some Caribbean islands.

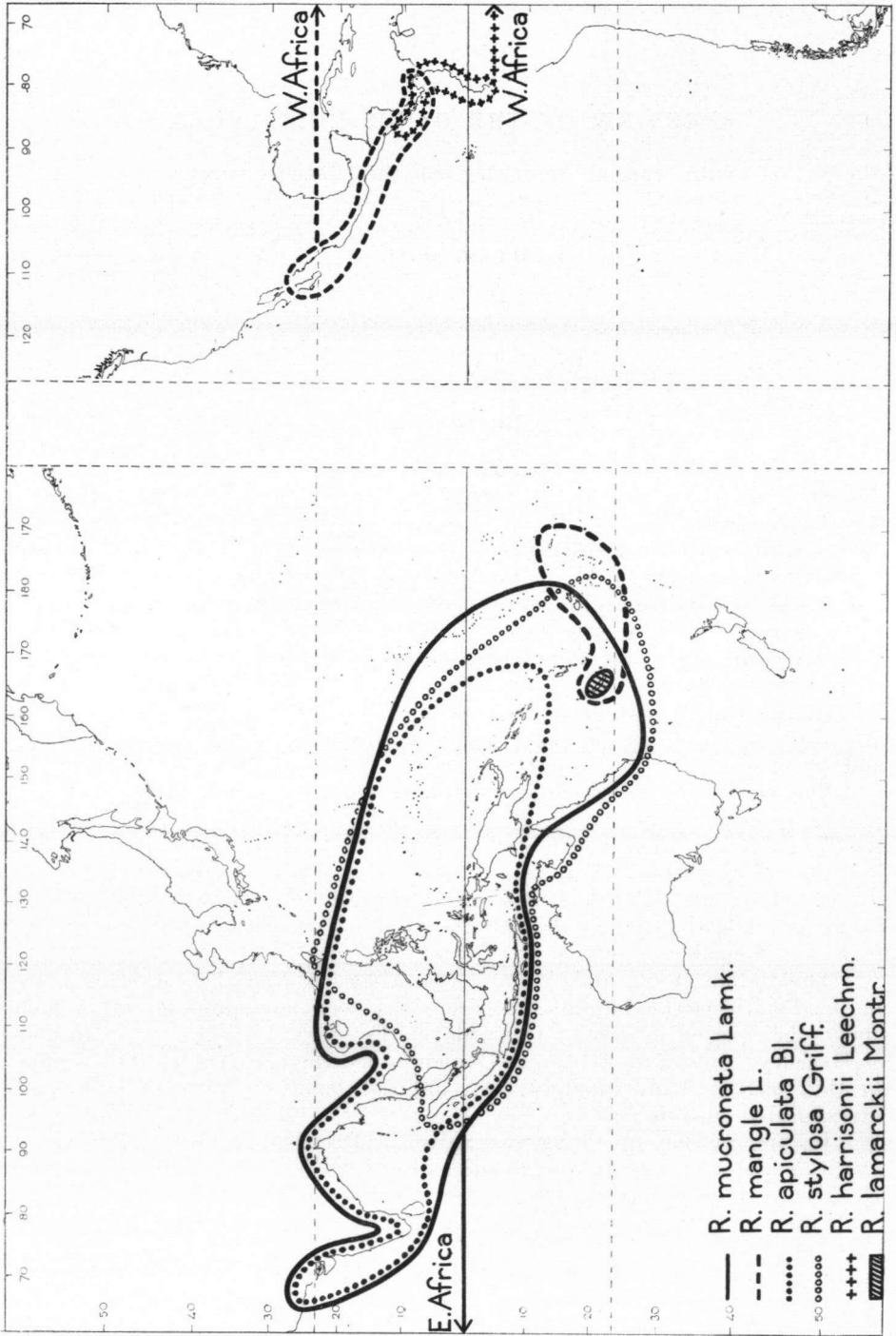
In the Old World, from the coast of East Africa to Malaysia, there are also three (other) distinct species as distinguished by many authors and by myself (7).

The occurrence of *Rhizophora* in the Pacific is remarkable as none of the species occurs native in the central part east of Micronesia and the Tonga group; there is a record by Forster (1) from the Society Islands, but this looks suspect as it has not been corroborated by any later collection. Eastward of the Tonga group *Rhizophora* appears first on the Galápagos Islands and on the Pacific coast of America from Lower California to Ecuador.

The Indian Ocean and Atlantic Ocean species find their meeting place in the Pacific Ocean but hitherto there has been no unanimity of opinion about the species involved. Onwards of Forster (1), such later authors as Hemsley (6) and also Guppy (4) maintained the occurrence of *R. mangle* in the Pacific. Unfortunately they did not make a thorough taxonomic investigation of the matter.

In his revision of the genus Salvoza (13) denied the occurrence of any Caribbean species in the Pacific, even on the west coast of America. He recorded various new species for the Pacific area, viz *R. brevistyla*, confined to the west coast of America, and *R. samoensis*, from the Pacific coast of America and from the West Pacific. Further he recognized another already described species, *R. lamarckii*, confined to New Caledonia.

I have come to the conclusion that the Pacific contains all species



of *Rhizophora* (except *R. racemosa*), viz *R. mangle* (incl. *R. samoensis*) on the American coast, the Galápagos Islands, the Fiji-Tonga group, and New Caledonia, *R. harrisonii* (incl. *R. brevistyla*) on the American coast, a local-endemic species *R. lamarckii* in New Caledonia, and *R. apiculata*, *R. mucronata*, and *R. stylosa* in the West Pacific.

On the accompanying map the distribution of the Atlantic *R. racemosa* has been omitted and it has not been attempted to draw the detailed distribution of *R. mangle* and *R. harrisonii* in the Caribbean because the map is primarily intended to show the generic distribution in the Pacific.

Plant-geographically it is most remarkable that a very large part of the Pacific seems to be devoid of any mangrove, the gap between the nearest stations of *R. mangle* being about 60 longitudinal degrees, if discarding the doubtful Forster record of the Society Islands from the discussion.

It is quite possible that Guppy (4) is right in part that the dispersal in living condition of the seedlings (hypocotyls) is impossible over very large distances, as he rightly assumes that the climate is no barrier for their distribution. This is also shown by the successful planting experiments of many mangrove genera in Hawaii where they thrive and multiply after their introduction in the twenties.

But it could be understood that seedlings cover smaller distances with success, provided there is a favourable sea current or wind causing a surface current for transport, and provided that they would arrive at suitable muddy coastal flats without injury in passing a heavy surf over sandy beaches, because surf on coral fringes or on rocky coasts is of course detrimental to the delicate plumule. In this way they could hop from one island to another.

It is probably the very scarcity of these ecologically suitable coastal conditions to receive seedlings which prohibits a wide dispersal and profusion of localities in the Pacific.

The identification of the Pacific *Rhizophoras* leads to a discussion on the history of the distribution of the genus. Obviously it was already present with a large distribution before the closing of the isthmus of Panama when the Atlantic and Pacific Oceans stood in open connection and the Americas were separated by open ocean. Two species are still present on both sides of the isthmus, viz *R. mangle* and *R. harrisonii*. And it is quite possible that future field work will also show the presence of *R. racemosa* on the American west coast.

As the coastal *Rhizophoraceae* are most abundantly developed in the Indian Ocean and West Pacific and five out of seven species are found in the West Pacific, it is most probable that the genus had its birthplace and ancient distribution in that part of the world and later spread through the Pacific to the Americas, passing between them, entered the Caribbean, and spread from there to the west coast of Africa. This explanation goes parallel with the explanation of distribution of several sea-grasses given by Den Hartog (5).

There occurs a slight indication of racial differentiation in two species.

The Pacific specimens reckoned to *R. samoensis* have generally a shorter style and ovary apex than those (cf. *R. mangle*) in the Caribbean,

but there is a range of intermediates defeating the use of this character even for varietal distinction.

The Pacific specimens of *R. brevistyla* have usually shorter pedicels than the Caribbean *R. harrisonii*.

*R. lamarckii* is the least understood species, but the collections of it are very homogeneous. In its hairy petals it approaches *R. mucronata*, but they are flat and thin as in *R. apiculata*. It has mostly two flowers per inflorescence and sometimes four as found in *R. mucronata* but never in *R. apiculata*. There is little possibility that it is of hybrid origin as it produces ripe fruit. Besides no hybrids are known in the genus, save a suggestion by Guppy (4) who believed to have found some specimens in Fiji with aborted pistils which he believed to be due to hybridisation.

Sterile specimens of *Rhizophora* and *Bruguiera* sometimes have been confused in the herbarium. However, the number and arrangement of vascular bundles in the leaf-scars provide a constant and reliable character to separate them. In *Rhizophora* each scar bears several vascular bundles arranged in two rows while in *Bruguiera* each scar has only one series of three bundles.

At the instigation of Dr van Steenis and with his indispensable help, I have undertaken to review the genus *Rhizophora* and to present a preliminary revision of the species concerned.

I have prepared a key to all seven species of *Rhizophora*, including also *R. racemosa* which may appear to occur on the west coast of America. All the specimens which I have examined have been enumerated in the "Identification Lists of Malaysian Specimens, 4. Rhizophoraceae, Sept. 1959".

I had the privilege of studying the material from the Herbaria at Leyden, Bogor, Kew, the Arnold Arboretum, the British Museum, Cambridge (England), Paris, and the Smithsonian Institution at Washington, D. C.

### Key to the species

- 1.a. Leaf-tips acute or even mucronate, not recurved, never rolled up. Mature fruit straight . . . . . 2
- b. Leaf-tips recurved or rolled up and appearing very blunt or sometimes slightly truncate in the herbarium. Mature fruit sometimes slightly curved . . . . . 5
- 2.a. Petals hairy. Inflorescences mostly in the axils of leaves. Flowers usually short-pedicelled . . . . . 3
- b. Petals glabrous. Inflorescences always in the axils of leaf-scars. Flowers sessile. Bracteole-cup at the base of the flower with irregularly lacerate or dentate margin . . . . . 4. *R. apiculata* Bl.
- 3.a. Petals with incurved margins, densely long-hairy on the margins, partly clasping the epipetalous stamens. Inflorescences 2—8(—16)-flowered. Bracteole-cup at the base of the flower distinctly 2-lipped. Stamens mostly 8 . . . . . 4
- b. Petals flat, sometimes slightly concave, sparsely short-hairy on the margins, sometimes also on the inside, usually covering the epipetalous stamens only on the back. Inflorescences 2(—4)-flowered. Bracteole-cup at the base of the flower with irregularly lacerate or dentate margin, not 2-lipped. Stamens usually 12—15. 3. *R. lamarckii* Montr.
- 4.a. Free part of the ovary high conical, in anthesis already emerging far beyond the disk; style obscure or very short up to 1½ mm. Stamens usually sessile. 1. *R. mucronata* Lamk.
- b. Free part of the ovary depressed-conical, in anthesis enclosed by the disk;

- 5.a. Inflorescences once or rarely twice branched, usually 2-flowered, occasionally 3- or 4-flowered. Flower bud usually slightly 4-angular in the herbarium, the tip slightly curved, one of the calyx lobes slightly longer than the others and cucullate. style filiform, 4—6 mm. Stamens distinctly short-filamentous 2. *R. stylosa* Griff.
- b. Inflorescences much branched, many-flowered. Flower bud straight, smooth, calyx lobes equal in length . . . . . 6
- 6.a. Inflorescences loose. Bracteole-cup at the base of the flower distinctly 2-lipped. Flower buds acute to acuminate. (Pedicels (3—)6—10 mm long) 6. *R. harrisonii* Leechn.
- b. Inflorescences rather contracted. Bracteole-cup at the base of the flower irregularly lacerate or dentate. Flower bud obtuse. (Pedicels 3—4 mm long). 7. *R. racemosa* G. F. W. Mey.

1. *Rhizophora mucronata* Lamk. For synonymy, references, and description see Fl. Mal. I, 5, 1958, 453.

This is the most widely distributed species of *Rhizophora* in the Old World tropics, occurring from the coast of East Africa throughout Malaysia and southeastern Asia to the Pacific islands as far as the Tonga group.

One specimen, collected by G. C. Moor, 132 (US) at Guam, has inflorescences borne in the axils of leaf-scars, each bearing 4 pedicelled flowers. The bracteole-cup at the base of the flower has an irregularly lacerate or dentate margin. The petals are slightly involute and sparsely hairy on the margins. It is similar to *R. mucronata* except for the position of the inflorescences and the shape of the bracteole-cups; these two characters resemble those of *R. lamarckii* and *R. apiculata*. It might be of hybrid origin.

2. *Rhizophora stylosa* Griff. For synonymy, references, and description see Fl. Mal. I, 5, 1958, 456.

This species is distributed from Formosa throughout Malaysia (no record for Borneo) to Melanesia (New Britain, Solomon Isl. and New Caledonia), northern Australia, Fiji and Micronesia (Guam and Marshall Islands).

It is quite closely related to *R. mucronata*, and Schimper had reduced it as a variety of the latter. In addition to the characters indicated in the key *R. stylosa* can easily be separated in the herbarium from *R. mucronata* by the rather smaller leaves and flowers, more-flowered inflorescences, and the petals with longer hairs along the margins. Furthermore they also differ in ecology: *R. stylosa* is exclusively found along sandy shores and on sand-covered coral terraces facing the open sea, while *R. mucronata* is generally gregarious near and on the banks of tidal creeks and on deep soft mud of estuaries.

3. *Rhizophora lamarckii* Montrouzier, Mém. Acad. Sc. Lyon 10, 1860, 201; Salvoza, Nat. Appl. Sc. Bull. Un. Philip. 5, 1936, 229, t. 9. — *R. pachypoda* Baillon, Adansonia 11, 1875, 309. — *R. conjugata* var. *lamarckii* Guillaumin, Not. Syst. 3, 1914, 56.

This species is known only from New Caledonia.

Montrouzier might not have kept a type specimen of it. I have had the New Caledonian material of *Rhizophora* on loan from the Muséum National d'Histoire Naturelle, Paris, but there is no type of this species.

Montrouzier described the calyx lobes and petals as varying from 4—5. I have examined this character in all specimens available and always found 4, the usual number in the genus.

Baillon might have overlooked Montrouzier's binomial in describing a new species, *R. pachypoda*, based on Balansa 2341 collected at Canala, New Caledonia.

Guillaumin, in 1914, reduced *R. lamarckii* as a variety of *R. conjugata* (= *R. apiculata*), from which it would be distinct by leaves which are broadly ovate, pointed at the apex, and abruptly attenuate at the base.

Salvoza, in revising the genus *Rhizophora* in 1936, retained Montrouzier's species.

The species is most allied to *R. apiculata*, especially by the usually 2-flowered, short, robust inflorescences, cupular and dentate bracteole-cup. It differs from the latter by the petals which are hairy on the margins and sometimes also on the inside, the usually short-pedicelled flowers, and (8—)12—15 stamens of which, in case there are 15, sometimes 3 of them are very small or staminode-like. The leaves are elliptic to broadly elliptic and in the herbarium usually reddish- to black-brown while those in *R. apiculata* are generally elliptic-oblong to sublanceolate and usually light brown to brown. This species seems more variable than *R. apiculata*, e. g. the inflorescences consist usually of 2, rarely of 4, flowers (not always 2 as in *R. apiculata*), the inflorescences are borne in the axils of the leaf-scars or in those of the leaves (not always in the axils of the leaf-scars), the petals are membranous, flat, sometimes slightly thicker and their margins are involute (not always membranous and more or less flat), and stamens vary in number between (8—)12—15 (not mostly 12).

**4. *Rhizophora apiculata* Blume.** For synonymy, references, and description see Fl. Mal. I, 5, 1958, 452.

This species is commonly found in most mangrove swamps in tropical Asia (India, Ceylon, Burma, Siam, Indochina and China) throughout Malaysia to Micronesia (Marianes and Caroline Islands) and Melanesia (New Britain, Solomon Islands and New Hebrides).

**5. *Rhizophora mangle* Linné.** For synonymy and references see Keay, Kew Bull. 1953, 123.

This species is widely distributed along the tropical coasts in West Africa, the Caribbean Islands, America and a few Pacific islands (New Caledonia, Fiji, Tonga, and Galápagos).

In tropical America, *R. mangle* occurs on both sides of the coastal regions. In 1936, Salvoza (13, p. 206) stated that "mangrove species on one side of the American continent differ from those on the other side. The Isthmus of Panama acts as a geographical barrier to natural dissemination and interbreeding among the different species." He separated the west coast population of *R. mangle* L. from that of the east coast and placed the former together with those of the Pacific islands as a distinct species, *R. samoensis* (Hochr.) Salvoza (13, p. 220).

Guppy (4, p. 445) made in a table a comparison of the species of *Rhizophora* in Fiji and Ecuador; as already rightly pointed out by Salvoza,

Guppy's "*Rhizophora mangle*" of Fiji and his "*mangle chico*" of Ecuador are conspecific and with the exception of minor vegetative differences must be referred to *R. samoensis*. In revising the *Rhizophoraceae* for the Flora of Panama, Gregory (2) accepted Salvoza's interpretation. There seems to be no doubt on the conspecificity of this *Rhizophora* from the Pacific islands with the population of the American Pacific coast. It would be much desirable to make a field study of *Rhizophora* on both sides of American coastal regions.

The specimens of *R. mangle* and *R. samoensis* have been on loan from the National Herbarium, U. S. A., and most of them have been cited by Salvoza in his revision. All these specimens have been sorted into three geographical groups: 1) Pacific islands, 2) American Pacific coast, and 3) American Atlantic coast. From the available herbarium specimens these three groups appear to be conspecific and certain minor quantitative differences vary only in degree. According to Salvoza one of the chief differences between *R. mangle* and *R. samoensis* would be the relative length of style which is 5 to 6 mm in the former and much shorter in the latter. However, he cited the style of *R. samoensis* as  $1\frac{1}{2}$ — $2\frac{1}{2}$  mm long in his description and 2 to 3 mm in his key. The ovary is half-inferior and its free part is conical, gradually narrowing into the style. Because of lack of a clear distinction between ovary and style, I have taken the measurements of the length of pistil from the top of the disk to the tip of the stigma as Gregory did (2). The measurements then range 4—5 mm,  $4\frac{1}{2}$ —6 mm, and 5—7 mm in the above mentioned three groups, respectively, which makes a separation impossible.

To explain the disjunct pattern of distribution, Guppy (4, p. 449) believed that the seedlings of this species are not well fitted for long voyages across the Pacific Ocean: he assumed it to have been once widely distributed over the tropics of the Old and New Worlds, and now on the "down grade" towards extinction so leaving it in two widely separate areas in the Americas and in the West Pacific islands.

Hemsley (6) postulated that this species is "perhaps accidentally introduced with ballast in the Tonga Islands as well as in Stewart Island". This is not very likely as Forster already knew it from many islands. Ridley (12) also considered that this seems quite impossible, because of "the soft nature of the seedling"; he thought "it must have been drifted by sea to those Polynesian Islands from America, although the distance (at least 6,000 miles), seems a very long one. It may, however, have formerly established itself on some of the intermediate islands, and either been overlooked or has disappeared, from changes in these islands".

Guppy (4, p. 443—448) recorded a seedless form of *Rhizophora*, "*selala*" (= "the tree with empty flowers"), which is intermediate between *R. mangle* and *R. mucronata* and is nearest to *R. mucronata*. Because of its intermediate characters and seedless condition, he first thought that the "*selala*" is a cross between those two species, with *R. mucronata* as the female parent, "but there are several difficulties in accepting the explanations"; after studying the means of renovation of "*selala*", he was inclined to the view that it is due to the "dimorphism" of *R. mucronata*, one fertile and the other seedless. Salvoza (13, p. 219), basing himself

on the characters given for "*selala*" in Guppy's table on p. 445, described it as *R. mucronata* var. *selala*. He did not give it a Latin diagnosis and according to the Code, Art. 34, this new taxon has not been validly published.

Forster (1) recorded *R. mangle* from the Society Islands and New Caledonia. There is a Forster specimen in the Kew Herbarium, on the label said to have been collected in the Society Islands with the common name "*wabitatin malabar*". So far I could not find any other specimen or record of the genus from the Society Islands; the specimen might have been collected on some Melanesian island.

Vieillard (16) recorded *R. mangle* with doubt from New Caledonia. His specimen (431, P) has rightly been pointed out by Guillaumin (3) to belong to *R. mucronata* Lamk. There is another specimen collected by Balansa (3355, K, P) at Diahot, New Caledonia, dated April 1871, with incurved leaf tips and good inflorescences and flowers, which is clearly *R. mangle*.

**6. *Rhizophora harrisonii* Leechm.** For synonymy, references, and description see Keay, Kew Bull. 1953, 124 and Salvoza's revision p. 211. — *R. brevistyla* Salvoza, Nat. Appl. Sc. Bull. Un. Philip. 5, 1936, 211, t. 2; Gregory, Ann. Mo. Bot. Gard. 45, 1958, 140. — *R. racemosa* (non G. F. W. Mey.) Benth. in Hinds, Bot. Voy. H. M. S. Sulphur 4, 1844, 92.

This species is occurring in the mangrove swamps in the New World and West Africa.

Salvoza described *R. brevistyla* based on his own collection (1007, A) at Bella Vista, along the Pacific coast, Panama. According to him, this species can be distinguished from *R. racemosa* (non G. F. W. Mey.) Salvoza, which is *R. harrisonii* Leechm. (cf. Keay, l.c. 125), "by its relatively small flowers or flower-buds and short style coupled with the length of the peduncles". The type specimen which I had on loan from the Arnold Arboretum Herbarium has three branchlets, broken inflorescences, fallen leaves and a hypocotyl. Salvoza only cited the type collection and I wonder if he had any duplicate of it as his drawing does not agree with the type specimen I have had on loan. Plate 2 in his paper seems to have been constructed from memory as far as measurements are concerned, e. g. the length of peduncle and pedicel and the width of the leaves.

There are two other collections in the National Herbarium, U. S. A., collected in Panama, Pearl Archipelago, viz San José Island (Erlanson 13), and Saboga Island (G. S. Miller Jr 1963), which match the type. Erlanson 13 is a very good specimen with a very well preserved inflorescence bearing flowers in different stages of development. It is very similar to *R. harrisonii* by the lax inflorescences and the free parts of the bracteole-cup at the base of the flower being distinctly 2-lobed and deltoid, differing from the latter by the shorter (3—4 mm) pedicels and slightly broader, ellipsoid, acute to slightly blunt flower bud. The pedicels of *R. brevistyla* are cited by Salvoza to be 5—10 mm long in the original description and 3 to 4 mm long in his key. The latter size agrees with that of the type. The length of the pedicels in Gregory's description of this species is 3 to 10 mm; not having seen all the specimens quoted by



him, I do not know whether this is based on the measurements of the specimens cited. There are some specimens of *R. harrisonii* in the Botanical Museum and Herbarium, Utrecht, especially those collected by the Jonkers (570, 571, 573) and by F. P. Jonker (600) in Suriname, which are very well prepared and with good preserved inflorescences. The length of pedicels of those specimens varies from 4 to 10 mm.

Guppy (4, p. 445) in comparing the species of *Rhizophora* in Fiji and Ecuador, listed two "forms" in the latter. One form "*mangle chico*" is *R. mangle* L. The other form, "*mangle grande*", bears leaves "very obtuse, with no twisted point", inflorescences "branching at least three times, sometimes four or five times, trichotomous or dichotomous, twelve to forty-eight flowers", and "well developed" bracts and bracteoles; all these characters match those of the present species very well. Salvoza has referred it to the present species. Guppy (p. 498) also noticed the "*mangle grande*" of Ecuador to exist in the Panama isthmus.

Bentham (l. c.) as early as in 1844, recognized two species of *Rhizophora* on the Pacific coast of America "to be perfectly distinct".

I have examined three old specimens of *R. harrisonii*: two of them were collected by Hinds in 1836—42 at Corinto, west coast of Nicaragua (s. n., BM), and Realejo, west coast of Guatemala (s. n., CGE), respectively, and one was collected by Spruce (6387, K, P) at Chanduy, Ecuador, in 1865; the latter has pedicels 5—7 mm long. This species occurs in a few localities on the Pacific coast between Guatemala and Ecuador as indicated above. It will probably appear to be more common than can be inferred from the available collections; it might have been confused sometimes with *R. mangle*. The distributional gaps would be filled up if one could have an opportunity searching it in the field as well as looking through the herbarium material identified as *R. mangle* from the Pacific coast of America.

**7. *Rhizophora racemosa* G. F. W. Meyer.** For synonymy and references see Keay, Kew Bull. 1953, 125.

This species is occurring on the Atlantic shores of West Africa and the Americas. According to Keay (9), it is "the most frequent species on the African coast, but the least frequent on the American side". It is the only species which has not yet been found on the Pacific side of America.

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