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Global distribution and genetic discontinuities of mangroves – emerging patterns in the evolution of *Rhizophora*

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Abstract Mangroves are often described as a group of plants with common features and common origins based mostly on their broad distributional patterns, together with an erroneous view of comparable abilities in long-distance dispersal. However, whilst mangroves have common needs to adapt to rigorous environmental constraints associated with regular seawater inundation, individual taxa have developed different strategies and characteristics. Since mangroves are a genetically diverse group of mostly flowering plants, they may also have evolved at quite different geological periods, dispersed at different rates from different locations and developed different adaptive strategies. Current distributions of individual taxa show numerous instances of unusual extant distribution which demonstrate finite dispersal limitations, especially across open water. Our preliminary assessment of broad distribution and discontinuities reveals important patterns. Discontinuities, in the absence of current dispersal barriers, may be explained by persistent past barriers. As we learn more about discontinuities, we are beginning to appreciate their immense implications and what they might tell us about past geological conditions and how these might have influenced the distribution and evolution of mangroves. In this article, we describe emerging patterns in genetic relationships and distributions based on both current knowledge and preliminary results of our studies of molecular and morphometric characteristics of *Rhizophora* species in the Indo West Pacific region.

Keywords Mangrove · Distribution · Discontinuity · *Rhizophora* · Evolution

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Global distribution and genetic discontinuities – unanswered questions

Despite recent important studies and review articles on the systematics, biogeography and evolution of mangroves (Duke 1995; Dodd et al. 1998; Saenger 1998; Parani et al. 1998; Ellison et al. 1999), progress has been slow since the earlier treatments by Tomlinson (1986) and others (e.g., McCoy and Heck 1976). For instance, we still know little about the so-called “centres” of mangrove evolution and we are still unclear about how or whether these relate to centres of extant diversity. Current consensus appears to be that the centres are not related; however, a dearth of primary data has meant that alternatives have not been properly explored. This situation has resulted in broadly different views of where mangroves might have originated and their possible evolutionary dispersal routes. Important questions remain unanswered, like why is the diversity of mangrove taxa greater in the Indo West Pacific (IWP) than in the Atlantic East Pacific (AEP). The overall debate has not progressed greatly and new observations continue to sway arguments in individual hypotheses based on limited additional facts.

There is an urgent need to promote greater understanding by gathering detailed new observations and appropriate data. We believe the answers lie in well-researched and rigorous systematic studies, taking one or all of three different approaches, namely:

1. thorough assessments of morphological, chemical and genetic variation among related taxa to develop phylogenetic understanding of individual taxa across their entire distributional ranges
2. comprehensive compilations of distributional records for revised morphological and genetic assessments of extant related taxa groups (e.g., multi-specific genera) across their entire distributional ranges
3. a complete review and synthesis of fossil records, which will identify gaps in time and space and demonstrate clear continuity between fossil and extant taxa

Three notable recent works contributing to the third approach in particular are the valuable and comprehensive assessments of fossil records by Saenger (1998), Ellison et al. (1999) and Plaziat et al. (2001). The treatment by Plaziat et al. (2001) notably provides current and critical insights into the early evolution of mangrove taxa and also highlights a serious gap in the fossil record during critical formative years in the Paleocene for key mangrove taxa like *Rhizophora* and *Avicennia*. As pointed out and implicit in all these works, such limitations also feature generally in systematic collections and taxonomic descriptions of ancestral and extant taxa. In addition, questions raised and gaps in knowledge concerning global distributions and genetic discontinuities (e.g., Duke 1995) have not been addressed. There are good reasons for many of these acknowledged gaps, but across all fields they seriously inhibit our intellectual progress in answering the fundamental questions concerning the origins and early dispersal of modern mangrove communities.

The problem is particularly evident in botanical taxonomy and systematics (notably the first and second approaches above), where extant mangrove taxa worldwide remain incompletely described and poorly identified. This is somewhat surprising considering that there are arguably only ~70 mangrove taxa in the world (Duke et al. 1998a). Furthermore, the unresolved taxonomic questions apply equally to restricted rare taxa as much as to widespread common taxa, like *Rhizophora*. The latter genus is noteworthy for its ubiquitous occurrence in mangroves throughout the tropical world (e.g., Tomlinson 1986). Our understanding of relationships within and among such mangrove groups has so far not been appreciably assisted by recent advances in molecular techniques, notwithstanding some excellent recent work in the field (e.g., Schwarzbach and Ricklefs 2000). Our limited progress has been due in part to a lack of firm links between field observations and laboratory analyses, i.e., in the coordination of genetic and morphological sampling.

In this article, we review a range of thoughts, observations and findings to identify some of the key trends and patterns. We also outline how we might contribute positively to the debate by combining systematic field collections and morphological assessments with genetic interpretations throughout the IWP. For this purpose, we have chosen to investigate in particular the common mangrove genus *Rhizophora*. We report some preliminary observations but we are particularly concerned at this stage to generate a rational and well-founded working hypothesis to help explain patterns and associations among taxonomic entities. It is the goal of our current field collections and laboratory analyses to test the hypothesis presented here for *Rhizophora*.

Global distributions of extant mangroves and what they tell us about dispersal

Mangroves occupy most sheltered coastlines throughout tropical regions of the world, with few exceptions (Duke

1992). They are absent where cold waters are forced towards the equator by western continental currents and ocean circulation patterns. Conversely, on eastern continental shorelines poleward-moving warm currents allow mangrove populations to expand into sub-tropical latitudes. However, this pattern has at least two exceptions, notably (1) the absence of mangroves from many islands in the eastern Pacific Ocean, despite the presence of suitable habitats sometimes occupied by introduced mangrove plants (Allen 1998), and (2) the occurrence of extensive mangrove populations in northern New Zealand and southeastern Australia, where they are found as far south as 38°S (Duke et al. 1998b). Apart from these exceptions, the overall distribution of mangroves in the world appears to be distinctly and uniformly temperature limited. Therefore, it seems reasonable to assume, since mangroves apparently occupy most available niches throughout the world, that they have already reached the limit of their ability to disperse buoyant propagules over long distances.

A view of apparent uniformity in mangrove distributions is tacitly supported further by neat concentric patterns of increasing species richness towards the centres of diversity in both IWP and AEP regions (Fig. 1). Based on such evidence, one might expect individual mangrove species to be distributed centrally about these respective centres, with more wide-ranging species extending further away, more or less concentrically. The impression of such simple distributional patterns is supported further by the idea that mangroves have uniform capabilities for long-distance dispersal of their propagules.

On closer inspection, however, these simple interpretations only apply as generalities at best. Mangroves have not evolved and dispersed uniformly. For example, propagule dispersal ability varies significantly even among species with comparable distributional ranges. The best example of this is seen comparing the equally distributed global genera *Rhizophora* and *Avicennia*. The propagules of *Rhizophora* have considerable longevity at sea, surviving over 3–4 months, while those of *Avicennia* last only 3–4 weeks (e.g., Rabinowitz 1978; Steinke 1986). Such differences would profoundly affect dispersal range and this is shown by the much greater eastward extent of IWP *Rhizophora* than *Avicennia* across the Western Pacific.

Based on such evidence, long-distance dispersal ability is expected to vary with each taxon. Mangrove dispersal is limited in different ways by both land barriers and wide expanses of water. Land barriers block all species completely. In contrast, sea barriers may be ranked on differing dispersal and establishment capabilities of each taxon, notwithstanding niche availability. The near total difference at species level between mangrove floras of the IWP and AEP is evidence of the effectiveness of the African land mass and the east Pacific Ocean barriers. Within each region, there are two additional barriers of varying but lesser degrees of effectiveness in blocking dispersal and gene flow. In the AEP, these include the American isthmus and the Atlantic Ocean; the IWP in-

Fig 1. Mangrove species numbers through (a) the Indo West Pacific (IWP) region and (b) more diverse part of the Atlantic East Pacific (AEP)

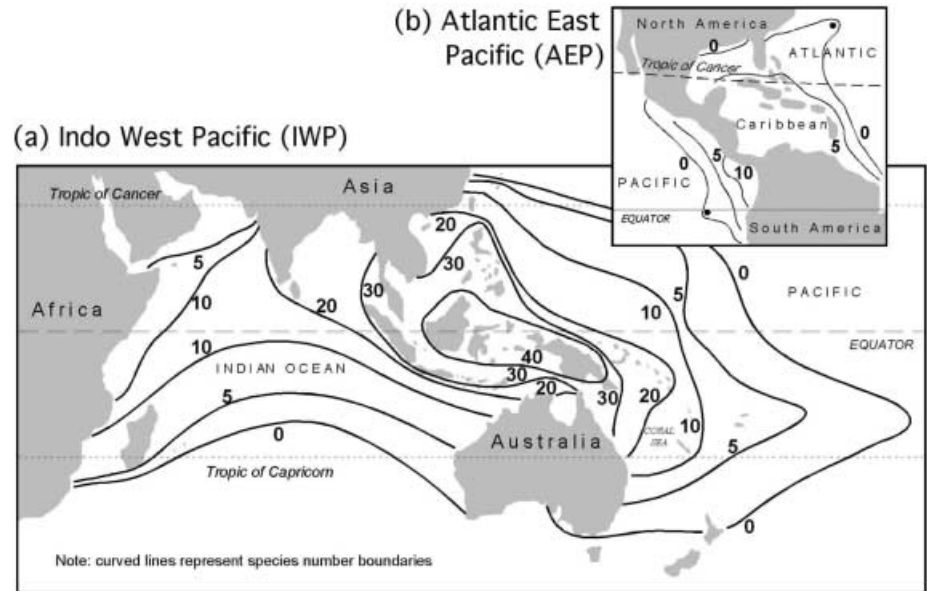
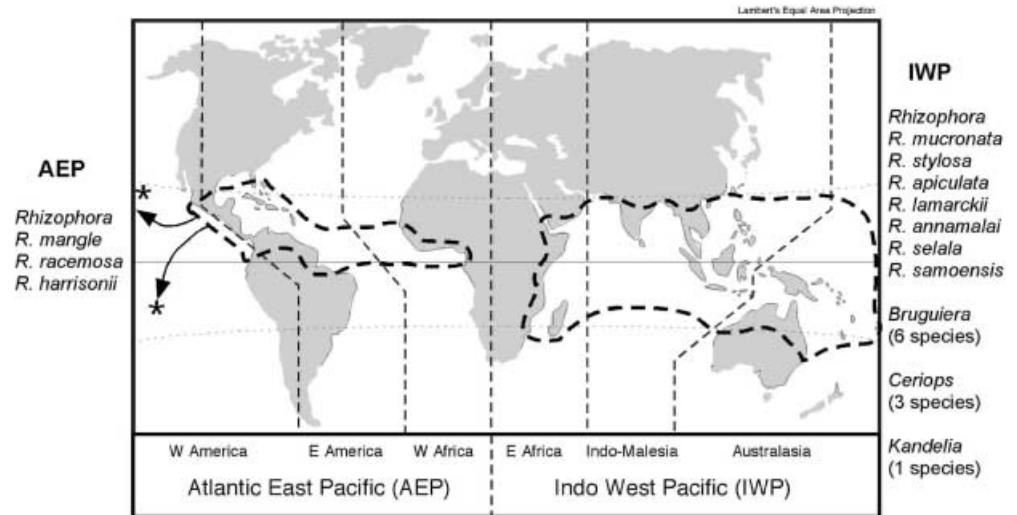


Fig. 2 World distribution of mangrove Rhizophoraceae. There are 17 taxa in the IWP and three taxa in AEP. Six dispersal barriers include two land barriers and variously effective water barriers. Recorded introductions of *Rhizophora mangle* have been made to Hawaii and Tahiti. For comparison, the distribution of *Avicennia* (=Avicenniaceae) is shown by the thin line along coastal margins



cludes the Indian Ocean in conjunction with the arid regions of the Middle East and the separation of Australasian biota from Asian biota (see Fig. 2).

Mangrove distributions are complicated. There are approximately one-third fewer taxa in the AEP (Duke et al. 1998a), even though there is an equivalent area of mangrove habitat in each region (Spalding et al. 1997). There is currently a full range of wet and dry tropical climates in each region, with equivalent ranges of habitat type and so on. In the AEP, the American continents currently separate east Pacific and west Atlantic coastlines. Similarly, the Atlantic separates east America from west Africa and the ocean distance between (comparable with the east Pacific barrier) suggests there is little, if any, genetic exchange between these sub-regions currently. In both cases, however, common species assemblages are apparently shared across all three sub-regions. Current distribution patterns in the AEP, there-

fore, cannot be explained by existing dispersal routes and geological conditions.

In the IWP, the Indian Ocean seems to be the only effective present-day barrier. East African communities are seen as a subset of the highly diverse mangroves of Malesia and Australasia. Mangroves might not be expected to cross the open water expanse of the Indian Ocean, but they may disperse and exchange genes currently via populations in the Middle East, India, across to SE Asia, to the NW Pacific Ocean and south to Australia and the SW Pacific Ocean. Furthermore, the contiguous island archipelago from SE Asia to Australasia suggests there might be ready gene flow also between these nominal sub-regions. This might be expected even for taxa with relatively limited dispersal capabilities. In the following sections, an examination of individual genera and species show distinctions in genetic make-up among the three IWP sub-regions.

Discontinuities within mangrove distributions

A discontinuity is a marked change in genetic or morphological character of one or more taxa over a short geographic distance (~100–200 km) where ecological and environmental conditions may be comparable. Discontinuities usually have distinct geographic locations, although these may in some cases be diffuse, or less apparent. Various discontinuities have been described for mangroves (see Duke 1992, 1995; Duke et al. 1998a, b).

Populations on either side of a discontinuity may comprise closely related taxa, or one taxa may simply be present on one side and absent on the other. Taxonomic levels making the discontinuity vary also and it is possible that they reflect the age of the discontinuity. Therefore, changes in taxa might be intra- or interspecific as sibling species. Based on prior notions of dispersal ability and incomplete taxonomy, some discontinuities in mangrove plants were unexpected occurrences of restricted dispersal and gene flow, especially within the global regions. By contrast, areas away from discontinuities have unexpectedly low diversity both within and among populations (e.g., see Huang and Chen 1997; Sun et al. 1998; Parani et al. 1998).

Expectations of gene flow in mangroves have been based on perceived wide dispersal abilities of their specialised water-borne propagules. In some cases, these expectations persist (as shown in Plaziat et al. 2001), despite acknowledged differences in this ability among otherwise equally distributed taxa (also see Rabinowitz 1978). The occurrence of discontinuities currently is used to support the chief argument against propagules as adaptations promoting long-distance dispersal (Duke et al. 1998a).

The New Guinea discontinuity

Perhaps the most notable mangrove discontinuity in the IWP is between the north and south coasts of New Guinea in the SW Pacific (Duke 1992; Duke et al. 1998a). This large island separates, in part, Malesian and Australasian mangrove floras. Species found chiefly on the north coast include *Sonneratia caseolaris* and *Avicennia alba* while those found on the south coast include *Sonneratia lanceolata*, *Avicennia marina*, *Avicennia officinalis*, *Campostemon schultzei*, *Osbornia octodonta*, *Bruguiera exaristata* and *Ceriops australis*. Based on differences between taxa like *Avicennia* and *Rhizophora*, there are several observations to be made about the New Guinea discontinuity.

Differences in *Avicennia* taxa from north to south coasts of New Guinea appear to be at the species level, at least for two taxa. *Avicennia marina* is the most widespread of *Avicennia* in the IWP (Duke 1991), ranging from east Africa through SE Asia to the edges of the western Pacific Ocean. In equatorial latitudes, however, *A. alba* is more broadly distributed than *A. marina* and apparently replaces it in northern New Guinea and immediately north.

Differences in *Rhizophora* taxa from north to south coasts of New Guinea are often at an intraspecific level, notably for *R. apiculata*. Morphological variation, indicative of possible intraspecific genetic variation, was reported for *R. apiculata* in Australasia (Duke and Bunt 1979) and was found to be consistent broadly through the IWP (Duke et al. 1998a). The leaves of *Rhizophora* species in the IWP typically have small reddish-brown spots (cork warts) on their undersurfaces, a diagnostic feature used to distinguish this genus from *Bruguiera* in the absence of reproductive parts (Ding 1958, 1960; Tomlinson 1986). Spots are present on *R. apiculata* from India to SE Asia and northern New Guinea. However, in southern New Guinea and Australia, the spots are absent in *R. apiculata* and the hybrid *R. lamarckii*. This is a good example of morphological differentiation at the intraspecific level.

Taxonomic differences about the New Guinea discontinuity appear related to dispersal abilities, where those taxa with lesser abilities have higher levels of taxonomic differentiation, e.g., as shown for *Avicennia* taxa at a species level; for *Rhizophora* this discontinuity was characterised by intraspecific variation. Levels of taxonomic differentiation for discontinuities are, therefore, expected to vary among taxa, as well as between each discontinuity. For this reason, the importance and comparative effectiveness of each discontinuity should be based, where possible, on comparable taxa when estimating their relative age.

The relatively high taxonomic level of taxa defining the New Guinea occurrence is considered indicative not only of the importance of this discontinuity but also of its relatively ancient origin. This pattern appears to have been a result of tectonic movement of the Australian plate, passing across the ancient Tethys Sea during the Eocene and Miocene eras. The strength of these patterns at genus and species levels implies that similar patterns also exist elsewhere in intraspecific characteristics. If so, knowing such patterns would support critical insights and understanding of dispersal and gene flow amongst mangrove populations and help answer important questions regarding the biogeography and evolution of mangroves.

Additional discontinuities in the IWP and AEP

Intraspecific discontinuities have been shown in genetic and morphological characters of at least five mangrove species: *Avicennia marina*, *A. alba*, *A. germinans*, *Ceriops tagal* and *Kandelia candel*.

Avicennia marina has three multilocus genotypes around the Australian mainland linked to specific morphological characters (Duke et al. 1998b). These intraspecific forms show variable levels of mixing depending on geographic distance from areas of highest concentrations of specific genes. In this case, overlap zones between these genotypes have broadly defined geographic locations over several hundred kilometres where mixing

is unrestrained and gene composition grades progressively from one form to the next.

A separate analysis of microsatellites for the same species (Maguire et al. 2000), however, supported a discrete subpopulation model rather than isolation by distance. The reason for this apparent discrepancy is believed to be based on the smaller number of populations sampled over the wide distribution range and particularly on the lack of sites around and within discontinuity and overlap zones. Such findings emphasize the sometimes variable and patchy nature of gene dispersal, especially when the mechanisms and extent of gene dispersal of particular taxa are poorly known. Limited evidence presented here suggests that wide mangrove distributions are sometimes characterised by discontinuities between parts of the range which otherwise and separately lack genetic divergence.

For instance, indications of intraspecific genetic differentiation have been observed in *A. germinans* from the Caribbean–eastern Pacific area, in the AEP (McMillan 1986). In this case, a preliminary investigation of allozymes revealed possibly three sub-groupings of alleles based on geographic locations in the western Caribbean, eastern Caribbean and eastern Pacific. These observations are indicative of two possible discontinuities: one is expected from the east to west coasts of Central America; but the other is unexpected, occurring between the eastern and western sides of the Caribbean Sea.

Some intraspecific genetic variation in *A. alba* also was observed between two SE Asian populations in Penang and Singapore, on the Malay Peninsula (Duke et al. 1998b). Based on a quite limited assessment of variation in allozymes and the nature of variation described in Australia for *A. marina*, it appears there may be comparable discontinuities in the Asian region. While the Singapore population had relatively little genetic variation, the population from Penang showed overlap at one locus (MDH-5), suggestive of possible further differentiation to the west.

This pattern was better shown in the study of inter-simple sequence repeat (ISSR) with *Ceriops tagal* by Ge and Sun (2001), who found eastern coastal populations of Thailand were more similar to populations from China than to populations from the western coastline of Thailand. These observations are consistent with a discontinuity across the Malay Peninsula, from the Andaman to the China Sea.

Kandelia candel has localised morphological characteristics across its range (Maxwell 1995). Leaf and propagule morphology of plants from Brunei, Thailand and Hong Kong were monitored in transplants over a 4-year period in Hong Kong. Two key observations were made: 1) saplings maintained their distinctive morphological characteristics with respect to source populations over time and 2) plants originally from milder tropical climates were severely affected by colder winter temperatures in Hong Kong. The cold tolerance of local populations was taken as further evidence of intraspecific variants in this

species, i.e., the presence of genetic variation in physiological traits that are adaptively important. Genetic studies based on collections from the China Sea region of Asia describe low levels of genetic diversity (Huang and Chen 1997; Sun et al. 1998). Further studies across the entire distributional range of taxa are required to determine broader geographic patterns which might better describe this apparent discontinuity across the Malay Peninsula.

Variation in *Rhizophora* – unresolved diagnostic issues

The genus *Rhizophora* is the most common mangrove genus worldwide and it is one of only three genera to span global regions (Duke et al. 1998a). Across this wide geographic range, *Rhizophora* species are primarily divided into two genetically isolated global regions by two currently effective dispersal barriers, namely the Eurasian–African land mass and the eastern Pacific Ocean (Fig. 2). The total number of species is around five, but there are also comparable wide-ranging hybrids in each region, as well as wide variation in diagnostic morphological characters for the known entities. This combination of factors has created considerable confusion for those wanting to identify the genetic composition of particular mangrove stands.

Rhizophora species comprise four distinct groupings of taxa: “mangle” and “racemosa” in the AEP and “mucronata-stylosa” and “apiculata” in the IWP (Fig. 3). There are also at least four reported hybrids in the world (Kathiresan 1995; Parani et al. 1997; Duke et al. 1998a) and there are likely to be more. In the IWP, there are four reported species [*R. mucronata*, *R. stylosa*, *R. apiculata* and *R. mangle* (= *R. samoensis*)] and three hybrids (*R. lamarckii*, *R. selala* and *R. annamalai*). The four chief systematic entities in Australasia (New Guinea, Australia and surrounding islands of the southwestern Pacific Ocean) were described some years ago (Ding 1958; Duke and Bunt 1979; Tomlinson 1978, 1986). There has been no reassessment since, despite acknowledgement that notable problems remained unresolved.

The chief issues concerning the systematics of *Rhizophora* in the IWP, based on Duke and Bunt (1979) and Tomlinson (1978, 1986) and on subsequent observations by Duke during recent surveys in northern Australia, Micronesia and China, include: (1) the closeness of *R. stylosa* (RS) in Australia and New Guinea to *R. mucronata* (RMw) in eastern Africa and the Middle East; (2) the divergence between Australasian *R. mucronata* (RMe) and east African *R. mucronata* (RMw); (3) the variation within *R. apiculata*, with one form in Australia and southern New Guinea (RAs) and another in northern New Guinea and throughout SE Asia (RAn); (4) the differences in hybrid intermediates depending on parental forms including *R. stylosa* (RS) and the two forms of *R. apiculata* (RAs or RAn), currently all known as *R. lamarckii* (RLs and RLn) in New Guinea, Australia, Micronesia and China; (5) the putative hybrid of *R. mu-*

Fig. 3 Relationships amongst the genus *Rhizophora* according to the occurrence of morphological taxa in two global biogeographic regions (Duke and Bunt 1979; Duke et al. 1998a). The proposed phylogeny is based on our current synthesis of information. Codes for taxonomic units: RAs *R. apiculata*, southern New Guinea, Australia and New Caledonia; RAn *R. apiculata*, India, Asia to Malenesia and northern New Guinea; RH *R. harrisonii*, putative hybrid RMa X RR; RLs *R. lamarckii*, putative hybrid RS X RAs; RAi *R. annamalai*, putative hybrid RMw X RAn; RLn *R. lamarckii* two, putative hybrid RS X RAn; RMa *R. mangle*, AEP and southwestern Pacific; RMe *R. mucronata*, Australasia and western Pacific; RMw *R. mucronata*, eastern Africa and India; RR *R. racemosa*, AEP; RSe *R. selala*, putative hybrid RS X RMa; RS *R. stylosa*, Asia, Australasia and western Pacific

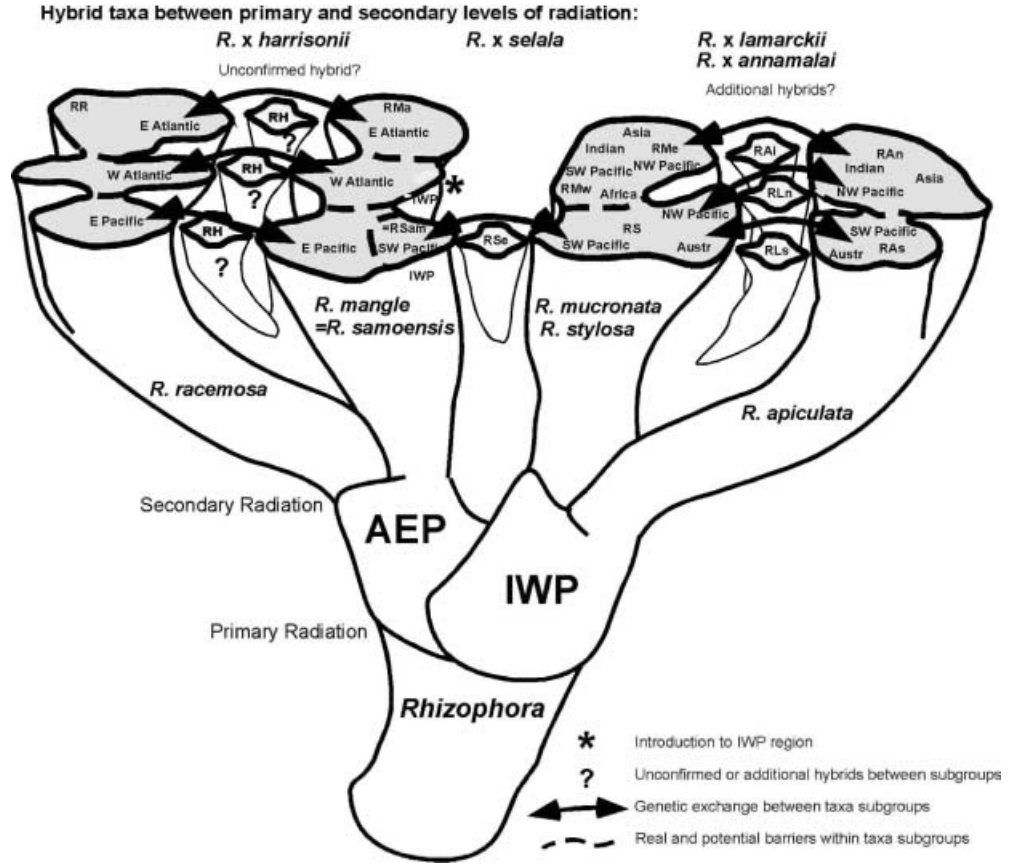
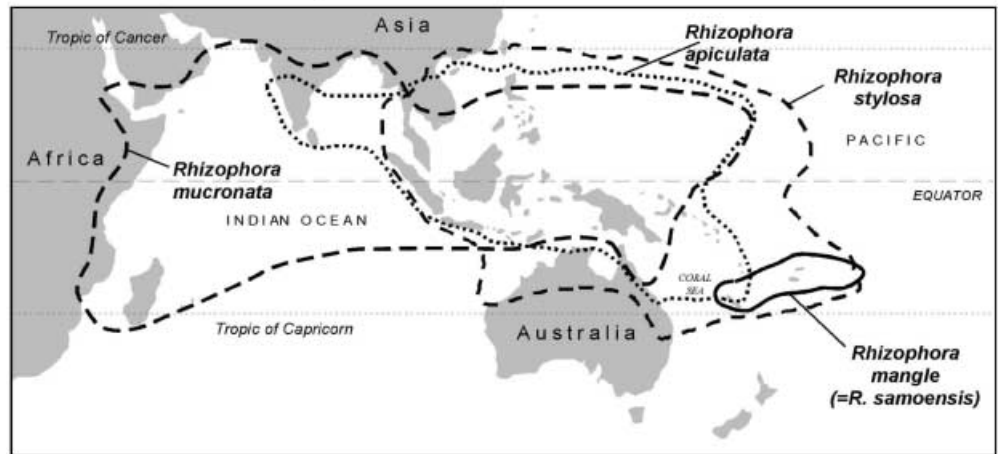


Fig. 4 Distribution of four chief *Rhizophora* taxa through the IWP region based on our current observations (noting some modifications after Tomlinson 1986)

Indo West Pacific *Rhizophora*



cronata (RMw) and *R. apiculata* (RAn), apparently described as *R. annamalai* in India (RAi) but sometimes referred to also as *R. lamarckii*; (6) the presence of the AEP species *R. mangle* (RMa) in several Pacific Island locations (introduced in Hawaii and Tahiti, but apparently natural in Fiji, Tonga and Samoa) and its putative hybrid with *R. stylosa* (RS), described as *R. selala* (RSe). The combination of these unresolved issues has resulted in inconsistent diagnostic determination of taxa throughout the IWP and has inhibited meaningful assessment of their distributional patterns and phylogenetic affinities.

Distribution of *Rhizophora* taxa in the IWP – unusual patterns for dispersal specialists

The four species (Fig. 4) and several hybrids of *Rhizophora* are distributed widely throughout the IWP (Ding 1958; Duke and Bunt 1979; Tomlinson 1986). One species, *R. samoensis*, appears to be an outlying population of the AEP species *R. mangle* (Ellison 1991). It is restricted to several island groups in the SW Pacific Ocean and it does not extend to New Guinea or Australia. This distribution pattern is unique in mangroves and repre-

sents an apparently isolated dispersal aberration. It is curious also why this species has not spread further west, since *R. stylosa* has dispersed east to these islands crossing similar water distances in the past.

Identification of hybrids is inconclusive, leaving gaps in apparent distributions. The best-known hybrid taxon, *R. lamarckii*, is the putative hybrid of *R. stylosa* and *R. apiculata* in Australasia (Tomlinson and Womersley 1976; Tomlinson 1978). Its distribution reflects the overlapping distributions of its parents (Duke and Bunt 1979). Recent reports of additional *Rhizophora* hybrids (e.g., *R. selala* and *R. annamalai*) might also be viewed in this way (consider Tomlinson 1978; Parani et al. 1997). This is important when assessing distributional records, since systematic field and herbarium determinations and descriptions of hybrid forms have been inconsistent and systematic distributional records are generally lacking in most places, except for Australasia.

The distributions of the three chief IWP *Rhizophora* taxa appear relatively well understood, although questions remain surrounding the distinctiveness of these "good" taxa. Briefly, *R. apiculata* is the most easily recognised of *Rhizophora* in the IWP. By contrast, *R. mucronata* and *R. stylosa* are often difficult to tell apart. However, *R. stylosa* appears dominant in eastern parts of the range, especially through Australasia and into the western Pacific Ocean, while *R. mucronata* appears to dominate the western range from east Africa to India. Both taxa occur in sympatry from SE Asia to the NW Pacific Ocean and to northern Australia.

Based on morphological evidence, it is certain *R. stylosa* and *R. mucronata* are closely related. The question is whether they are sibling species or variants of the one species. Given the nature of *Rhizophora* taxa to hybridise amongst all chief taxa (including those from the AEP and IWP), these two might be expected to hybridise when they occur in sympatry, but there are no distinct hybrid forms. In summary, the current evidence for their

close genetic relationship includes the difficulty in distinguishing these taxa using morphological criteria and no clear evidence of reproductive isolation. For instance, while there is some divergence in both flowering period and niche specialisation, both characteristics overlap between taxa. These characteristics also appear to have greatest divergence at eastern sections of the distribution of each taxon.

Similar overall distribution patterns and irregularities appear in other IWP mangrove genera (Tomlinson 1986), particularly for multi-specific taxa: 1) widespread taxa which are morphologically distinct and extend to east Africa, despite the relative isolation of some populations today; 2) taxa that are centrally located and dominant within SE Asia, but sometimes absent in the Philippines; 3) taxa that are dominant chiefly in Australasia, often limited at or near the New Guinea discontinuity. These patterns reflect notable restrictions in gene flow in current circumstances, because there are both notable distributional limits and species absences, as well as the presence of discontinuities.

Intraspecific variation in *Rhizophora*

Preliminary results of variation in 12 diagnostic characters of *Rhizophora* taxa are summarised in Tables 1, 2 and 3. Data are grouped for four geographic areas: NW Pacific Islands, China, East Africa and Australia. Groupings are made for up to four nominal taxa in each sub-region, noting intra-taxa variation described earlier, including: *R. apiculata* (northern form, RAn, and southern form, RAs), *R. lamarckii* (northern form, RLn, and southern form, RLs), *R. stylosa* (RS) and *R. mucronata* (western form, RMw, and eastern form, RMe).

Rhizophora apiculata is the most distinct of IWP taxa with fundamental differences observed in many characters, including lower position of inflorescences, corky

Table 1 Summary of chief diagnostic morphological characters (range with median in brackets) of *Rhizophora* taxa in NW Pacific island sites, including Palau, Yap, Guam, Chuuk, Pohnpei, Kosrae and Kiribati. Blank cells indicate no data (*Bb* mature flower bud,

Fb mature fruit, *Hb* mature hypocotyl, *L* length, *L1* style length from corolla base, *L2* style length above swollen base, *SW* style width at corolla base, *W* width)

| Diagnostic characters | | <i>R. apiculata</i> | <i>R. X lamarckii</i> | <i>R. stylosa</i> | <i>R. mucronata</i> |
|-----------------------|-----------|---------------------|-----------------------|-------------------|---------------------|
| Leaf mucro (mm) | <i>L</i> | 0.8-(2.1)-3.5 | 1.5-(3.3)-5.6 | 2.0-(4.4)-6.7 | 2.7-(5.0)-7.0 |
| | <i>W</i> | 0.3-(0.5)-0.6 | 0.3-(0.5)-0.8 | 0.5-(1.0)-2.5 | 0.7-(1.0) |
| Leaf undersurface | Spots | Spots | Spots | Spots | Spots |
| Inflorescence | <i>Bb</i> | 6-11 | 3-6 | 2-5 | 2-3 |
| Position no. | <i>Fb</i> | 8-10 | | 4-7 | 4-5 |
| | <i>Hb</i> | 9-13 | 8-9 | 4-9 | 5-10 |
| Bract surface | | Corky | Smooth | Smooth | Smooth |
| Inflorescence joints | No. | (1)-2 | 1-2 | 0-4 | 1-4 |
| Style dimensions (mm) | <i>L1</i> | 0.1-(0.6)-1.3 | 1.7-(2.7)-3.7 | 1.6-(3.4)-5.7 | 0.5-(1.3)-2.3 |
| | <i>L2</i> | 1.5-(2.2)-3.0 | 3.2-(4.3)-5.8 | 3.0-(4.9)-8.0 | 2.5-(3.8)-5.8 |
| | <i>SW</i> | 2.6-(3.6)-4.8 | 3.2-(4.1)-5.4 | 2.0-(2.5)-3.0 | 2.5-(3.3)-4.2 |
| Petal margin | | Glabrous | Slightly hairy | Very hairy | Hairy |
| Petal shape | | Linear | Linear-lanceolate | Lanceolate | Lanceolate |
| Stamen | No. | 8-(10)-13 | 6-(11)-16 | 6-(7)-8 | 7-(8) |
| Calyx lobes | No. | (4)-6 | 3-(4) | 3-(4) | 4 |

Fig. 5 Variation in calyx lobe number through the IWP region for (a) *Rhizophora apiculata* and (b) *Rhizophora stylosa*. Four calyx lobes are normal for the genus. Geographic ranges are shown for respective species. Inset shows typical mature bud inflorescences for *R. apiculata* RA, *R. lamarckii* RL, *R. stylosa* RS and *R. mucronata* RM

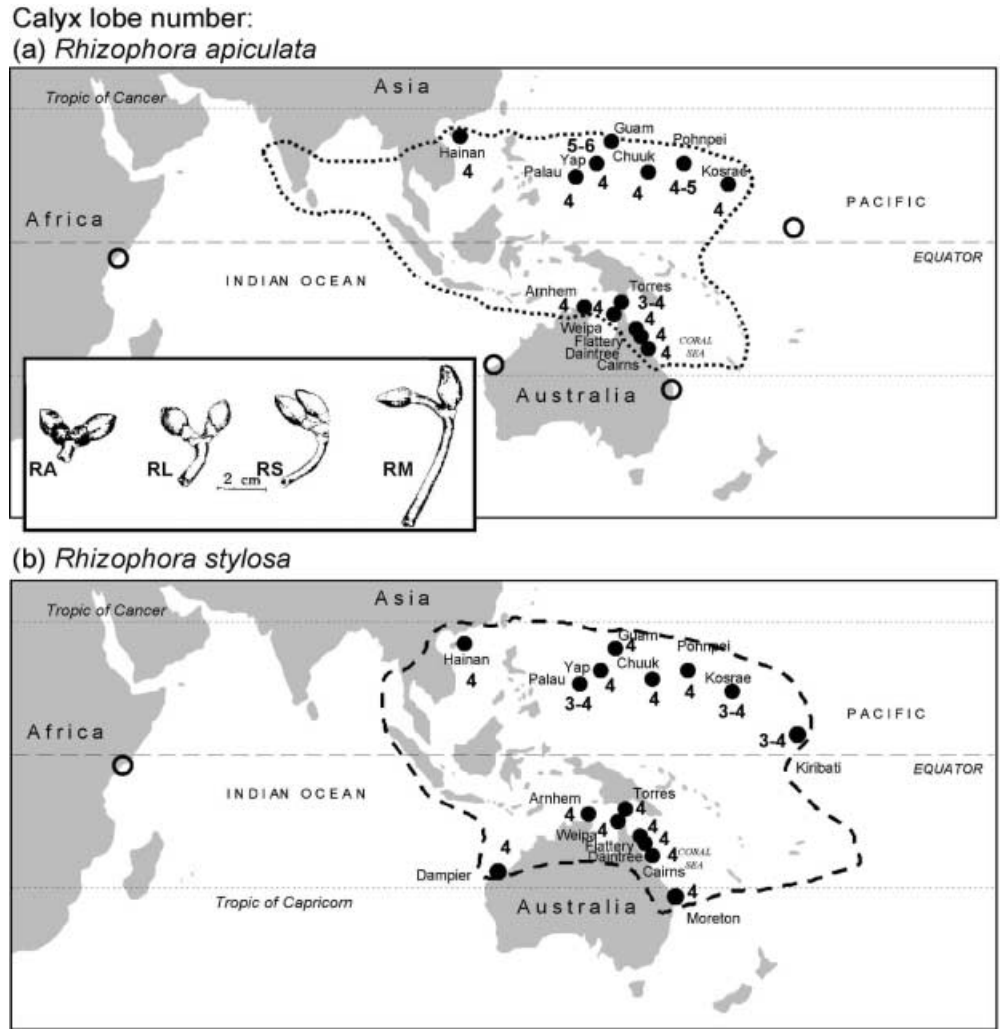


Table 2 Summary of chief diagnostic morphological characters (range with median in brackets) of *Rhizophora* taxa in Australian sites, including Western Australia (Dampier), Northern Territory (Arnhem Bay) and Queensland (Weipa, Torres Strait, Cape Flat-

tery, Daintree River, Trinity Inlet, Moreton Bay). Blank cells indicate no data (*Bb* mature flower bud, *Fb* mature fruit, *Hb* mature hypocotyl, *L* length, *L1* style length from corolla base, *L2* style length above swollen base, *SW* style width at corolla base, *W* width)

| Diagnostic characters | | <i>R. apiculata</i> | <i>R. X lamarckii</i> | <i>R. stylosa</i> | <i>R. mucronata</i> |
|-----------------------|-----------|---------------------|-----------------------|-------------------|---------------------|
| Leaf mucro (mm) | <i>L</i> | 1.3-(2.8)-4.9 | 2.3-(3.9)-7.1 | 1.9-(4.6)-7.4 | 2.1-(4.5)-7.5 |
| | <i>W</i> | 0.4-(0.7)-1.2 | 0.4-(0.8)-1.4 | 0.6-(0.9)-1.2 | 0.5-(0.9)-1.2 |
| Leaf undersurface | | No spots | No spots | Spots | Spots |
| Inflorescence | <i>Bb</i> | 4-10 | 3-5 | 1-4 | 1-2 |
| Position no. | <i>Fb</i> | | | 5 | 4 |
| | <i>Hb</i> | 7-9 | | 5-8 | 4-7 |
| Bract surface | | Corky | Smooth | Smooth | Smooth |
| Inflorescence joints | No. | 1 | 0-2 | 0-5 | 0-3 |
| Style dimensions (mm) | <i>L1</i> | 0.4-(0.8)-1.3 | 1.3-(2.0)-2.9 | 2.1-(3.6)-5.5 | 0.6-(1.3)-2.5 |
| | <i>L2</i> | 1.3-(2.1)-2.7 | 2.2-(3.6)-4.5 | 2.9-(4.4)-5.5 | 2.4-(3.4)-4.3 |
| | <i>SW</i> | 3.7-(4.2)-6.0 | 2.4-(4.1)-5.3 | 1.8-(2.5)-3.3 | 2.5-(2.8)-3.1 |
| Petal margin | | Glabrous | Slightly hairy | Very hairy | Hairy |
| Petal shape | | Linear | Linear-lanceolate | Lanceolate | Lanceolate |
| Stamen | No. | 9-(12)-16 | 7-(11)-15 | 6-(8) | 8-(9)-11 |
| Calyx lobes | No. | 3-(4) | 4 | 4 | 4 |

bract surfaces, single inflorescence joints, short style length, glabrous petal margin and linear petal shape. For Australia, the southern variant (RAs) characteristically lacks spots (cork warts) on leaf undersurfaces (Duke and Bunt 1979). The number of calyx lobes (Fig. 5), normal-

ly 4 in the genus, is 3-6 in this and other species. Australian sites mostly have 4, but there were 3-4 in at least one location. In China, there was no apparent deviation from 4, but in the islands of the NW Pacific the number of lobes was greater than 4 (4-6) at two locations. There

Fig. 6 Variation in stamen number through the IWP region for (a) *Rhizophora apiculata* and (b) *Rhizophora stylosa*. Eight stamens are common for most species in the genus except *R. apiculata*. Geographic ranges are shown for respective species. Inset shows typical floral diagrams for *R. apiculata* RA, *R. lamarckii* RL, *R. stylosa* RS and *R. mucronata* RM

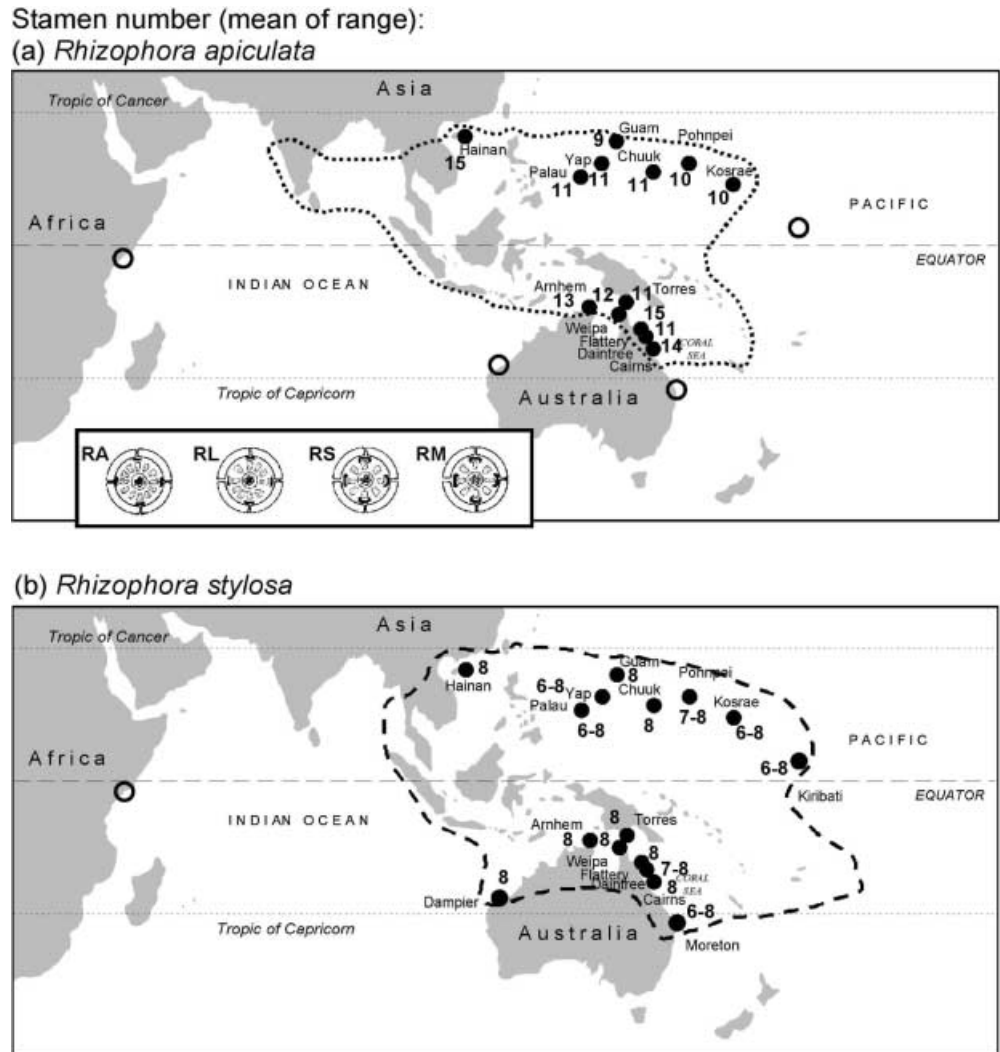


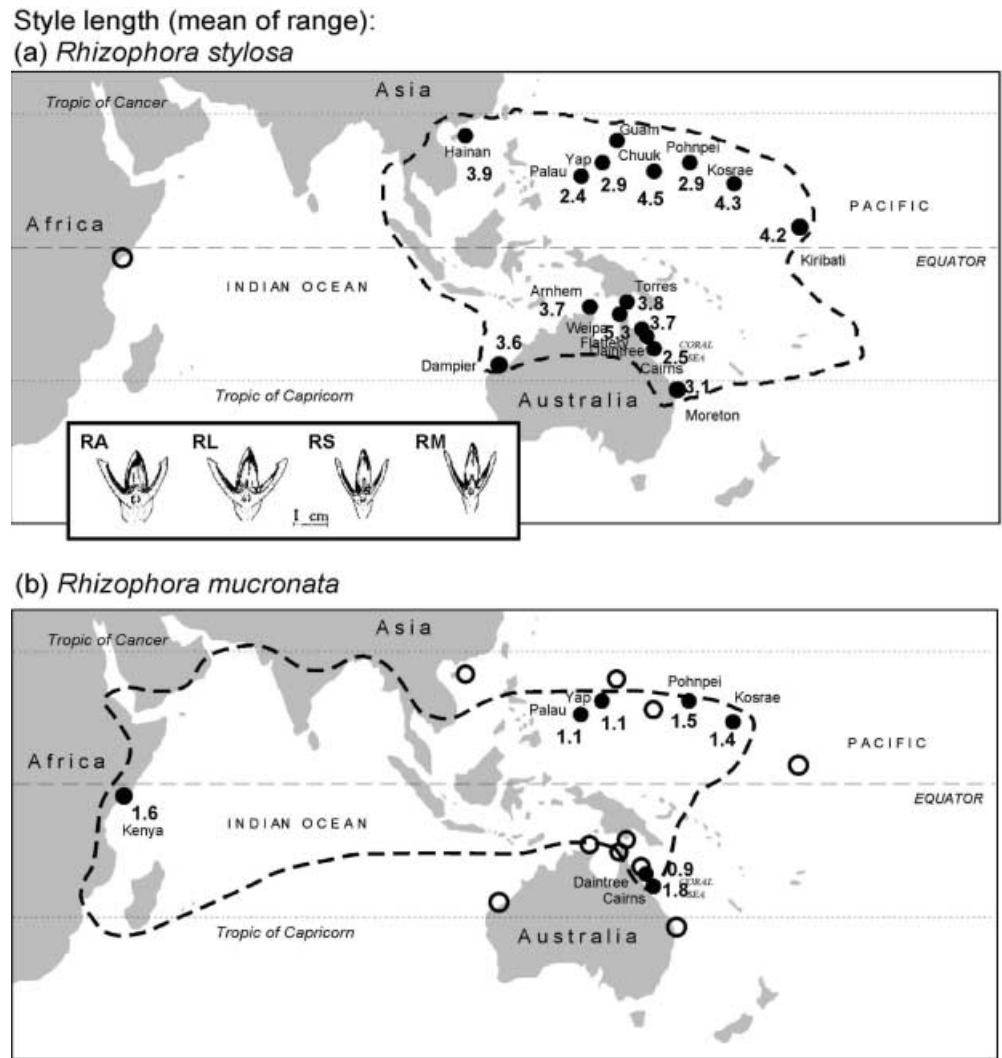
Table 3 Summary of chief diagnostic morphological characters (range with median in brackets) of *Rhizophora* taxa from sites in China (Dongzhai and Wenchang, Hainan Island) and East Africa (Gazi Bay and Mida Creek, Kenya). Blank cells indicate no data (*Bb* mature flower bud, *Fb* mature fruit, *Hb* mature hypocotyl, *L* length, *L1* style length from corolla base, *L2* style length above swollen base, *SW* style width at corolla base, *W* width)

| Diagnostic characters | China | | Kenya |
|-----------------------|----------------------------|-------------------|---------------------|
| | <i>R. apiculata</i> | <i>R. stylosa</i> | <i>R. mucronata</i> |
| Leaf mucro (mm) | <i>L</i> 1.6-(2.8)-4.0 | 3.5-(5.4)-7.3 | 4.2-(5.8)-7.4 |
| Leaf undersurface | <i>W</i> 0.5-(0.7)-0.8 | 0.6-(0.8)-1.0 | 0.7-(1.1)-1.4 |
| Inflorescence | Spots | Spots | Spots |
| Position no. | <i>Bb</i> 7 | 3-4 | 2-3 |
| | <i>Fb</i> 8 | 5-6 | 5 |
| | <i>Hb</i> 8 | | 8 |
| Bract surface | Corky | Smooth | Smooth |
| Inflorescence joints | No. 1 | 1-3 | 1-3 |
| Style dimensions (mm) | <i>L1</i> 0.6 | 3.4-(3.9)-4.4 | 1.3-(1.6)-1.8 |
| | <i>L2</i> 1.9-(2.1)-2.3 | 4.3-(4.6)-4.9 | 3.9-(4.5)-5.0 |
| | <i>SW</i> 3.4 | 3.4 | 2.9-(3.2)-3.5 |
| Petal margin | Glabrous | Slightly hairy | Hairy |
| Petal shape | Linear | Linear-lanceolate | Lanceolate |
| Stamen | No. 13-(15)-16 | 8 | 8 |
| Calyx lobes | No. 4 | 4 | 4 |

was also a notable decline in stamen number for islands towards the furthest northeastern limit of the species range (Fig. 6). Such patterns suggest trends brought about by increased isolation where geographic distance between populations is great.

Rhizophora lamarckii has consistently intermediate characteristics between *R. apiculata* and *R. stylosa* (and/or *R. mucronata*?) in both NW Pacific Islands and Australia. Morphological differences between *R. stylosa* and *R. mucronata* are also sometimes difficult to discern

Fig. 7 Variation in style length through the IWP region for (a) *Rhizophora stylosa* and (b) *Rhizophora mucronata*. Style length here is the length above the swollen base *L1* in Tables 1, 2 and 3). Geographic ranges are shown for respective species. Inset shows typical flower bud cross-sections for *R. apiculata* RA, *R. lamarckii* RL, *R. stylosa* RS and *R. mucronata* RM



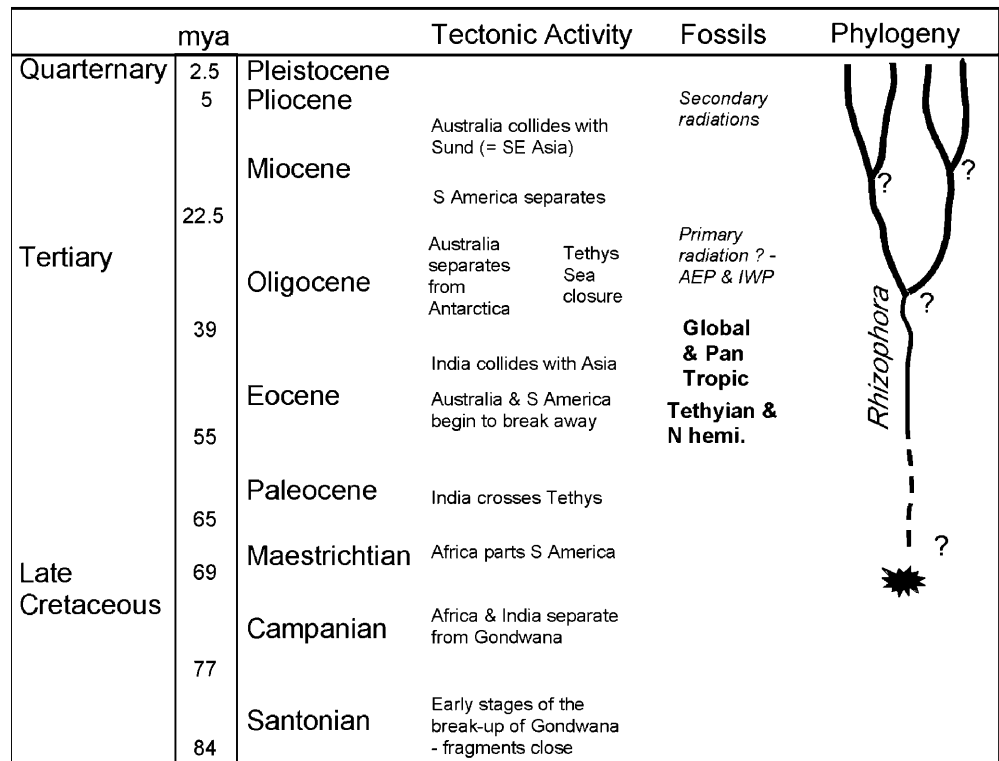
in sympatric mixed communities in both NW Pacific Islands and Australia. However, based on the key diagnostic character of upper style length ($L1$ = length above basal ovary swelling), both taxa are present in both sub-regions. This becomes less apparent when considering full style length ($L2$ = length above the corolla base) and, by contrast, this measure is not considered diagnostic in itself. Clearly, the choice of style length measure as the diagnostic character presents confusion in discriminating these taxa, especially where they might otherwise be grouped together based on other characteristics. A range of supportive characters was described by Duke and Bunt (1979) for Australian populations, but these characters were not considered diagnostic on their own, or definitive.

Furthermore, in both sub-regions, some individuals had intermediate style lengths ($L1$). Our observations suggest the two forms are genetically as well as morphologically close. The occurrence of undefined intermediate individuals (notable as those which are difficult to assign to either taxa) is indicative of mixed genotypes be-

tween variants of one species rather than between genetically distinct, sibling species. This view is supported by our preliminary genetic assessment (unpublished data) showing very close but distinct genetic characteristics between *R. stylosa* and *R. mucronata*, compared with other *Rhizophora* taxa in the IWP, including: *R. apiculata*, *R. lamarckii* and *R. mangle*.

Variations in $L1$ style length in *R. stylosa* and *R. mucronata* are summarised in Figure 7 for the four sub-regions in the IWP. For *R. stylosa*, there is a tendency for longer styles in some NW Pacific Islands, but overall no consistent pattern emerged based on this key character. Currently, there are relatively few data for *R. mucronata*, since sampling has concentrated so far in eastern parts of the IWP range of *Rhizophora*, but there is a tendency to longer styles in populations at the distributional limits of this taxon. Again patterns here show variation in basic characters that tend to diminish their overall diagnostic value.

Fig. 8 Time line for the appearance, radiation and divergence of *Rhizophora* taxa in the IWP region. Concurrent significant tectonic events and fossil occurrences have been listed for comparison with the proposed phylogeny



Origin and early dispersal of *Rhizophora*

Plaziat et al. (2001) provide a comprehensive re-assessment of fossil records for mangrove taxa around the world. In this treatment, ancestral *Rhizophora* forms were reported first in deposits of the northerly located, ancient Tethyan archipelago during the Early Eocene (~50 million years ago). At that time, the genus was already relatively widespread in the area, although it apparently did not surround the globe until about 10 million years later in the Late Eocene. This appears to have been a period of measured expansion for *Rhizophora* and other common mangrove taxa. Prior to this, notably during the Paleocene (~55 million years ago), there are apparently no records of *Rhizophora* taxa. These observations imply that *Rhizophora* mangrove evolved during this period of relatively warmer conditions somewhere in the ancient Tethys Sea area. Warmer and milder climates which prevailed during Eocene times are also shown by high latitude locations of *Rhizophora* and other mangroves (Fig. 8).

The position of continental masses at the time was also quite different from today. During the 15 million years from Paleocene to Late Eocene, the dispersing fragments of the old Gondwanan supercontinent were clearly unsettled and mobile. In the Paleocene, the Indian subcontinent was more or less equatorial, traversing north but still distant from Eurasia. Meanwhile, Australia was only just beginning to detach and move northward away from Antarctica and toward SE Asia. As these were formative times for mangrove communities, we suggest that continental drift significantly affected *Rhiz-*

ophora dispersal and diversity. In the IWP, these tectonic movements appear to have contributed to the major genetic discontinuities, especially those of higher level, taxonomic differences.

Phylogeny and divergence of *Rhizophora* taxa

Taxa in the genus *Rhizophora* are primarily divided into IWP and AEP groups based on morphological characters, notably presence/absence of leaf mucro. This basic division is indicative of a primary radiation in the genus, most likely to have occurred after closure of the Tethys Sea and as warm conditions contracted during the Oligocene, around 30 million years ago. Current isolating barriers have remained in place over a very long period and there are few instances where IWP and AEP taxa occur sympatrically. This feature is in marked contrast to subsequent patterns of radiation and divergence of the genus. Each of the two global sub-regions appears to have undergone separate periods of secondary radiation, promoted by quite different circumstances.

In the AEP, two chief *Rhizophora* taxa dominate, namely *R. mangle* and *R. racemosa*. There appears to be confusion with the second taxa only where it may also be named *R. harrisonii*. However, if a third taxon exists, it may be the hybrid of the other two, but there are no data (morphological or genetic) to support this claim (e.g., Breteler 1969; Dodd et al. 1995). The distributions of these taxa reportedly extend equally and largely in sympatry, from western shores of Central and South America, through the Caribbean and eastern shores of

South America and across to the west coast of Africa (Tomlinson 1986). Saenger (1998) argued that *Rhizophora* reached West Africa via the Mediterranean with its earlier appearances in southern France (~50 million years ago; Gruas-Cavagnetto et al. 1988), Great Britain (~45 million years ago; Chandler 1951), North America (~40 million years ago; Berry 1916, 1936) and South America (~38 million years ago; Germeraad et al. 1969; van der Hammen and Wymstra 1964).

In the absence of suitably detailed information on these taxa across this wide distribution range, it is not possible to make any further observations about their subsequent radiation and early dispersal. However, it is odd that these taxa cross two existing dispersal barriers, namely the Central American isthmus and the Atlantic Ocean (e.g., Domínguez et al. 1998), in view of patterns of more restricted dispersal in IWP taxa.

In the IWP, the description and distribution of taxa are becoming better known and there is sufficient information now from which to develop hypotheses on dispersal and diversification of *Rhizophora* taxa in this region. Comparable in one sense with the AEP, there are also two groupings of taxa in the IWP, including *R. apiculata* and a sub-group combining *R. mucronata* and *R. stylosa*. This is apart from the limited incursion of *R. mangle* in the SW Pacific and the occurrence of hybrid forms. Also in common with the AEP, taxa in the IWP have overlapping distributions, but in the IWP the patterns are relatively complex. In general, however, nearly all taxa occur in sympatry from India to Australia. In contrast to the AEP, the only potential barrier to present-day dispersal and gene flow is the Indian Ocean, which separates populations of *R. mucronata* along the East African coast from those further east.

Divergence and dispersal of *Rhizophora* in the IWP

As noted earlier, the divergence of *Rhizophora* in the IWP appears to have taken place after closure of the Tethys Sea during the Oligocene (Fig. 8). At this time, the Indian subcontinent was joined to the Asian continent, but Australia had just separated from Antarctica and was moving north towards SE Asia. Fossils in the Late Eocene demonstrate that *Rhizophora* ranged widely at the time and was present in Australia. Although specific taxa have not been identified in Australian deposits, particular species might logically match present-day distribution patterns and genetic relationships among extant taxa.

The major discontinuity around New Guinea reflects the convergence of two floras from Malesia and Australasia. Common characteristics in genera of these floras show their previous union. However, the degree of difference between floras is also indicative of the period of isolation that existed before these communities were reunited. They clearly shared many elements shown in other mangrove genera. For example, the presence of sibling taxa, like *Ceriops tagal* and *C. australis* and *Bruguiera gymnorrhiza* and *B. exaristata*, *Sonneratia*

caseolaris and *S. lanceolata*, are all considered taxa that reflect ancient Malesian and Australasian floras, respectively. For *Rhizophora*, an arguably comparable sibling relationship appears to be shown for *R. mucronata* and *R. stylosa*, where *R. stylosa* appears to be the Australasian form and *R. mucronata* the Malesian form. Clearly, their respective current distributions now overlap to such a degree that this relationship across the New Guinea discontinuity appears quite obscure. But there are notable supportive observations including: 1) dispersal ability and gene flow in *Rhizophora* are considered the greatest of all mangrove taxa, hence it is expected these species might disperse more widely and rapidly; 2) there is a close genetic relationship between *R. mucronata* and *R. stylosa*; 3) *R. mucronata* and *R. stylosa* occur in the west and east, respectively, of their combined distributional range in the IWP; 4) very recent data (unpublished) show close genetic association of *R. stylosa* in southern Australia with *R. mucronata* in East Africa.

The current widespread occurrence of *R. stylosa* through the western Pacific region in both northern and southern hemispheres appears consistent with the wide dispersal ability of this taxon. It is also consistent with its greater presence in coastal areas, away from riverine estuaries which often restrict and limit the distribution of most other mangrove species.

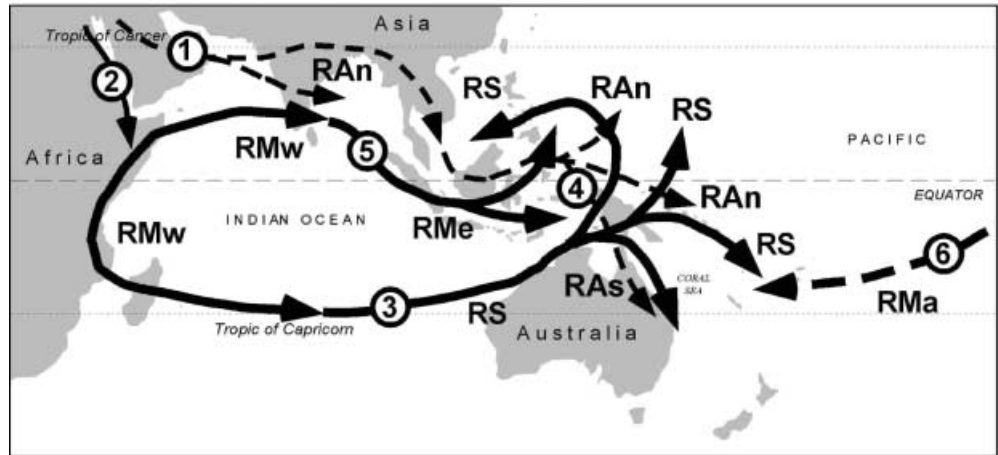
In contrast, the distribution of *R. apiculata* has been quite different although apparently affected also by the joining of Australian and SE Asian land masses. Unlike the situation for *R. stylosa* and *R. mucronata* in the region, *R. apiculata* shows a distinct and close correlation with the New Guinea discontinuity, where the different forms of this species occur on north and south coasts (Duke and Bunt 1979). By comparison, the differences between *R. apiculata* forms are subtle and more closely intraspecific, where populations differ only by the presence or absence of cork wart (spots) on leaf undersurfaces. No other morphological characters consistently support the nominal forms of *R. apiculata* on northern and southern coasts of New Guinea. Furthermore, the absence of spots is unique in the genus, so it might be assumed that the Australian form is the most recently derived of the two. Based on these observations and the dominance of *R. apiculata* through India and SE Asia, it appears *R. apiculata* only arrived in Australian mangroves after the continent got within dispersal range of SE Asia during the Miocene, around 20 million years ago.

These observations may be used to explain distributions of *Rhizophora* taxa surrounding the New Guinea discontinuity. However, there are important and significant distributional ranges, genetic relationships and dispersal events still to be explained, including: 1) the close relationship between Australian *R. stylosa* and East African *R. mucronata*; 2) East African *R. mucronata* and Malesian *R. mucronata*; 3) the earlier divergence of these forms and *R. apiculata*.

The latter event is the basis for the secondary radiation in the genus and the primary radiation in IWP taxa.

Fig. 9 Proposed paths of radiation and dispersal for *Rhizophora* taxa through the IWP region (Oligocene to present day, see Fig. 8). Coding of taxa names are those used in Figure 3 and numbered arrows refer to stages described in the text. Note the eastern reunification of disparate ends of the distributional range of the *R. stylosa*–*R. mucronata* complex sensu lato. Note that stages 1–3 at least would have occurred prior to closure of the ancient Tethys Sea

Dispersal and Evolution of IWP *Rhizophora*



Associated geological and ecological events are less apparent in the separation of these distinct taxa, but once again there are observations to be made from present-day distribution patterns and genetic characteristics of extant taxa.

The dispersal of *R. apiculata* is relatively uncomplicated, especially in view of the hypothesis for the late expansion of this taxon into the Australasian region, as outlined above. Distribution ranges in themselves do not provide the complete picture and species dominance must also be considered, especially in relation to other *Rhizophora* taxa. *Rhizophora apiculata* typically dominates in northern areas from India through Asia to China. In contrast, *R. stylosa*, is mostly dominant in Australasian mangroves. In East Africa, there is only *R. mucronata*, while a mix of *R. mucronata* with *R. apiculata* in India appears roughly equal.

These observations imply the following primary dispersal centres of ancestral *Rhizophora* taxa: 1) *Rhizophora apiculata* in Asia; 2) *Rhizophora mucronata* in East Africa; 3) *Rhizophora stylosa* in Australasia. The early dispersal of ancestral IWP taxa, therefore, appears to have resulted in geographically isolated populations of the genus to either northern or southern coasts of eastern remnants of the ancient Tethys shoreline. Over time and/or during initial dispersal, the ancestral form evolved into the three extant taxa. The close association between East African *R. mucronata* and Australian *R. stylosa* may be because *R. stylosa* evolved as a later derivative of an earlier east African form during the Oligocene when Australia was at the eastern end of the southern Tethys shoreline.

Meanwhile, the dispersal of *R. mucronata* may also have followed the northern coastline through Asia and down to Australia, apparently reaching its eastern limit after the Miocene, when Australia reached the Asian land mass. In the process, the eastern entity could have developed specialised traits not obvious in the western form (Ding 1958; Duke and Bunt 1979). These traits include: 1) its ecological preference for larger riverine es-

tuaries with relatively constant freshwater influences; 2) distinct morphological features such as long hypocotyls, long inflorescence pedicels and an usually small number of inflorescence joints.

Rhizophora apiculata is unique in the genus for its exceptionally long reproductive cycle, taking over 2.5 years from appearance of bud primordia to maturation of hypocotyls (Duke et al. 1984). This is 1 year longer than other IWP and AEP *Rhizophora*. Because all species have similar leaf production rates in leafy shoots, the position of inflorescence stages in the shoot are clearly different in *R. apiculata* compared with other *Rhizophora* (Tables 1, 2 and 3). This leaves East African *R. mucronata* as the one most closely allied with AEP species.

Primary dispersal may have taken place towards the west where divergence took place between northern *R. apiculata* and western *R. mucronata*–eastern *R. stylosa*. Subsequently, *R. stylosa* formed in Australasian mangroves.

Our hypothesis describing dispersal routes and evolution of each taxon in IWP *Rhizophora* may be summarised in six chief stages (also see Fig. 9):

1. Primary establishment of northern *R. apiculata* (RAn)

- well-established dominance along old northern shores of Tethys Sea
- distinct morphology and genetics suggest early divergence
- Australasian plate initially beyond dispersal range

2. Primary establishment of western *R. mucronata* (RMw)

- well-established along old southern shores of Tethys Sea from E Africa to India
- species notable along exposed seashore habitats, as well as estuaries
- possibly restricted by the barrier of the Sund Peninsula

3. Primary and secondary establishment of *R. stylosa* (RS)

- well-established along old SE shores of Tethys Sea to Australia
- species of exposed seashore habitats, as well as estuaries
- genetically allied with RMw before other IWP variants
- possibly restricted initially to Australasian plate

4. Secondary establishment of southern *R. apiculata* (RAs)

- well-established along old N shores of Australia and S New Guinea
- unique morphological character for genus implies recent appearance

5. Secondary establishment of eastern *R. mucronata* (RMe)

- apparently recent variant, quite restricted ecological range in upstream estuaries
- genetically allied with RMw before RS

6. Primary establishment of *R. samoensis* = *R. mangle* (RMa)

- apparently recent but natural introduction to SW Pacific region

Conclusions

The questions arising from these observations and deductions are the basis of our emerging hypothesis on the dispersal, divergence and evolution of *Rhizophora* taxa in the IWP region. Our current observations were based upon a range of features, including extant and fossil distributions, distributional discontinuities, morphological and genetic characteristics of taxa and, to some extent, their ecological characteristics. An understanding of all these aspects is considered essential for progress in these studies. The relationships within this genus are clearly complex but a rudimentary understanding is emerging of how each taxon may have evolved and achieved its current form and distributional range. Over the coming years, we will challenge and test these ideas further to refine and build upon the findings presented here.

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