Genetic diversity, distributional barriers and rafting continents – more thoughts on the evolution of mangroves

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Abstract

Without continental drift, the diversity and distribution of many species, including mangrove plants, would be very different today. First, there would be fewer pantropic genera and many more endemics. Second, their characteristics would not be as common and widespread as some are today. Continental drift has brought about the massive mixing and dispersal of genes in geologically recent times, greatly enhancing the evolutionary process; particularly for flowering plants - the angiosperms, which evolved during this period.

Mangrove plants are comprised of approximately 70 species from 20 quite different angiosperm families. Most taxa are characterized by special physiological abilities and structural forms, enabling them to live in both seasonally fluctuating saline conditions, and water-saturated soils. Their occurrence is mostly tropical, perhaps because of harsh physiological conditions of intertidal habitats; but distributions of specific taxa do not fully concur with the idea of a completely tropical evolution, at least for some important species.

At least one genus of mangrove tree, *Avicennia*, occurs around the world, chiefly in tropical estuarine habitats, although they also range into temperate latitudes, especially in the south. Around the world, there are no more than ten species of *Avicennia* recognised today, but their diagnostic determinants were inadequate prior to recent studies using both numerical analyses of morphological parameters and isozymes. Such analyses significantly reduced the number of apparent species, notably around Australia, and provided a basis for the revision of distributional records throughout the Indo West Pacific region. One species, *A. marina*, was found to be widespread and morphologically variable with genes divided into characteristic groupings of at least three geographic areas in the region. Based on these findings, there are several novel inferences to be made regarding the evolution of this genus. A western Gondwanan origin is proposed, with subsequent radiation of several taxa facilitated via the tectonic dispersal of southern continental fragments.

Introduction

There are two important paradigms associated with the evolution and biogeography of mangrove plants. One is the idea of a common centre-of-origin for all taxonomic entities and species. The second is the idea of a centre-of-diversity linked with a centre-of-origin. These are quite old concepts, and they still form the basis of our present understanding of the evolution of mangrove plants. When applied to specific taxa however, they do not explain present-day distributions (Duke, 1992; Tomlinson, 1986), leaving fundamental questions un-answered. For instance, why do mangroves have such remarkable distributional disjunctions and discontinuities? And why do they occur so widely around the world, especially in view of these discontinuities and their overall genetic uniformity? It appears that hypotheses based on centre-of-origin and centre-of-diversity concepts are chiefly based on a precept of exaggerated long-distance dispersal to explain the presence of certain taxa in widely disparate regions. In view of these doubts, and some recent findings on intra-specific variation, it is time for a re-appraisal of evolutionary models of mangroves.

The genetic composition of todays mangrove flora, while subject to present-day climatic and geographi-

cal conditions (Duke, 1992), is largely relict. Species are presumably where they are today because of past events and circumstances. And, these were influenced by respective physiology, ecology, dispersal success, geological circumstances, evolutionary rate, and origin of each taxon. These concepts are summarized in eight generalized statements concerning the biogeography and evolution of mangroves, based on Tomlinson (1986) and expanded here:

1. *Ecological and Climatic Conditions*. Mangroves are generally restricted to sheltered tropical coastlines where mean monthly seawater temperatures rarely drop below 20 °C. Some mangrove taxa are further restricted to areas of higher rainfall and to larger riverine estuaries.

2. *Topographic Height*. Mangroves are generally restricted to a very small topographic range from around mean sea level to high water of spring tides.

3. *Distribution by Sea*. Mangroves have water-buoyant propagules which are dispersed by sea and estuarine currents, driven by wind, waves, tides and ocean circulation. Note: sea-drift, and its possible deposition as fossil beds, may extend far beyond the range of growing plants.

4. *Distributional Change*. Where climatic conditions and sea levels change, the distributional ranges of mangroves expand or contract.

5. *Appreciable Geological Age*. Mangroves have long fossil records extending back to the Cretaceous era, at least to around 100 million years ago. This often applies to specific genera, demonstrating their genetically conservative nature and relatively slow rates of genetic change.

6. *Diversity and Systematic Groupings*. Some extant mangrove taxa extend around the world, while others have very restricted ranges. The concentration of most species in the Indo-Malesian area defines the chief centre of diversity.

7. *Disjunctions of Distribution*. There are several major distributional disjunctions for mangroves around the world. Two chief examples are: the disjunction between the Atlantic East Pacific and Indo West Pacific populations; and, the disjunction to the north and west of New Guinea.

8. *Continental Drift Theory*. The evolution of mangroves, and angiosperms generally, took place at the same time as the southern super-continent of Gondwana broke apart. Continental fragments were scattered around the world, carrying their respective complements of plants and animals. Some parts of the former southern continent are now in contact with the old northern land mass of Laurasia.

The relative importance and influence of each statement above is species-dependent. The first two identify the predominant and major physiological constraints which particularly influence within-site species distributions. They can be considered primary factors, chiefly based on temperature, moisture and tides. The third concerns dispersal of propagules. This has been greatly over-rated, and I suggest that propagules do not primarily provide for long-distance dispersal, but rather for enhanced re-establishment locally. Briefly, there are two major problems encountered in assessments of the dispersal capabilities of mangroves: one is the assumed uniformity of this ability in all taxa; and the other is the often exaggerated claim of long-distance dispersal capabilities, despite contradictions encountered in records of extant distributional disjunctions.

Consider the global disjunction which separates conspecifics within either the Indo West Pacific or Atlantic East Pacific regions. These are joined at present by the Pacific Ocean which forms a major biogeographic barrier to most mangrove species, with one exception, a species of 'New World' (Atlantic East Pacific) *Rhizophora* in the south-western Pacific islands of Fiji to New Caledonia. This distribution is discontinuous with American mangroves, and the trans-Pacific distribution is interrupted by the absence of this species from intervening islands with suitable habitats. Clearly, this demonstrates present limitations of long-distance dispersal for Rhizophora. The reason for such a situation must involve a change in current environmental conditions which restrict present-day dispersal. This is covered in the remaining statements, 4 to 8, which all relate to historical change in geological and climatic conditions, including changes in genetic make-up and speciation.

McCoy & Heck (1976) investigated similarities between mangroves and two other tropical shallow water habitats, finding they shared global patterns of occurrence, species diversity, and fossil transitions, despite their different genetic make-up and dispersal capabilities. For example, compare the non-buoyant propagules of seagrasses with the dispersal specialist taxa in corals and in mangroves. In addition, there is considerable variation of dispersal capabilities within these groups; further challenging the importance of long-distance dispersal. But, other evidence describes markedly similar floral elements from widely disparate regions around the world; noting five major exam-

ples described by Hutchinson (1973): eastern North America and eastern Asia, western Africa and eastern Brazil, Mascarene and southern India, southern Africa and western Australia, and New Zealand and southwestern South America. There must be an explanation which encompases all these observations, based on both a better understanding of changing distributional constraints, and the dispersal capabilities for each taxon.

Mangrove species are typically sea-water dispersed by buoyant propagules. They are expected therefore to be less influenced by sea barriers which restrict most other plants. But, even so, their ability to disperse across water has definable limits. These are notably species-specific, and often far less than expected; for example, *Avicennia* propagules apparently travel less than 200 nautical miles before they perish, based on personal observations and studies of buoyant longevity by Steinke (1975, 1986). This contrasts dramatically with *Rhizophora* propagules which survive several months at sea (Rabinowitz, 1978), and are capable of traveling much greater distances. It is therefore unreasonable to lump all mangrove genera in one combined evolutionary model based on extant distributions alone.

Given all the different ancestral sources of mangrove plants and their present-day wide distributions, their co-evolution appears more circumstantial since they almost certainly originated at different locations and at different times. The fact that distributions overlap so much attests to some greater influence, and I suggest this was the direct result of movements in continental fragments described in the theory of continental drift. To unravel the major processes involved, each taxon must be dealt with separately, tracing both their extant populations and their putative fossil remains. The following discussion deals with this at three levels, notably habitats, selected families, and one specific genus, the *Avicennia*.

Origin of mangroves and ancestral groups

It is convenient first to investigate the origin of mangrove taxa, making up the habitat. Were they ancestral to land plants, or were they derived from land plants? The latter seems more plausible since the majority of mangrove plants are angiosperms and these first appeared in the fossil record as sparse montane shrubs during the Early Cretaceous (Takhtajan, 1980). Furthermore, while mangrove orders and families are diverse, none include appreciably primitive characteristics. For this reason, it is assumed that mangrove species were derived from either freshwater swamp plants or halophytes, or both. These observations are implicit in any discussion of the origin and evolution of the various taxa, and the habitat they form.

The intertidal habitat is inhospitable to most plants, it has obvious spatial limitations, and similar 'mangrove' capabilities and characteristics have evolved in only a few members of several very different plant groups (Duke, 1992). In view of these comments, it is important to ask whether mangrove ancestors would have dispersed into intertidal habitats without some dynamic physical processes 'directing' genetic change. One such physical process might have been extended periods of progressive sea level rise. In these circumstances, coastal environments would have been subject to constant encroachment of marine conditions, leaving selection of marine-tolerant offspring as the only possibility for survival. However, sea level changes are notably dynamic and they generally fluctuate widely in geological time. Another process might meet the constant encroachment model described above, and it occurs irrespective of sea level change. This is the formation of new intertidal habitat when continental land masses break apart over millions of years; for example, consider the break-up of the Gondwanan supercontinent since Cretaceous times.

In Fig. 1, world maps show four geological eras, based on Lambert equal-area projections with both poles shown at the same time, used by Briggs (1987). Black shapes depict the present day world map, while shaded ones represent postulated maps for Early Cretaceous, Late Cretaceous and Eocene eras. By presenting these as overlays, the relative movement of land masses is shown through time. Note the separation of the Gondwanan supercontinent parts, South America, Africa, Antarctica, India and Australia. Their dispersal took place at different times and rates. In this depiction, Antarctica has moved very little while others have moved considerably. For example, note the rapid northward movement of India. Also note that all, except Antarctica, are now in relatively close contact with portions of the old northern supercontinent, and all are disconnected from each other.

These tectonic events and the evolution of angiosperms, including mangroves, all took place over the same period. I suggest that mangrove species, and their habitat, evolved and diversified because of the breakup of Gondwanaland. This would account for the
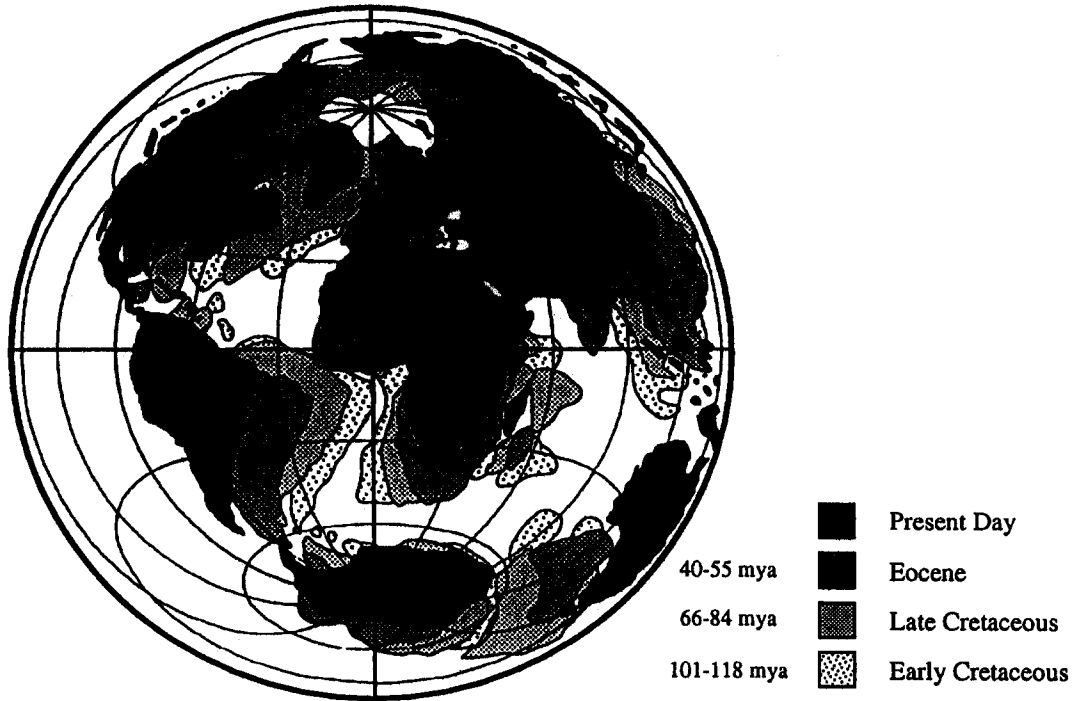
Fig. 1. World maps of four geological eras, from early Cretaceous to present day. These are overlaid to depict the movement of continents during the latter stages of the breakup of the Gondwanan supercontinent, as described in the theory of continental drift. Maps are presented in Lambert equal-area projection based on Briggs (1974). Note: 'mya' is an abbreviation for the unit, 'million years ago'.

wide dispersal and distribution of species around the earth (Fig. 1).

The next question concerns speciation, notably in the creation of genetically unique plant species. This process is implicit in an evolutionary model, and there are at least three ways a new species might form (Takhtajan, 1980). First, where species disperse from a centre-of-origin, those at the centre might multiply by subtle mutation and genetic drift. The pattern created is of younger more recently evolved taxa toward the centre and older conservative ones around the margins. In this way, the centre-of-diversity marks the centre-of-origin. A second mechanism is where the process of diversification takes place where a continuous range of one taxon is divided and each sub-group becomes genetically isolated. The sub-groups become different over time in this vicariant process as each is subject to different biological selection pressures and the influence of different mutations. A third mechanism is where new species evolve by 'budding' in a process also called the 'founder' effect. In this process,

small satellite populations become genetically isolated either by range contraction of the larger population, or by exceptional long distance dispersal events. In each instance, genetic diversification from the original population could occur quite dramatically since genes of the founder population might comprise only a limited subset of the original larger one. Furthermore, any mutant genes would have a proportionally greater influence (Takhtajan, 1980), permitting rapid change in the new population.

The circumstances of continental drift might have greatly enhanced these evolutionary processes. Land masses breaking apart could create vicariant populations with sibling species and varieties, while land masses moving closer together might form founder populations, also resulting in new taxa.

There are problems however, with inferring evolutionary processes from extant distributions. The major difficulty is in discerning those taxa which have retained ancestral characters from those that are derived or new. This may be resolved in a number

of ways using anatomical and other morphological comparisons, or from genetic comparisons, or from direct observation of fossils. Unfortunately, the latter more direct approach is not possible since mangrove fossils are generally scarce. Nevertheless, inferences from comparative studies do provide important insights, provided phenotypic and genetic differences of morphological characters have been clearly distinguished. Note that mangrove trees often include a wide range of growth forms, and degrees of growth expression, correlated directly with environmental parameters. These include salinity, temperature, and inundation frequency (Soto & Corrales, 1987; Duke, 1990a), as well as available light; for example, there is significant morphological variation within single individuals between leaves from the upper and lower canopy (Duke, 1990a). Using comparative anatomical, morphological and genetic information, it is possible to construct phylogenies for comparison with the limited fossil evidence. This would test various hypotheses and provide an evolutionary model for on-going evaluation of clearly defined taxa.

Hypotheses on the evolution of mangroves

Several hypotheses proposed explanations for extant distributions of mangroves. In one, van Steenis (1962) suggested a primary radiation in the Malesian area prior to dispersal chiefly eastward across the Pacific. While advocating long-distance dispersal, he expressed reservations about suitability of apparently drier habitats along the ancient Tethys coastline leading to the Atlantic. This route, however, was later advocated by Chapman (1976, 1977) in a second hypothesis which accepted the Malesian centre-of-origin and subsequent radiation in the Late Cretaceous. In a third hypothesis, McCoy & Heck (1976) proposed the centre-of-diversity differed from the centre-of-origin, which, they suggested, occurred along the ancient Tethys coastline. Fourthly, Specht (1981) accepted an Australasian centre-of-origin, based chiefly on pollen observations by Churchill (1973), and postulating Early Cretaceous (or even earlier) origins. Mepham (1983), in a fifth hypothesis, accepted a Late Cretaceous time of origin with radiation from the Gondwanan-east Tethyian area; a migration northward would have been achieved by tectonic movements of India and Australia, making it possible for dispersal westward through the Tethys.

These hypotheses have essential differences, but they are generally similar, reflecting available evidence at respective dates of writing. In most cases, a centre-of origin is proposed, and this was altered when fossil records apparently contradicted earlier proposals matching centre-of-diversity and centre-of-origin concepts. There are, however, two views on subsequent radiations. Most hypotheses suggest that particular radiation routes led to extant taxa en route. The hypothesis of McCoy & Heck however, proposed that radiation was initially uniform before contracting and leaving disjunct refuge populations that evolved into extant taxa. But in either case, Tomlinson (1986) pointed out that extant distributions were not explained by any hypotheses, and he suggested that they generally used greater time spans than were likely. A greater criticism is that none of these hypotheses fully considered individual taxa, taking into account their major differences in morphology and life history processes, including dispersal ability and habitat preference. It is worth noting that downstream estuarine mangroves might simply drift along a continuous coastal niche, while upstream forms might 'estuary hop'; the latter being reminiscent of terrestrial plants which 'island hop'. Presumably, those less dependent on particular estuarine conditions, preferring more coastal conditions rather than upstream lower salinities, would have the greatest chance of wider dispersal.

In addition, Tomlinson (1986) pointed out that mangrove taxa were geologically old and included some remarkably conservative and stable genera. These observations were based chiefly on the detailed review of fossil pollens provided by Muller (1981). This review is summarized in the schematic of Fig. 2, where all families with mangrove genera are depicted, showing oldest records of orders, families and genera since the earliest angiosperm pollen. Muller recorded this earliest pollen occurred around the Early Cretaceous, approximately 110 million years ago in the Aptian period. The first mangrove orders and families appeared during the Santonian in the Late Cretaceous, around 80 million years ago. The first mangrove genus recognized was *Nypa* in the Maestrichtian, around 69 million years ago. *Rhizophora* pollen appeared in the Late Eocene. *Avicennia* and *Sonneratia* in the Early Miocene. These observations however appear remarkably conservative compared with limited macro-fossil data. For example, *Nypa* fruit (Whitmore, in Heywood, 1978) in Mid Cretaceous, fruit and leaves of *Avicennia* (Berry, 1916, 1936) in Eocene, and the earliest angiosperm fossil dating from 135 million years ago

(Takhtajan, 1980). There is also the disputed (Muller, 1981) claim by Churchill (1973) of *Avicennia* pollen from the Eocene. The time lines of mangrove evolution (Fig. 2), based on the review of palynological evidence by Muller (1981), therefore appear relatively conservative.

Connections between Indo West Pacific and Atlantic East Pacific regions

Possible dispersal routes of mangrove genera occurring in both world regions may have followed three possible paths, and in either direction. Each was approximately the same distance, considering past conditions, but two further factors must be considered. One is the proximity of sites for growth and further dispersal, and the other is the suitability of climatic conditions along the way.

The first route, via the ancient Tethys Sea, was favoured in one hypothesis of mangrove evolution (McCoy & Heck, 1976). This route was tropical and it was apparently available until the Miocene. Potential problems for dispersal of mangroves were suggested by van Steenis (1962) however, who noted that dry climatic conditions would have severely restricted the range of suitable mangrove habitat.

The second route, across the east Pacific, was suggested but dismissed because of its need for 'island hopping' and long distance dispersal. Current phanerozoic maps (Fig. 1) however, show an almost continual coastline between eastern Asia and western North America during Late Cretaceous and Paleocene times. The tropics during that time were reportedly around 52 ° latitude North and South, and climate was subtropical at cooler sections of the route. This route therefore cannot be dismissed so easily although there is no fossil evidence to support it. There is evidence however, suggesting the limited western migration across the southern Pacific (Duke, 1992) of one mangrove species, *Rhizophora samoensis*, which is indistinguishable morphologically from *R. mangle* (Tomlinson, 1986). The presence of unoccupied suitable habitats within their range suggests a Late Cretaceous connection between western Pacific and Atlantic East Pacific, possibly crossing to South America via an old island archipelago present during the early formation of the Pacific Plate (Schlanger & Premoli-Silva, 1981; Schlanger *et al.*, 1981). The migration appears to have been one-way, and distances between the putative ancient islands was

large enough to restrict all mangroves except the dispersal specialist, *Rhizophora*.
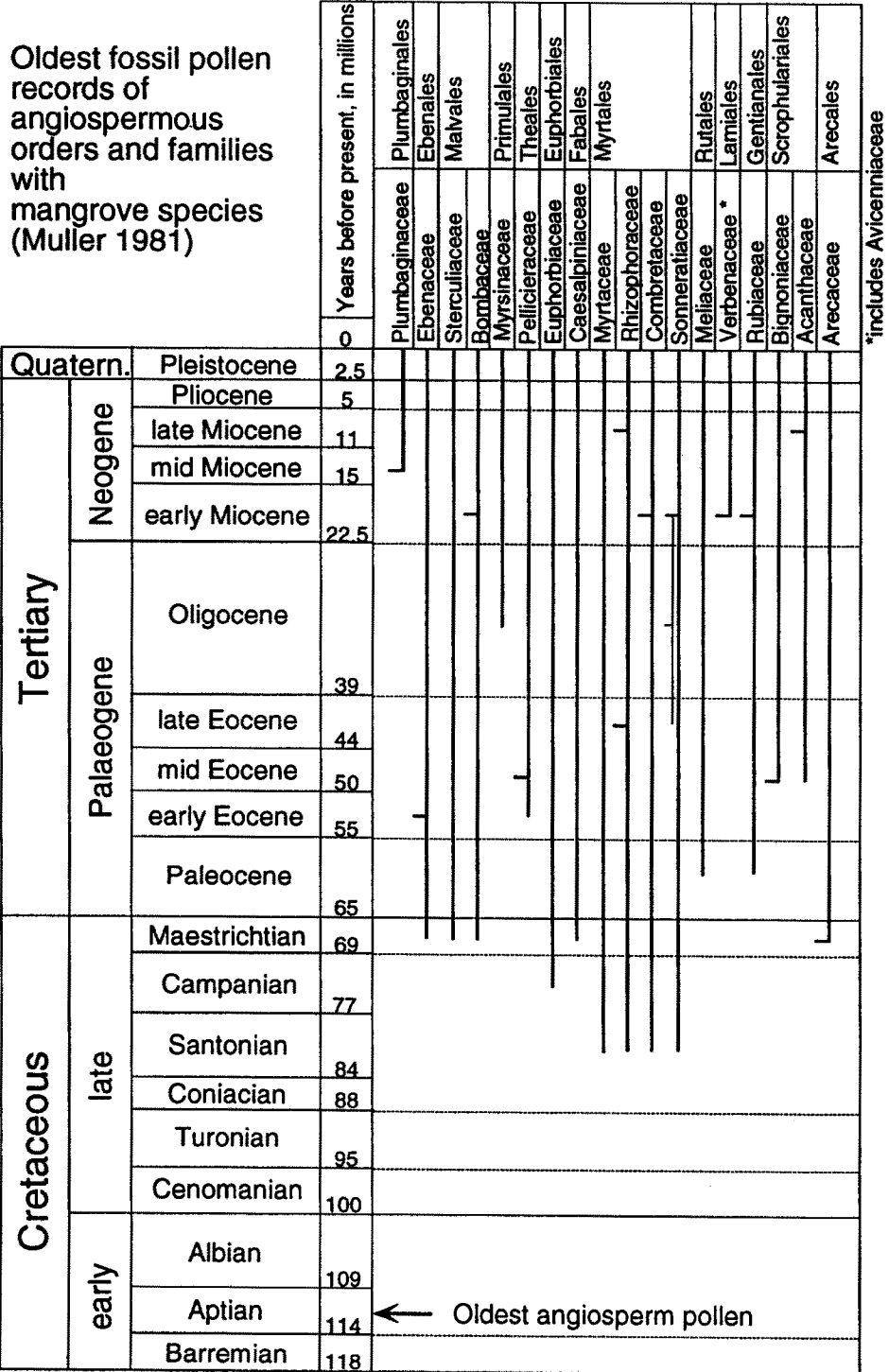
A third path around Antarctica or southern Africa has never been discussed, although evidence of *Avicennia* in Gondwana was accepted by Specht (1981) and Mepham (1983). Clearly, if *Avicennia marina* occurred there, it could have migrated around the subtropical-warm temperate shores of Antarctica, connecting between eastern South America and Australia at some time prior to the Eocene. There are no fossil records of *Avicennia* to support this idea, other than those disputed (Muller, 1981) ones from Western Australia (Churchill, 1973). Migration between southern Africa and Australia was also possible apparently via an island archipelago which included the Indian subcontinent during the Late Cretaceous (Kemp & Harris, 1974; Norton & Molnar, 1977). In any case, a southern connection appears to be a plausible alternative, comparable with other routes.

Evolution of *Avicennia*

Phylogenies from morphological and genetic evidence

The large polymorphic genus, *Avicennia*, is well-known ecologically, systematically and genetically (Duke, 1988, 1990a, 1990b, 1991, 1992) in comparison with other mangrove taxa. Accordingly, this genus has the best information for the development of a specific evolutionary model.

All *Avicennia* taxa in the world (Duke, 1991, 1992; Tomlinson, 1986) were evaluated in multivariate analyses using diagnostic morphological characters. The results show four major groupings of species (Fig. 3), including (1) *A. marina* and *A. alba*; (2) *A. officinalis* and *A. integra*; (3) *A. rumphiana*; and, (4) *A. germinans*, *A. schaueriana* and *A. bicolor*. The last group comprises all Atlantic East Pacific species. In this analysis, three groups were arranged around *A. rumphiana*, which could be interpreted as suggesting a central or intermediate phylogenetic role of this species. However, a detailed appraisal of anatomical features of Indo West Pacific species (Tan & Keng, 1965), suggested that *A. officinalis* was more primitive. The groups were also divided by flower-size, making two important associations within *Avicennia*, notably groups 1 and 3 with small flowers, and groups 2 and 4 with larger flowers.

Oldest fossil pollen records of angiospermous orders and families with mangrove species (Muller 1981)

Years before present, in millions

Plumbaginales — Plumbaginaceae
Ebenales — Ebenaceae
Malvales — Sterculiaceae
— Bombaceae
Primulales — Myrsinaceae
Theales — Pellicieraceae
Euphorbiales — Euphorbiaceae
Fabales — Caesalpiniaceae
Myrtales — Myrtaceae
Rhizophoraceae
Combretaceae
Sonneratiaceae
Rutales — Meliaceae
Lamiales — Verbenaceae *
Gentianales — Rubiaceae
Scrophulariales — Bignoniaceae
— Acanthaceae
Arecales — Arecaceae

*includes Avicenniaceae

Quatern.	Pleistocene	2.5
Tertiary — Neogene	Pliocene	5
	late Miocene	11
	mid Miocene	15
	early Miocene	22.5
Tertiary — Palaeogene	Oligocene	39
	late Eocene	44
	mid Eocene	50
	early Eocene	55
	Paleocene	65
Cretaceous — late	Maestrichtian	69
	Campanian	77
	Santonian	84
	Coniacian	88
	Turonian	95
	Cenomanian	100
Cretaceous — early	Albian	109
	Aptian	114
	Barremian	118

← Oldest angiosperm pollen

Fig. 2. Timelines of fossil pollen observations for all orders and families of angiosperm mangrove plants reviewed by Muller (1981). The oldest record of angiosperm pollen, accepted by Muller, is included for reference. Note: solid lines depict oldest records of mangrove families; bar flags depict oldest records of mangrove genera; and, dashed lines depict oldest records of mangrove orders.
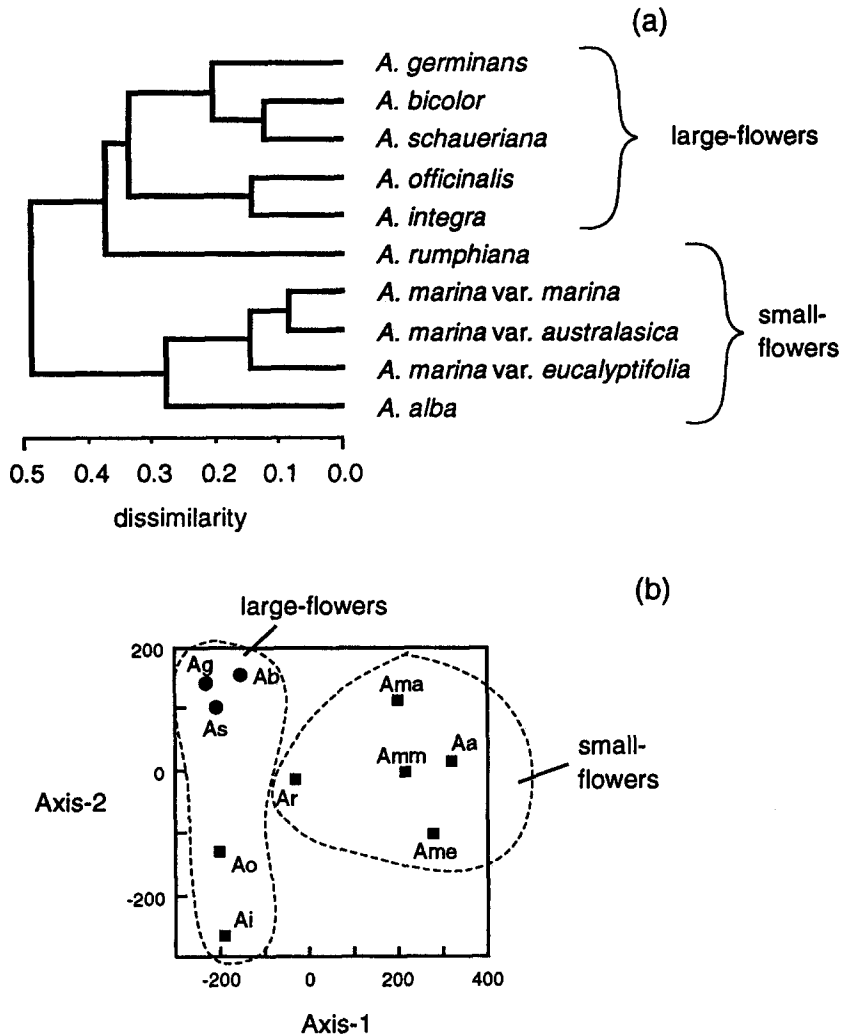
Fig. 3. (a) Dendrogram showing fusion sequence using morphological characters for major *Avicennia* taxa in the world. Data consisted of ordered multistate attributes of major morphological characters (Duke, 1988). The cluster analysis used the UPGMA method on dissimilarity measures derived from Gower's algorithm. Note, taxa are also grouped as small and large-flower forms. (b) Plot of principal coordinate analysis of morphological characters for major *Avicennia* taxa in the world, as listed in Fig. 3a. The analysis used dissimilarity measures derived from Gower's algorithm. Note, circles depict Atlantic East Pacific taxa, squares depict Indo West Pacific taxa, and all are also grouped as small and large-flower forms.

Detailed studies of the widespread small-flower species, *A. marina*, revealed three varieties based on morphology (Duke, 1990a), electrophoretic patterns and carbohydrate composition (Duke, 1988). Measures of genetic identity, determined by electrophoresis suggest an order of phylogenetic derivation of *A. marina* varieties from var. *marina*, to var. *australasica*, to var. *eucalyptifolia*. This was deduced from the first and second criteria for recent progenitor-derivatives which have less variation than progenitors (Gottlieb, 1973; Crawford, 1983). Morphological differences also suggested an intermediary role of *A. marina* var. *marina* to other varieties (Duke, 1990a).

Limitations of dispersal and growth for Avicennia

The chief mode of reproduction in *Avicennia* is the sexual production of water-borne propagules. These apparently withhold root development for around four days, depending on salinity and temperature, after which they sink (Steinke, 1975, 1986). This would limit dispersal to within 100–200 nautical miles in average

sea conditions, influenced by currents and wind-blown drift. Dispersal is also limited by the inability of adults to reproduce in the colder climates of higher latitudes (Duke, 1990b). Growth is limited further by salinity conditions (Burchett et al., 1984; Clough 1984), and each of these characters is expected to differ for each species. For example, A. marina has a wide estuarine range upriver from the mouth, while A. integra has a much smaller range midway in mostly hyposaline conditions (Duke, 1992). This has the effect of limiting the latter species to estuaries with continuous, although variable, freshwater input. All these factors are subject to present-day geological and climatic conditions; and the distributional disjunctions observed now between estuaries, might be the result of differing conditions in the past.

Genetic variation is also an important consideration, although it is believed to be relatively stable. Evidence of genetic stability is apparently shown in two examples where diagnostic characteristics were maintained in populations believed to have been isolated for approximately 40 million years, notably: A. germinans in North America and west Africa (Tomlinson, 1986); and, A. marina var. australasica in south-eastern Australia and New Zealand (Duke, 1991).

Disjunctions and discontinuities of Avicennia distribution

Evidence of disjunctions and discontinuities in distributions are found for all levels of species occurrence; notably global, regional, and within regions. The division of Avicennia species within two different hemispheres of the world represents a global disjunction where no species are shared (Duke, 1992). They are isolated by natural barriers of both land and sea, preventing exchange of genetic material. Reasons for this occurrence might be explained by historical considerations providing the necessary genetic and physical links in the past. In this way, the two global regions are also thought to be centres of secondary radiation with lesser differences between taxa and other distributional disjunctions; based on smaller changes to both genes and distributional barriers. All this combines to create additional levels of complexity in the mosaic of present-day distributional anomalies.

Examples of disjunctions and discontinuities within regions are shown by the occurrence of Avicennia marina varieties in Australasia, A. officinalis in New Guinea, and A. integra in Australia (Duke, 1991, 1992). In general, historical changes in the Indo West

Pacific are more complex than those in the Atlantic East Pacific (Briggs, 1987). This is reflected chiefly in respective numbers of species and is used as evidence for the centre-of-origin in hypotheses of mangrove evolution, specifically suggesting either locations in Indo-Malesia (van Steenis, 1962; Chapman, 1976, 1977), or Australasia (Specht, 1981; Mepham, 1983). The duality of these putative centres is reflected in equal numbers of species, and a high proportion (ca. 20%) of species with localized affinities and endemism (Duke, 1992). For Avicennia, this situation was partially shown with A. alba and A. officinalis predominantly found in Indo-Malesia, A. integra and A. marina var. australasica and A. marina var. eucalyptifolia in Australasia.

Avicennia marina var. australasica occurs in northern New Zealand and south-eastern Australia (Duke, 1991). These countries have not been sufficiently close for crossmigrations for at least 40 million years, and maybe even 65 million years, back to the Late Cretaceous. This all sounds rather unlikely considering the reported Early Cretaceous beginnings of the evolution of angiosperms, but some scenario like this does match the southward disposition of this taxon today. It also concurs with fossil Avicennia-like pollen recorded by Churchill (1973) from Late Eocene deposits in southwestern Australia. The strength of this latter evidence, as already noted, was weakened by doubts expressed by Muller (1981).

The richer bio-diversity of the Indo West Pacific region is also generally explained by the tectonic dispersal of continental fragments (Briggs, 1987). For example, the major zone of faunal and floral overlap observed between Malesia and Australasia presumably resulted from the relatively recent contact between these areas in the late Miocene. This zone included many closely related (sibling) species of mangroves with wider distributions in their respective areas (Duke, 1992).

This important discontinuity and zone of phylogenetic duality, however, is not particularly clear for species of Avicennia. The most common species, A. marina, occurs widely through both regions, and other species have overlapping and different Malesian or Australasian affinities. This is particularly evident around New Guinea where many mangrove species are distributed along either northern or southern coastlines according to their respective floral affinities (Duke, 1992). Therefore, while a species like A. alba (Indo Malesia to northern New Guinea only) might be considered part of the Indo Malesian flora, A. officinalis

(Indo Malesia to southern New Guinea only) is difficult to categorize. Similarly, the occurrence of *A. rumphiana* along both coastlines cannot be classified either. The reasons may be related to different stages of phylogenetic development and dispersal, possibly shown by ever greater respective eastern limits of occurrence, where greater ranges were observed in putatively younger ancestral forms, *A. officinalis*, *A. rumphiana*, and *A. alba*, respectively.

There are two major species groupings for Indo West Pacific species, represented by *A. marina* with small flowers, and *A. officinalis* with large flowers (Fig. 3). The latter group includes Atlantic East Pacific species, and I suggest that a common progenitor of this large-flower group migrated between regions. However, small-flower taxa are more widely distributed in the Indo West Pacific today, and they exclusively occupy all putative dispersal routes to extant, large-flower Atlantic East Pacific habitats. If this phylogenetic inference is correct, the range of large-flower forms must have decreased while that of the small-flower group increased. In any case, an evolutionary model for *Avicennia* must account for this distributional discontinuity.

The direction of dispersal between regions is another problem, depending on where *Avicennia* evolved first. There is little evidence to suggest where this might be, although the genus appears to have developed early in the evolution of angiosperms (Barlow, 1981), suggesting a South American, or western Gondwanan origin. In support of this idea, it is suggested that the breakup of the continents would have created vast inter-continental estuaries, slowly changing from riverine swamps and flood plains to more marine conditions. The largest example was the division of Africa and South America (Fig. 1), and considering the combined river catchments involved, it is difficult to imagine a better environment and circumstances for the evolution of mangrove characteristics. This would have taken place over millions of years, providing the opportunity for a wide range of riverine and terrestrial taxa to develop the specialized characters we see in mangroves today.

The earliest fossil evidence of Avicennia

The early evolution of flowering plants is currently unresolved, although there are some implications of both the area and the time of origin (Takhtajan, 1980; Barlow, 1981). The story is complicated however by possible polyphyletic beginnings with at least three major groups arising at different times and places (Krassilov, 1977), although this concept was dismissed by Cronquist (1981). In any case, taxa with tricolpate pollen (note: *Avicennia* pollen is tricolpate) first appeared in western Gondwana (Brenner, 1976) in the Early Cretaceous, and by the mid-Cretaceous they were dispersed widely (Barlow, 1981). Their radiation included Australia where tricolpate pollen first appeared in the latter part of the Early Cretaceous, around 115 million years ago (Dettman, 1981). This arrival in Australia was characterized by plants already showing wide ecological adaptation (Raven & Axelrod, 1974). There were two routes available to plants at that time. Firstly, a tropical one, from Africa via India and an island archipelago (Kemp & Harris, 1974), which reportedly remained open until the Late Cretaceous, around 65–70 million years ago. Second, there was a polar route from South America via Antarctica which remained open until the Oligocene, around 35 million years ago (Raven, 1979). The first route was limited by access between South America and Africa which ended much earlier, and the latter route was restricted by its mostly, at best, warm subtropical climate.

The scant older fossil record for *Avicennia*, summarized in Table 1, indicates a wide distribution extending from the Atlantic East Pacific to Indo West Pacific regions by the Eocene, around 40 million years ago. Observations of pollen by Muller (1964,, 1981) suggest a relatively late arrival in Malesia during the middle Miocene, around 20 million years ago. However, these records are likely to be remarkably conservative; for *Avicennia*, this might be a function of the active collection of pollen by insects, thus reducing its concentration in sediments and future fossil beds. In any case, fossil records for *Avicennia* are very limited, and some are considered doubtful. The remarkable report by Churchill (1973) of *Avicennia* pollen in south-western Australian Eocene deposits, was questioned by Muller (1981); such doubts must be resolved by both a re-assessment of the relevant samples, and the collection of new pollen material and macro fossils from more sites around the world.

A model for the evolution of Avicennia taxa

The model draws on the points already raised, notably the phylogenetic affinities of the different taxa, based on morphological and genetic evidence, the fossil record, and the most recent records of extant distribution. It is also described in the context of past geolog-

Table 1. Oldest fossil records of *Avicennia* and '-like' forms, noting: age (mya = million years ago), location and source reference.

Taxa	Component	Greatest age	mya	Site	Authority
A. nitidaformis	leaves	Eocene	38–55	Mississippi	Berry (1916)
A. eocenica	fruit	Eocene	38–55	Tennessee	Berry (1916)
Avicennia-like*	pollen	late Eocene	40	SW Australia	Churchill (1973), * doubted by Muller (1981)
Avicennia	pollen	early Miocene	20	Marshall Islands, west Pacific	Leopold (1969) in Muller (1981)
Avicennia	pollen	mid Miocene	14	Borneo	Muller (1964)
Avicennia	pollen	late Miocene	10	N South America	van Steenis (1969)
Avicennia	pollen	late Miocene	10	Nigeria	van Steenis (1969)
Avicennia	pollen	late Miocene	10	NW Borneo	Muller (1981)
A. miocenica	leaves	Miocene	6–22	Columbia	Berry (1936)
A. lanceolata	leaves	Tertiary	3–65	Columbia	Moldenke (1960)
Avicennia	pollen	Pliocene	4	Guyana	Wymstra (1971) in Muller (1981)
A. germinans	leaves	Pleistocene	<2.5	Trinidad	Moldenke (1960)

ical and climatic conditions as presently known (e.g. Smith *et al.*, 1981; Briggs, 1974, 1987). This evaluation is also taken in appreciation of the evolution of other plant and animal groups, as described by Briggs (1987). Clearly, there is great benefit in comparing other biota whose fossil records are more complete and informative. This is especially so for biota having similar dispersal limitations, and similarly demonstrating the biological effectiveness of putative dispersal routes or barriers.

A western Gondwanan origin of Avicennia

I suggest that the earliest *Avicennia* ancestors appeared during the Early Cretaceous, along the north-western coast of Gondwanaland. This is based chiefly on two pieces of evidence. First, this was the site of the earliest angiosperm fossils. Second, this was the future site of the slow-expanding super-estuary between South America and Africa. This condition, occurring over a prolonged period, I believe to be essential for the selection and development of the specialized traits which characterize mangrove plants today. Based on the occurrence of large-flower forms in both regions today, it is assumed this form also had large-flowers. It might also have had glabrous inner surfaces of the petal lobes, a fully hairy radical on the propagule, and ovate to lanceolate leaves with rounded apices; possibly linking *A. schaueriana* in the Atlantic East Pacific

and *A. officinalis* in the Indo West Pacific. It is of interest that these forms cannot be easily distinguished on present botanical descriptions. I propose that these represent western and eastern derivatives of an ancestral pan-Tethyian equatorial distribution during the mid Cretaceous (Fig. 4). It was apparently restricted to the northern shores of the southern continent. The preferred habitat was possibly in larger estuaries and in mid- to upstream locations like their present day relatives. *Avicennia bicolor* and *A. integra* are in this group, and their occurrences on the American Pacific coast and the north Australian coast respectively, perhaps represent outlier populations at the extremes of this ancient range. The events which would isolate these populations and allow their eventual speciation probably took place at different times. The first step occurred when the continents of Africa and South America separated during the Late Cretaceous, around 80–90 million years ago. Around this time the formation of an earlier isthmus between North and South America might also have isolated the future *A. bicolor* populations. The last of this group, *A. integra*, might have been isolated from *A. officinalis* in relatively recent times. This will be discussed later. Meanwhile, as the Gondwanan break-up continued into the Late Cretaceous, this further isolated the ancestral *Avicennia* populations. Those in South America stayed much as they are today, but those in north-western Africa, north-eastern Africa, India and Australia were subjected to major changes, leading

them to change and speciate further. The populations in Africa were presumably divided in the north (and possibly the south) by very dry climates.

Populations in north-western Africa eventually came within dispersal range of the spreading fragments of the northern super-continent, Laurasia, during the Late Cretaceous (Fig. 4, also Fig. 1) and the Paleocene, around 60–80 million years ago. It is likely these were restricted to the western hemisphere of the northern continent by a channel connecting with the Arctic Sea (Fig. 4). In view of the warmer climatic conditions and the connection between Europe and North America at the time, it is proposed that Avicennias spread west to North America via southern Europe. By this time, the character of the ancestral species had changed to that of *A. germinans*. This might have occurred during the original crossing of the narrowing Tethys Sea when small founder populations flourished on the northern continent once they crossed from Africa. Or it could have occurred earlier when South American and African populations first became separated. In any case, by the late Eocene, around 50 million years ago, the wide- ranging *A. germinans* was split by the formation of the North Atlantic Ocean and the slow contraction of tropical climates, which had reached 50-60 ° N. This forced species toward the more equatorial distributions of today. During this time the older American isthmus had gone, but it was reformed in the late Pliocene, around 2–3 million years ago. This resulted in the isolation of *A. germinans* on Atlantic and Pacific coasts of North and Central America.

In the east, the situation became more complex as the breakup of the ancient supercontinents continued, and warmer climates contracted. I suggest a model that took place in two stages, based on the development and dispersal of large and small-flower forms. The large-flower, *A. officinalis*, ancestor probably began its crossing to the northern continent and Malesia during the Late Cretaceous, around 65–100 million years ago, as the Indian sub-continent brushed past the north-eastern part of Africa (Norton & Molnar, 1977). Apparently, this enabled such a taxon with relatively poor dispersal abilities and restricted habitat requirements to invade the northern super-continent, notably in the area of Indo Malesia. When this took place it was probably isolated from the *A. germinans* progenitor to the west, initially by a physically divided east and west sides of Africa, and later by dry climatic conditions (van Steenis, 1962). Presumably, the species became extinct in east Africa as conditions dried. Once reaching south-eastern Laurasia in the Eocene, around 38-54 million

years ago, it spread relatively quickly east along the wet tropical southern shores of the old Sund Peninsula. Later, with the approach of the Australian continent in the Miocene, around 10-27 million years ago, it probably spread there via New Guinea. The retraction of this range later on, presumably left the populations in northern Australia which became *A. integra*.

The appearance of small-flower taxa

Meanwhile, I suggest that the evolution of small-flower taxa took place around the south-eastern shores of the ancient Tethys Sea, during the mid Cretaceous. At this time, the eastward spread of large-flower forms had reached north-eastern Africa. Evolution of the first small-flower form, *A. marina*, possibly took place in one of two very different ways however, depending on the progenitor. In each case, it was a large flower-form, but it could have been either *A. officinalis* or *A. schaueriana*, depending on whether it migrated around the northern or southern shores of Africa, respectively. The northern route provides a simple model with only one dispersal route, but the southern route would help explain apparent comparable cold tolerances in *A. schaueriana* and *A. marina*, shown by their extreme southern distributions in respective hemispheres (Duke, 1991, 1992). In the first case, founder populations possibly formed on offshore islands, via Madacascar and India. In the second case, founder populations might have been established around the southern coast of Africa.

In either case, it seems likely that the taxon reached the Indian subcontinent prior to contact with north-east Africa. After its contact with Africa, India was also colonized by the large-flower form, *A. officinalis*. This being the case, *A. marina* would then have followed two migration routes, one north to Malesia, and the other south-east to Australia and New Zealand. This southern migration probably took place across an old archipelago which crossed the developing Indian Ocean (Kemp & Harris, 1974) linking Australia and Africa until the Late Cretaceous. After *A. marina* arrived in Australia, the continent apparently became fragmented as sea levels rose in the mid to Late Cretaceous, causing further isolation of these populations; presumably leading to the formation of the two other varieties in northern Australia, and south-eastern Australia and New Zealand. The New Zealand population has been isolated ever since. Meanwhile those in Australia were re-united preventing further genetic separation, while retaining their sub-specific identities. At
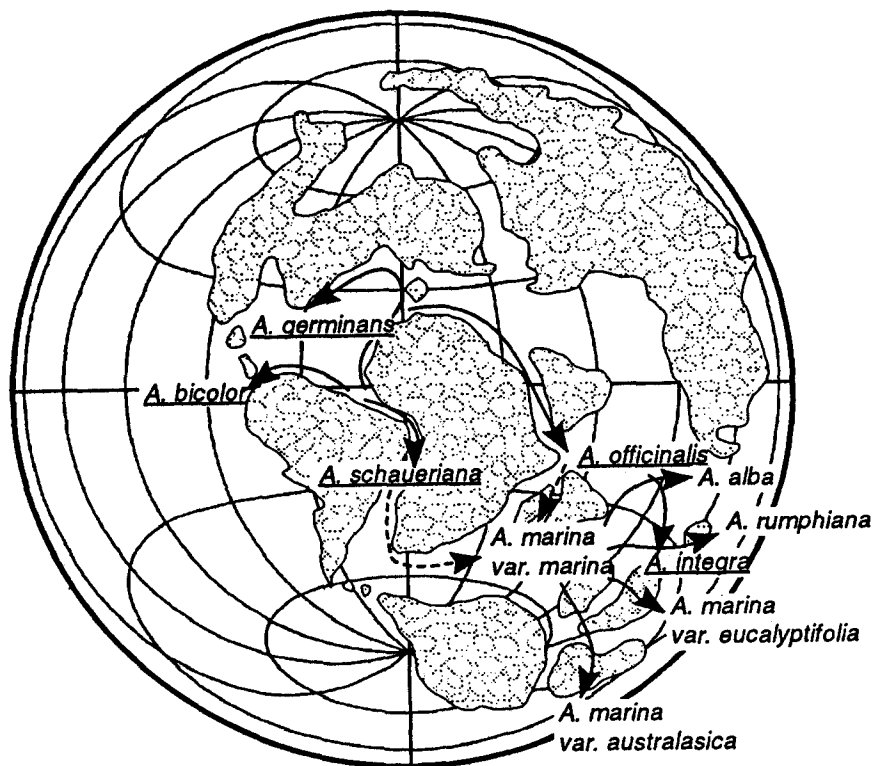
Avicennia

Fig. 4. A model for the evolution of all existing *Avicennia* taxa, based on an early Cretaceous map of the world. Also refer to Fig. 1. Arrows depict spatial and evolutionary links between progenitors and derived forms. Although an early Cretaceous map provides the basis for this representation, many developments occurred subsequently, notably those in the Indo West Pacific. Underlined taxa names depict large-flower species. Note: 'mya' is an abbreviation for the unit, 'million years ago'.

this time, *A. rumphiana* may also have evolved, possibly on a chain of islands to the north of Australia. Meanwhile, the Indian subcontinent carried the original A. marina variety together with *A. officinalis* to Malesia and southern Asia. During this crossing, the most recent species of *Avicennia*, *A. alba*, possibly developed from founder populations of *A. marina* as the Asian continent drew nearer.

Conclusion

In developing this model, the chief principle was to have new species and varieties evolve only whilst ancestral species invaded new sites, or, after a wider

distribution was divided. It is notable that taxa are remarkably conservative, changing very little over millions of years, where populations remained large and fixed in one location. In any case, where small populations became genetically isolated, either by founder or vicariant events, this may have allowed greater expression of their mutant genes (Takhtajan, 1980). These were normally present in larger populations, but their low frequency precluded significant expression. Of course, this process was driven by both the changing climate and by the breakup of the Gondwanan supercontinent. This may also be the reason why the mangrove flora of today is so rich in species and diversity of morphological characters. In the first instance, the expanding super-estuary provided the geographic cir-

cumstances for the evolution of major mangrove characteristics. Second, the dispersal of continental fragments made sure those new forms and their derivatives were distributed around the world.

Mangrove forests are as complex and variable in makeup and evolutionary processes as any forest habitat. Plant species comprising these ecosystems have come from a variety of ancestral groups, and their co-occurrence in the present time should not be taken as a measure of common evolution or origin. Clearly, changes taking place in this habitat were greatly influenced by the massive displacement of continents during the last 100 million years. Mangrove evolution, diversification and dispersal apparently were accelerated by continental drift. Although perhaps not all taxa were involved in these changes, there appears to be no other explanation for the extant distributional ranges and disjunctions of most, especially polyspecific, genera. This being the case, we may find that some groups will extend back further than our present fossil records indicate, and in different places than we may at first expect.

Acknowledgements

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