RHZOPHORA IN AUSTRALASIA — SOME
CLARIFICATION OF TAXONOMY AND DISTRIBUTION

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The western Pacific is known as an area of floristic discontinuity where many species with a wide distribution in the Indo-Malayan region terminate their range (Thorne, 1969). Consequently, precision is required in mapping plant distribution in this area. The important pantropical genus Rhizophora is an example of particular interest because it has long been recognized (Salvoza, 1936; Ding Hou, 1960) that in the western Pacific there is an area of overlap between the group of four taxa with an “Indo-Pacific” distribution (i.e., R. apiculata Bl., R. × lamarckii \(^1\) Montr., R. mucronata Lamk., R. stylosa Griff.) and the three species with an “Atlantic” distribution (R. harrisonii Leechman, R. mangle L., R. racemosa G. F. W. Meyer). The overlap is occasioned by the extension of the range of the Atlantic species into the western Pacific via a form of Rhizophora mangle sufficiently distinct to be recognized and named as either a variety (var. samoensis Hochr.) or even a separate species (R. samoensis (Hochr.) Salvoza). A consequence of this overlap is the production of hybrid populations in the form of a taxon here recognized as R. × selala. Problems have arisen because the diagnostic features which are clear in the field (although small) are often obscured in herbarium specimens, resulting in frequent misidentification of dried material. Also, the area falls outside that covered by Flora Malesiana, so the account by Ding Hou (1958) of the genus in Malesia does not provide details of distribution in the area considered here.

Recent field work in this area, partly summarized here, now allows further precision to be brought to generalized statements and confirms earlier evidence of hybridization (Guppy, 1906; Tomlinson & Womersley, 1976) which is of phytogeographic and evolutionary interest. Direct observation of wild populations in several countries has been supplemented by study of herbarium materials at A, BRIS, GH, K, SUVA, NOU. Measurements reported later were all made on fresh or fluid-preserved specimens.

Since New Caledonia is one of the areas visited, and as it is particularly rich in Rhizophora species, some of which have been confused in earlier accounts, this island has been given special consideration. One taxon new to its flora, R. × selala, is recognized here. Fiji is also considered in some detail. My present understanding of the distribution of these taxa is summarized in Maps 1–3.

\(^1\)The name Rhizophora × lamarckii (Montr., Mém. Acad. Sci. Lyon 10: 201, 1860, \textit{pro sp.}) indicates the hybrid status of this entity (Tomlinson & Womersley, 1976).
Map 1. Distribution of Rhizophora in Australasia. A–C, R. stylosa: A, generalized distribution in the southeastern part of its range; B, details of distribution in New Caledonia; C, details of distribution in Fiji. D–F, R. samoensis: D, distribution in the south-central Pacific (New Caledonia to Samoa); E, details of distribution in New Caledonia; F, details of distribution in Fiji. G–I, R. × selala: G, total known distribution; H, distribution in New Caledonia; I, distribution in Fiji. (Most localities refer to herbarium specimens seen by the author, but supplemented by field observations in Fiji, New Caledonia, Queensland, and New Guinea.)
TYPIFICATION AND DISTRIBUTION OF RHIZOPHORA × SELALA

Guppy (1906) described and illustrated a form of Rhizophora in Fiji which was characterized by the absence of fruits and, consequently, of viviparous seedlings. He used the name “Selala” to refer to this plant, from the native name signifying empty (“lala”) flowers (“se”), but did not validly describe it. He considered it likely that this entity was a hybrid between the two fertile species he recognized in Fiji (which he called R. mucronata and R. mangle). More recent work supports this interpretation, although with changes in Guppy’s nomenclature. On the basis of Guppy’s descriptions, Salvoza (1936) used the name R. mucronata var. selala. This is unfortunate because Guppy’s use of the name mucronata is incorrect. Modern work shows that he confused R. stylosa and R. mucronata. It seems certain that R. mucronata does not occur in Fiji (cf. Richmond & Ackermann, 1975), and that the one parent of the hybrid is actually R. stylosa. The other parent may be referred to most conveniently as R. samoensis. Guppy discussed the difference between Fijian and American populations of R. mangle and concluded that they were morphologically distinct. This is supported by the present work,

F I G U R E 1. Floral features and diagnostic details of Rhizophora × selala. A–C, just-opened flower, × 2: A, side view; B, median longitudinal section; C, from above. D–F, floral details, × 2: D, style; E, dehisced stamen; F, petal. G, H, inflorescences, × ½: G, 5-flowered; H, 4-flowered and with regular dichotomy. I, floral diagram; J, diagram to show one type of inflorescence branching. (All drawn from P. B. Tomlinson & T. Richmond 18.XI.74 A, from Kinoya, Viti Levu, Fiji.)
and the name *R. samoensis* provided by Salvoza (1936) recognizes this distinction. In contrast, neither Ding Hou (1960) nor Breteler (1977), on the basis of herbarium studies, considers the small differences between the two forms sufficient to merit segregation of *R. samoensis* from *R. mangle*. The further problem of *Rhizophora* in Pacific America can only be solved by extensive field work and the establishment of further diagnostic differences, which is not within the scope of the present account.

Most recently, *R. × selala* has been shown to occur abundantly in New Caledonia. This suggests that the name used by Guppy should be given formal recognition.

*Rhizophora × selala* (Salvoza) Tomlinson, comb. et stat. nov.

"Selala" Guppy, Obs. Nat. Pacific 2: 445, 487, frontisp. 1906.

*Rhizophora mucronata* Lamk. var. *selala* Salvoza in Bull. Nat. Appl. Sci. Univ. Philip. 5: 219. 1936.

*Rhizophora 'selala'* Tomlinson & Womersley in Contr. Herb. Austral. 19: 9. 1976. Nomen illegit.

A *Rhizophora mangle* differt: foliis mucronatis mucrone demum recurvato (Figure 4); axe inflorescentiae crassiore longiore et floribus (2–9) plus quam *R. mangle* (2–6) praeedito; gemmis maturis albis ad 14 mm. longis, pedicellum versus angustatis, in sectione transversali rotundis; bracteola manifesta sub flore omni; ovario apice conico in stylum ca. 1 mm. longum produco.

Type. Frontispiece (and p. 445). "Selala, Vanua Levu, Fiji," Guppy. 1906.

Other collections. Fiji: Kinoya Village, near Suva, Viti Levu, P. B. Tomlinson & T. Richmond 18. XI.74 A (A). New Caledonia: common in association with its putative parents in mangrove swamps on both coasts (e.g., Teremba, P. Morat, J.-M. Veillon, & P. B. Tomlinson 18. VII.77 B (A, NOU); Poindimié, P. Morat, J.-M. Veillon, & P. B. Tomlinson 19. VII.77 C (A, NOU).

This species differs from *Rhizophora samoensis* in having a leaf apex with an appreciable but ephemeral mucro, which becomes recurved with age (Figure 4). The inflorescence axis (Figure 1, G, H) is longer, thicker, and often with more flowers (2 to 9, sometimes more). The flower buds at maturity are white (not yellow), rounded (not angular) in cross section, up to 14 mm. long, and gradually (not abruptly) narrowed to the pedicel. The bracteole below the flower is distinct (2–3 mm. long) and not obscure as in *R. samoensis*. The top of the ovary is conical, with a distinct style scarcely 2 mm. long (Figure 1, D), i.e., shorter than in *R. stylosa* (Figure 3, C) but longer than in *R. samoensis*, which has a steeply conical ovary (Figure 2, E). Populations of *R. × selala* in New Caledonia and Fiji seem indistinguishable.

With fresh material of mixed populations at hand, it is easy to allocate a given specimen to one of the three species; to provide comparative in-
Figure 2. Comparison of *Rhizophora samoensis* and *R. mangle*. Above: *Rhizophora samoensis*. A–C, just-opened flower, × 2: A, side view; B, median longitudinal section; C, from above. D–G, details of flowers: D, dehisced stamen, × 2; E, style, × 2; F, relation between style and dehisced stamens, in median longitudinal view; G, petal, × 2. H, 2-flowered inflorescence, × 1 and × ½. I, 3-flowered inflorescence at the same magnifications; flowers removed in larger figure to show obscure bracteoles. J, floral diagram. (All drawn from P. B. Tomlinson & T. Richmond 18.XI.74 C, from Queen Elizabeth Drive, Suva, Viti Levu, Fiji.) Below: *Rhizophora mangle*, details of inflorescence to show diagnostic features. A–C, 2-, 5-, and 3-flowered inflorescences, respectively, all × ½. D, E, details of 2 inflorescences, × 1, showing obvious bracteoles. F, examples of typical branching patterns of inflorescence, often with trifurcation at first node. (All drawn from P. B. Tomlinson s.n., Fairchild Tropical Garden, Miami, Florida.)
formation, a series of illustrations emphasizing certain diagnostic features is included in Figures 1–3. Apart from the morphology of the leaf tip (Figure 4), \( R. \times \text{selala} \) also can be recognized because it often has a trichotomy of the first node of the inflorescence, whereas branching in \( R. \text{stylosa} \) is exclusively dichotomous. Flower buds in \( R. \times \text{selala} \) are white rather than yellow as in \( R. \text{ samoensis} \). In addition, illustrations of \( \text{Rhizophora mangle} \) from South Florida show how it differs from \( R. \text{ samoensis} \) in its conspicuous bracteoles (Figure 2).

Guppy (1906) referred to two forms of \( \text{Rhizophora} \times \text{selala} \), the second distinguished from the one described above by its larger numbers of flowers (up to 24) because the inflorescence is branched 4 to 5 times. I have not seen this second form.

**RHIZOPHORA IN AUSTRALASIA**

With the above clarification, it now becomes possible to provide a diagnostic key to \( \text{Rhizophora} \) species in this area of overlap in the western

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**Figure 3.** \( \text{Rhizophora stylosa} \), habit and diagnostic features. A, leafy shoot with axillary inflorescence, \( \times \frac{3}{4} \); inset, leaf apex. B, same with leaf blades removed to show extensively branched inflorescence. C, style, \( \times 3 \). D, constructional principle of inflorescence. (All drawn from P. B. Tomlinson 30.X.74 C, from Bootless Bay, Port Moresby, Papua New Guinea.)
Pacific. Distributional information summarized in the key is shown in detail in Maps 1–3. These are drawn up from limited sampling of herbarium material together with field study. Undoubtedly, the range of species needs to be expressed with further precision in the future, but the present summaries are more accurate than the generalized map of Ding Hou (1960). In the following key, measurements represent approximate values and may be exceeded in individual specimens. Only Rhizophora stylosa, R. samoensis, and R. × selata are illustrated; detailed drawings of R. apiculata and R. × lamarckii are given in Tomlinson and Womersley (1976).

Map 2. Rhizophora mucronata. Distribution in Australasia (continued), based on herbarium specimens seen by the author. Its absence from New Caledonia and Fiji is supported by field observation. It is likely to occur in the Bismarck Archipelago and the Solomon Islands.

Key to Rhizophora in Australasia

1a. Apex of leaf with a persistent extended mucro 2–3 mm. long (e.g., Figure 4, D–F); leaf blade usually 10–20 cm. long; inflorescence branching exclusively by dichotomy (e.g., Figure 3, B, D), never trifurcated, peduncle scarcely flattened. Flowers never in 3’s. Mature flower buds white or greenish yellow (never yellow), 15 mm. or more long, rounded in cross section, pedicel of individual flowers often short or obscure. Stamens 8, 12, or 16; petals glabrous or hairy. (“Indo-Malayan group”; species group ranging from East Africa to the Western Pacific.) ... 2.

1b. Apex of leaf without a prominent apical mucro (e.g., Figure 4, A–C, G–M); leaf blade usually <10 cm. long. Inflorescence axis flattened and frequently trifurcated at the first (rarely subsequent) nodes. Peduncle often flattened. Flowers commonly in 3’s. Mature flower bud white or yellow, somewhat angular in cross section, <15 mm. long. Pedicel of individual flowers always distinct. Stamens 8; petals always
woolly-hairy. ("Atlantic group"); species group ranging from New Caledonia to West Africa.) ........................................... 5.

2a. Stamens 8; petals conspicuously woolly-hairy on the margins. Leaf blade usually less than 15 (to as short as 8) cm. long. Mature flower buds white, ca. 15 mm. long. Inflorescence long-stalked, peduncle usually longer than 2.0 cm., usually branched to more than 2 orders. Flowers usually more than 4 per inflorescence; pedicel evident.

3a. Apex of ovary extended abruptly into a style ca. 3 mm. long. (Common and widely ranging throughout the South Pacific to Samoa and Tonga (Map 1, A–C).) .................................................. Rhizophora stylosa (Figure 3).

3b. Apex of ovary bluntly conical, lacking a distinct style. (Extending into the South Pacific as far as the New Hebrides, apparently absent from New Caledonia and Fiji (Map 2).) Rhizophora mucronata.

2b. Stamens most commonly either 12 or about 16; petals glabrous or with inconspicuous marginal hairs. Leaf blade commonly 15 cm. long (sometimes more). Flower buds greenish yellow, never white, 15–20 mm. long at maturity. Inflorescence short-stalked, peduncle 1–2 cm. long, never branched to more than 2 orders. Flowers 2 to 4 per inflorescence; pedicel short and more or less obscured by bracteoles. .......... 4.

4a. Stamens usually 12, petals glabrous. Flowers usually 2 per inflorescence, peduncle short (usually <1 cm.). Inflorescence developing slowly and at maturity borne below the leafy crown. Bracts and bracteoles thick, rough, corky. Style absent. Plants fertile, with corky fruits and viviparous seedlings on the older parts of the twigs. (Common and wide ranging, but not further east than the New Hebrides; in New Caledonia restricted to the northeast coast (Map 3, A, B).) .................................................. Rhizophora apiculata.

4b. Stamens varying in number, but based on 16; petals sparsely hairy on the margins. Flowers usually 4 per inflorescence, peduncle moderately long (1–2.5 cm.). Inflorescence borne within the leafy crown. Bracts and bracteoles not corky. Style distinct. Plants sterile, virtually lacking fruits and viviparous seedlings. (Scattered in Papuasia (Map 3, C); always in association with its putative parents, e.g., in New Caledonia restricted with R. apiculata to the northeast coast (Map 3, D).) .................................................. Rhizophora × lamarckii.

(A probable F, hybrid, R. stylosa × apiculata; Tomlinson & Womersley, 1976.)

5a. Leaf apex blunt, recurved (Figure 4, A–C). Peduncle 2–2.5 cm. long or longer, 2–2.4 mm. in diameter, uncommonly branching beyond 2 orders. Flowers usually 2 to 5 per inflorescence. Bracteoles scarcely developed and represented by a narrow rim of tissue (Figure 2, H–I). Mature flower buds yellow, angular in cross section and with a distinct basal shoulder, i.e., abruptly narrowed below, 10–12 mm. long at maturity. Apex of ovary steeply conical and without a distinct style. Plants fertile, with fruits and viviparous seedlings (Figure 2). (Apparently restricted to New Caledonia, Fiji, Samoa, and Tonga (Map 1, D–F); its status in South America is disputed (cf. Breteler, 1977). Rhizophora mangle, apart from its distribution in West Africa and Tropical America, is distinguished by its conspicuous bracteoles and pointed flower buds, as shown in Figure 2.) .................................................. Rhizophora samoensis.

5b. Leaf apex initially with an indistinct but usually soon deciduous or recurved mucro (Figure 4, H–M). Peduncle 2.5–3.0 cm. long but often
longer, 2.6–3.2 mm wide, commonly branched beyond 2 orders. Flowers 2 to 9 per inflorescence. Bracteoles distinct, ca. 1 mm long. Mature flower buds white, neither sharply angular in cross section nor abruptly narrowed to a distinct shoulder at the base, 12–14 mm long. Apex of ovary extended into a distinct style 1–2 mm long. Plants sterile, lacking fruits and viviparous seedlings. (Presently known from Fiji and New Caledonia; always in association with its putative parents (Map 1, G–I).) Rhizophora × selala.

(A probable F1 hybrid, R. stylosa × R. samoensis.)

**Figure 4.** Leaf morphology of two Rhizophora species and their putative hybrid. A–C, R. samoensis: A, leaf outline, × ½; B, C, details of leaf with blunt recurved apex, × 5. D–F, R. stylosa: D, leaf outline, × ½; E, F, details of leaf apex with pronounced erect and persistent mucro, × 5. G–M, R. × selala: G, leaf outline, × ½; H–M, examples of variation in leaf apex (but always with a persistent but recurved mucro, i.e., intermediate between B, C, and E, F), × 5.
Map 3. Distribution of Rhizophora in Australasia (continued), based on herbarium specimens seen by the author and field observations. A, B, *R. apiculata*: A, generalized distribution, not extending further west than New Caledonia and the New Hebrides; B, details for New Caledonia to show its apparent restriction to the northeast coast. C, *R. × lamarckii*, generalized distribution from all known localities (all except those in the Bismarck Archipelago based on field observations). D, details for New Caledonia. All known sites in proximity with sites of its putative parents, *R. stylosa* (cf. Map 1, A–C) and *R. apiculata*.

The characters listed in the key might appear to be elusive, but in the vicinity of Poindimie, New Caledonia, where no less than three species together with two of their hybrids can be found growing within a few hundred meters of each other, there is no problem in naming any indi-
Figures 5, 6. 5, quantitative variation in certain features of inflorescence morphology in populations of some species of Rhizophora. Measurements are averages for about 50 samples. R. apiculata (above); R. × lamarckii (center); R. stylosa (below). Parameters represented are theoretical flower number (left), and actual flower number (center). On the right the lines compare average di-
vidual once the appropriate diagnostic features have been recognized. This demonstrates that field knowledge is essential for identifying Rhizophora taxa. The presence or absence of a persistent mucro will allow preliminary segregation of species. *Rhizophora apiculata* can be recognized at a distance by its larger dark green leaves, an identification confirmed at close quarters by the paired flowers borne below the leafy crown and protected by thick corky bracteoles. *Rhizophora × lamarckii* has leaves almost equally large, but lighter green. It never has seedlings, and its flowers are borne within the leafy crown in 4’s on a rather lax inflorescence. Any remaining trees with mucronate leaf blades are *Rhizophora stylosa*; this has medium-sized flowers that are white in bud, and a lax inflorescence usually with several branch orders and more than four flowers. Although *Rhizophora mucronata* has been recorded for New Caledonia (Guillaumin, 1948) neither field nor herbarium study has revealed its presence. It would be recognizable by its sessile stigma.

The two species without a persistent mucro are much more alike, but can be distinguished by the form of the leaf apex, together with the color and shape of the flower bud, and the bracteole structure. *Rhizophora × selala*, in general, has longer inflorescences with more numerous flowers than *R. samoensis*.

**QUANTITATIVE VARIATION**

Since *Rhizophora* species are not easily distinguishable, methods were sought to quantify differences between them. Analysis of certain populations by simple biometric methods shows that although variation is large, consistent average differences do exist. Figures 5 and 6 summarize data from populations of *R. apiculata*, *R. stylosa*, and their putative hybrid, *R. × lamarckii*, mainly in Queensland. Parameters measured were:

1. “Theoretical flower number,” which is the number of nodes in the dichotomously branched inflorescence. Were every axis to terminate in a flower, this would indicate the maximum possible flower number.

2. “Actual flower number,” which is often less than the theoretical number because of abortion of certain inflorescence axes.

3. “Stamen number,” including larger aborted stamens which are quite numerous in *R. × lamarckii*.

4. Average length and diameter (at half length) of the peduncle.

In these histograms the data for the Queensland *Rhizophora stylosa*
include two sets from two different but nearby populations (CC and BC), the latter a more vigorous group of trees.

To show differences between more distant populations, the data for *Rhizophora apiculata* include measurements for a population in New Guinea characterized by quite frequent twice-branched (and therefore 3- or 4-flowered) inflorescences and flowers often with less than 12 stamens. It is not known if these differences are genetic. The general result of these histograms is to show that *R. × lamarckii* is intermediate between its putative parents in certain measurable characters (cf. Tomlinson & Womersley, 1976).

An attempt to produce similar histograms for *R. × selala* was abandoned because the differences between this species and its putative parents were smaller, and insufficient samples were measured. Precise analysis of larger populations would undoubtedly lead to quantifiable expression of differences on a statistical basis, but this morphometric approach is likely to be superseded if other diagnostically useful characters (e.g., chemical) are recognized.

**CONCLUSIONS**

In summary, it appears that *Rhizophora mucronata* has a restricted distribution in the western Pacific, since it is not yet known to range further east than the New Hebrides, but precise assessment of the limits of its eastward range depends on future collecting. *Rhizophora stylosa*, on the other hand, ranges as far east as Samoa, although it is not known from tropical South America. *Rhizophora apiculata* does not seem to occur further east than New Caledonia, where it is restricted to the eastern coast. *Rhizophora × lamarckii* clearly has a wider range in the western Pacific than hitherto appreciated, and it always occurs with its putative parents, *R. apiculata* and *R. stylosa*. *Rhizophora samoensis* extends as far as New Caledonia, and the result of this overlap between “Indo-Malayan” and “Atlantic” forms appears to be crossing with *R. stylosa* and the production of the sterile hybrid, *R. × selala*, in both Fiji, from where it was first reported, and (as shown here) New Caledonia.

These observations are but simple preliminaries to the larger questions about reproductive isolation between *Rhizophora* species, the breakdown of usual sterility barriers, and the apparent persistence of F₁ populations without backcrossing. Evidently more precise knowledge of the breeding mechanism of *Rhizophora* is needed. This should allow hypotheses about the origin and dispersal of *Rhizophora* in evolutionary time to be put on a less speculative basis.

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