

Global Patterns of Diversity in Mangrove Floras

Robert E. Ricklefs and Roger Earl Latham

During the past three decades, ecologists have developed a body of theory that attempts to explain global patterns of species diversity in terms of interactions that limit the local coexistence of species (Pianka 1966; MacArthur 1972; Connell 1978; Tilman and Pacala, chap. 2). The outcome of these interactions is thought to depend on local conditions of the environment; as a result, patterns of diversity would parallel patterns of climate and other features of the physical world. Theories of diversity based upon local interactions predict that similar habitats in different parts of the world, in which biological communities have developed independently, should support similar numbers of species (Recher 1969; Cody 1975; Orians and Paine 1983; Ricklefs 1987). This is the principle of convergence. Although species richness generally does reflect physical factors in the environment (Rosenzweig and Abramsky, chap. 5; Wright, Currie, and Maurer, chap. 6), many comparisons of similar environments in different parts of the world have revealed strikingly different numbers of species (Orians and Paine 1983; Ricklefs 1987; Latham and Ricklefs, chap. 26; Morton, chap. 14; Schluter and Ricklefs, chap. 21; Westoby, chap. 15). Such "diversity anomalies" challenge our understanding of the origin and maintenance of biodiversity.

Diversity anomalies may result from local factors other than competition, including the effects of predation and disturbance (Orians and Paine 1983). However, these causes, to the extent that their influence is governed by local physical factors, should produce convergent diversity in similar habitats. Ecologists have also rightly pointed out that what appear to be similar habitats may, in fact, differ in fundamental attributes that affect species richness (Morton and James 1988). At the same time, however, ecologists must entertain the idea that differences in local species richness might arise from the particular history and biogeographical circumstances of each region, quite apart from the contemporary local environment.

Of the many examples of diversity anomalies, mangrove floras are one of the most enigmatic. Mangroves of the Indo-West Pacific (IWP) region have several times the species richness of comparable associations in the Atlantic-Caribbean-East Pacific (ACEP) region (Chapman 1976; Hadač 1976; Barth 1982; Tomlinson 1986; Duke 1993; see fig. 20.1). This anomaly parallels similar differences in the diversity of other associations in shallow

tropical seas, notably seagrasses, reef-building corals, and their associated faunas (McCoy and Heck 1976; Rosen 1988; Woodroffe and Grindrod 1991). In both the ACEP and IWP regions, one may find mangrove¹ associations in the deltas of large rivers or along protected coasts, in areas with both wide and narrow tidal ranges, and bordering upon both arid and wet terrestrial environments. However, mangrove habitats in the IWP region consistently support more species than similar habitats in the ACEP region. On a global scale, the IWP has four times the number of genera (17 versus 4) and about six times the number of species (40 versus 7) as the ACEP (Saenger, Hegerl, and Davie 1983; Tomlinson 1986; table 20.1). Furthermore, the present ACEP flora is, with the exception of a single endemic genus, a subset of the IWP flora at the genus level. In the absence of obvious differences in the physical habitat, the difference in mangrove diversity between the IWP and ACEP regions may require an explanation based on regional processes or unique history. In this chapter, we address the mangrove diversity anomaly by considering the taxonomic positions of mangrove plants, their geographical distribution and fossil record, and the paleogeography and paleoclimatology of the mangrove habitat.

Taxonomic affinity provides clues to the historical development of present-day mangrove floras, suggesting the number of independent origins of modern mangrove taxa and, to the extent that their terrestrial sister taxa are geographically restricted, the region of their origin. The fossil record of mangroves is incomplete, but can help to distinguish regional differences in extinction and origination that may be causes of global patterns in species richness (Latham and Ricklefs, chap. 26; Van Valkenburgh and Janis, chap. 28; Valentine and Jablonski, chap. 29). Paleoclimatological and paleogeographical information may contribute to our understanding of the geography of origination and dispersal of mangrove taxa.

The considerations outlined below suggest that

1. Tomlinson (1986) suggests that "mangal" be used as a term for the community, and reserves "mangrove" for the plants themselves (Macnae 1968). Accordingly, the environment and habitat can be referred to by either term. Mephram and Mephram (1985) and Duke (1993) do not favor "mangal" because it is not commonly used in the English-language literature. In this chapter, we use "mangrove" as both noun and adjective in reference to both habitat and individual plants or taxa.

Table 20.1. Taxonomy and Biogeography of Exclusive Mangrove Trees and Shrubs

Subclass ^a	Order	Family	Genus	Total spp. ^b	Distribution ^c							F ^e	Life form				
					2	1	6	5	4	3	A ^d			V ^e	I ^f		
Arecidae	Arecales	Arecaceae	<i>Nypa</i>	1*	1	1						-	+	Sf	*	Palm	
Hamamelidae	Plumbaginales	Plumbaginaceae	<i>Aegialitis</i>	2*	1	1						-	+	G		Shrub	
Dilleniidae	Malvales	Bombacaceae	<i>Camptostemon</i>	2+	1	2						+	-	G	+	Tree	
		Sterculiaceae	<i>Heritiera</i>	2 ⁺	1	2	1						±	-	S		Tree
Rosidae	Primulales	Myrsinaceae	<i>Aegiceras</i>	1 ⁺	1	1						-	+	G	+	Shrub	
	Theales	Theaceae ^g	<i>Pelliciera</i> ^h	1+					1			-	+	G	*	Tree	
	Euphorbiales	Euphorbiaceae	<i>Excoecaria</i>	1 ⁺	1	1						-	-	S		Tree	
	Myrtales	Combretaceae	<i>Laguncularia</i>	1*				1	1	1			+	-	Tr	*	Sh/tr
			<i>Lumnitzera</i>	2 ⁺	2	2	1							+	-	G	*
			Lythraceae	<i>Pemphis</i>	1+	1	1	1					-	-	S		Sh/tr
			Myrtaceae	<i>Osbornia</i>	1+	1	1						-	-	G		Shrub
			Rhizophoraceae ⁱⁱ	<i>Bruguiera</i>	6*	6	5	1					++	++	Tr	*	Tree
				<i>Ceriops</i>	2 ⁱⁱ	2	2						++	++	Tr	*	Tree
				<i>Kandelia</i>	1*		1						-	++	Tr		Tree
		<i>Rhizophora</i>		8 ⁱⁱⁱ	6	3	1	3	3	2			++	++	Tr	*	Tree
		<i>Sonneratia</i>		5*	3	5	1						++	-	G	+	Tree
Asteridae	Sapindales	Meliaceae	<i>Xylocarpus</i>	5 ⁺	3	5	2					++	-	S		Tree	
	Lamiales	Avicenniaceae	<i>Avicennia</i>	11 ^{iv}	5	5	1	1	2	3		++	+	F	*	Tree	
	Rubiales	Rubiaceae	<i>Scyphiphora</i>	1+	1	1						-	-	G		Shrub	

Note: Table includes only exclusive mangrove species recognized by Tomlinson (1986). Saenger, Hegerl, and Davie (1983) additionally recognize *Conocarpus* (Combretaceae, 1 species), *Cynometra* (Caesalpinaceae, 2 species), *Acanthus* (Acanthaceae, 3 species), and *Phoenix* (Arecaceae, 1 species); Saenger et al. do not include *Pemphis* (Lythraceae, 1 species). Duke (1993) includes the fern *Acrostichum* (Pteridaceae), *Diospyros* (Ebenaceae, 1 sp.), *Cynometra*, *Mora* (Caesalpinaceae, 1 sp.), *Conocarpus*, *Pemphis*, *Aglia* (Meliaceae, 1 sp.), *Acanthus*, and *Dolichandrone* (Bignoniaceae, 1 sp.).

^aHigher taxonomy largely after Cronquist (1981).

^bNumber of species according to Saenger, Hegerl, and Davie (1983). *, major elements of the mangrove flora; +, minor elements (Tomlinson 1986, table 2.1).

^cRegions described by Saenger, Hegerl, and Davie (1983): 2, Australia and New Guinea; 1, Asia and Indonesia; 6, East Africa and Madagascar (western Indian Ocean); 5, West Africa (eastern Atlantic Ocean); 4, western Atlantic Ocean and Caribbean Sea; 3, western Central and South America (eastern Pacific Ocean).

^dAerial roots or pneumatophores well developed (++), present (+), absent (-) (Hutchings and Saenger 1987).

^eViviparity well developed (++), present (+), absent (-).

^fTaxonomic isolation at the level of species (S), genus (G), subfamily (Sf), tribe (Tr), or family (F).

^gindicates Paleogene fossil record; + indicates earliest fossils in Miocene.

^hDuke (1993) recognizes 3 species.

ⁱTomlinson (1986) and Duke (1993) recognize 2 species.

^jAiry Shaw (Willis, 1966) and Tomlinson (1986) place *Pelliciera* in a separate family, the Pellicieraceae.

^kGenus name is *Pelliciera* according to Airy Shaw (Willis, 1966).

^lDuke (1993) recognizes 2 species.

^mThe Rhizophoraceae are sometimes placed in a separate order, Rhizophorales (Tomlinson 1986). On the basis of a very thorough examination, Dahlgren (1988) considers the Rhizophoraceae as belonging to the order Celastrales and separates several terrestrial genera, including *Combretocarpus*, into the Anisophyllaceae (Rosales).

ⁿDuke (1993) recognizes 6 species and 3 hybrids.

^oTomlinson (1986) recognizes only 1 species; Duke (1993) recognizes 2 species.

^pTomlinson (1986) and Duke (1993) recognize only 8 species.

throughout most of the Tertiary, conditions for the invasion of mangrove habitat by terrestrial taxa and their specialization as mangroves occurred primarily in Southeast Asia/Malaysia and, to lesser extent, East Africa/Madagascar. These conditions probably included the presence of a diverse terrestrial flora adjacent to mangrove habitat in areas of high, relatively aseasonal rainfall. Strong evidence supports the origin of only a single mangrove taxon in the Western Hemisphere, sometime prior to the early Eocene. The restriction of most mangrove taxa to the Indo-West Pacific region may have resulted from poor dispersal and from closure of the Tethys connection to the Atlantic Ocean in the middle of the Tertiary.

THE MANGROVE SYSTEM

Mangroves are defined as halophytic, generally woody plants that inhabit the upper intertidal zones of saltwater areas, primarily within tropical and subtropical regions (Tomlinson 1986; Hutchings and Saenger 1987; see Mepham and Mepham 1985 for a more detailed, critical evaluation). Mangrove vegetation usually occurs on soft sediments protected from extreme wave action, although

many taxa may establish themselves on protected rocky shores (Thom 1982). Within the mangrove habitat, taxa are specialized and segregated (zoned) with respect to tidal height, salinity of the water, range of salinity of the soil, and aeration of the soil (Watson 1928; Macnae 1968; Chapman 1976; Oliver 1982; Snedaker 1982; Hutchings and Saenger 1987; Bunt et al. 1991; Duke 1993). Macnae (1966) recognized six zones in IWP mangrove habitat, distinguished by the dominant genus of mangrove tree: the landward fringe, *Ceriops* thickets, *Bruguiera* forests, *Rhizophora* forests, the seaward *Avicennia* zone, and the *Sonneratia* zone at the lowest level. The landward fringe is the most variable zone. Its floristic composition depends on the climate and vegetation of adjacent terrestrial habitats. In arid climates, owing to the evaporation of water between infrequent tidal coverage, the highest zone in the mangrove habitat can become so salty as to exclude woody plants, or even all vegetation (Walter 1985). In wet climates, salt concentration in the soil decreases landward, and terrestrial species may intermingle with mangrove species in the highest zone. In estuaries, saline conditions grade continuously into brackish and then fresh water. The palm *Nypa* and representatives of the genus

Acanthus, which some regard as mangrove taxa, occupy brackish-water zones. Because woody plants of freshwater swamp communities have no floristic relation to mangroves, they appear to have evolved independently.

Mangrove plants exhibit a variety of striking adaptations to salt stress and anoxic soils (Saenger 1982; Tomlinson 1986; Hutchings and Saenger 1987). Principal among these are various mechanisms of salt exclusion from roots or salt excretion from leaves; aerial roots and pneumatophores with openings (lenticels) to admit air; and viviparity. In the Rhizophoraceae, the seed germinates while still attached to the parent plant and is dispersed as a seedling with developing shoot and root axes. In several other mangrove taxa, embryonic development commences prior to dispersal, but the embryo does not break the pericarp of the seed. In all species of mangroves, propagules float and are dispersed by marine currents.

Mangrove vegetation consists of "exclusive" species that are limited to mangrove habitat and "nonexclusive" species that are distributed widely in terrestrial habitats but which also occur in the upper mangrove zones. Authors generally agree on which taxa belong in which group (but see Mepham and Mepham 1985 for a different, more inclusive, viewpoint): in a global mangrove flora of perhaps 20 genera and 50 species of exclusive mangrove taxa, Saenger, Hegerl, and Davie (1983) include 4 genera (7 species) that Tomlinson (1986) omits, but Tomlinson includes 1 genus (*Pemphis*: one mangrove species) not considered by Saenger et al. Chapman (1976) lists 16 genera and 55 species (10 are *Xylocarpus*). Duke (1993) includes 27 genera and 62 species plus 7 hybrids. In this chapter, we recognize 19 genera and 54 species or hybrids of exclusive mangroves (table 20.1); although mangroves have been studied intensively, their taxonomy is subject to revision (e.g., Duke 1991b; Duke and Jackes 1987; Juncosa and Tomlinson 1988a), and geographical ranges are imperfectly known in some areas (e.g., Bunt, Williams, and Duke, 1982).

Botanists also distinguish "major" elements of the flora, which are trees capable of forming dense stands (principally Rhizophoraceae, Avicenniaceae, Combretaceae, and Sonneratiaceae), from "minor" elements. Finally, mangroves harbor a diverse associated biota of marine and terrestrial plants and animals that may or may not be exclusive to the habitat but frequently occur there. Among plants, these include numerous epiphytes, parasites, climbers, and other herbaceous species that avoid salt stress by using mangrove plants as substrates for growth.

In general, mangrove species are widely and continuously distributed in suitable habitat within the region of their occurrence (Tomlinson 1986). Disjunctions (subpopulations separated by unoccupied suitable habitat) between populations within a species have been reported only in *Bruguiera hainsii* and *Pemphis acidula* (IWP region); disjunctions between sister taxa occur in the genera *Aegialitis* and *Camptostemon* (also IWP). However, Duke (1993) has called attention to the distinct mangrove floras of the northern and southern coasts of New Guinea, suggesting that "New Guinea marks a fusion boundary between two previously isolated and different mangrove

floras." Duke further makes the point that the distributional limits of many individual mangrove taxa are not well understood in terms of dispersal and ecological factors. In addition, Woodroffe and Grindrod (1991) emphasize the role of Pleistocene climate and sea level changes in modifying the present distributions of taxa.

TAXONOMIC AFFINITIES OF MANGROVES

Mangrove attributes appear to have evolved independently at least 15 times in 9 orders and 15 families (see table 20.1). Taxonomic isolation of mangrove species from non-mangrove sister taxa varies from the level of species within genera (*Heritiera*, *Excoecaria*, *Pemphis*, *Xylocarpus*) to the level of tribe (Rhizophoreae), or family if one separates the Avicenniaceae from the Verbenaceae (Tomlinson 1986). Taxa endemic to mangrove habitat at the species level generally are represented by single mangrove species, particularly if one accepts that all the mangrove taxa of *Xylocarpus* belong to a single species (Tomlinson 1986). Taxa endemic at the genus level also are represented mostly by single species, or by allopatric species (*Aegialitis* and *Camptostemon*). The exceptions are *Lumnitzera* (2 species) and *Sonneratia* (5 species); according to Cronquist (1981), the latter constitutes a family with only one other genus (*Duabanga*: 2 species of lowland rainforest trees), although Dahlgren and Thorne (1984) place *Sonneratia* in the Lythraceae. More than half the worldwide diversity of mangrove species is included within the Avicenniaceae and the Rhizophoreae, which evidently have undergone substantial diversification after invading the mangrove habitat (see below).

THE DIVERSITY OF MANGROVE TAXA

Saenger, Hegerl, and Davie (1983) tabulated the occurrence of species within six areas, three within the IWP region and three within the ACEP region (fig. 20.1). Although the IWP and ACEP regions presently have roughly equivalent total areas of suitable habitat (table 20.2), mangrove diversity differs between the regions by a factor of four for genera and about six for species. Within the ACEP region, most mangrove taxa, with the exception of *Pelliciera*, are widespread, and diversity does not vary markedly from site to site (Tomlinson 1986).² On the

2. Gentry (1982) lists 13 species of exclusive mangrove trees on the Pacific coast of Central and South America from southern Mexico to northern Peru, belonging to the genera *Avicennia*, *Crenea** (Lythraceae), *Laguncularia*, *Mora** (Leguminosae), *Pavonia** (Malvaceae), *Pelliciera*, *Phryganocydia** (Bignoniaceae), *Rhizophora*, *Tabeuia** (Bignoniaceae), and *Tuberostylis** (Compositae) (asterisks indicate taxa not found on the Caribbean side of the Isthmus). This area includes the Choco region of Columbia, one of the wettest on earth, where salt stress may be minimized and where uplifted mangrove habitats may permit intermixing of more terrestrial, flood-tolerant (as opposed to salt-tolerant) vegetation. Such conditions may represent evolutionary entryways of terrestrial taxa into mangrove habitat. *Crenea* pollen appears in the Caribbean region in the Upper Eocene and Lower Miocene in association with *Rhizophora* pollen in coastal sediments, suggesting the presence then of a mangrove taxon within the genus (Germeraad, Hopping, and Muller 1968).

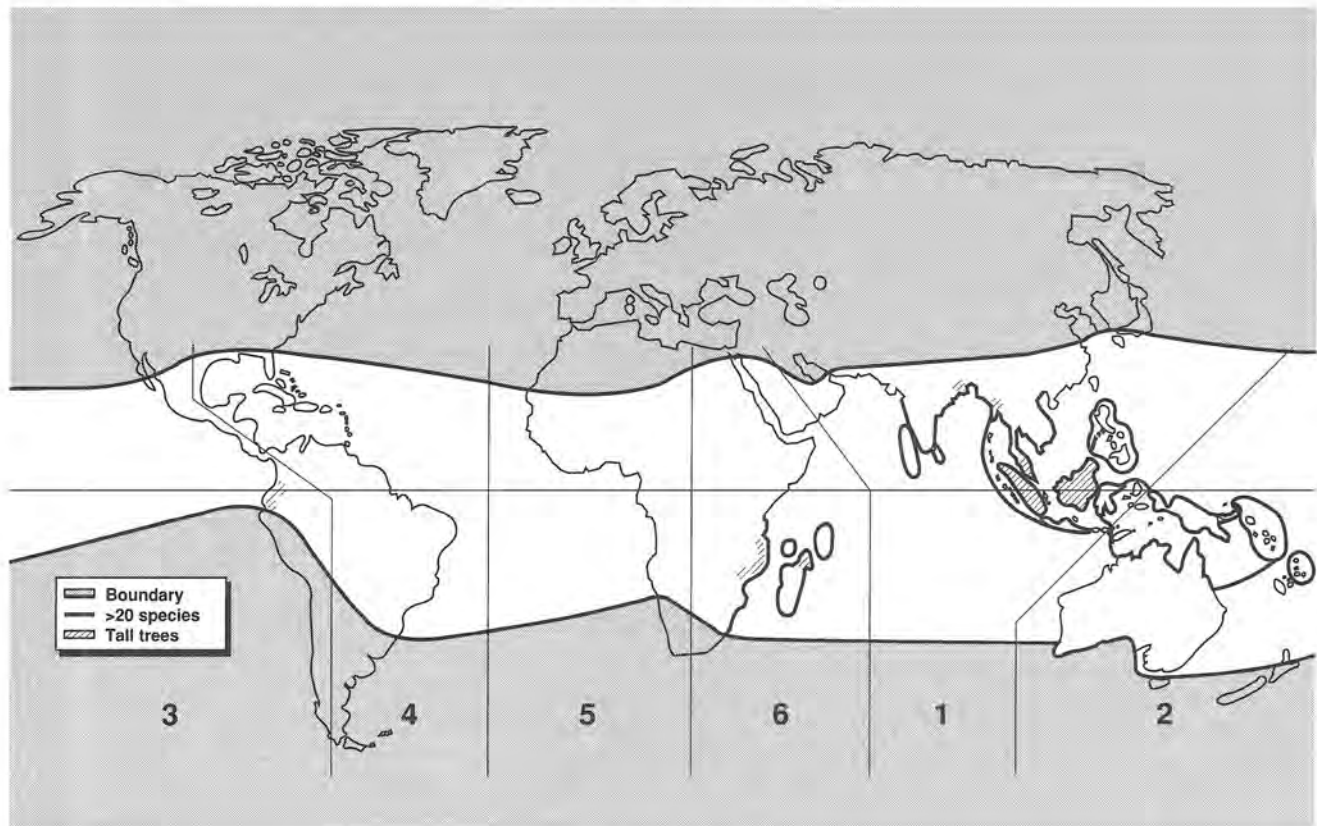


Figure 20.1 Worldwide distribution of mangroves. Coasts with more than 20 species are indicated by heavy lines; areas supporting very tall trees are indicated by hatching. (Distributions from

Chapman 1970.) Vertical lines separate geographical areas used by Saenger, Hegerl, and Davie (1983) to tabulate regional diversity.

Table 20.2 Taxonomic Diversity of Mangrove Taxa in Different Biogeographical Regions

Region and subregion	Area of mangrove habitat (km ²)	Number of genera	Exclusive species
IWP			
2. Australia/New Guinea	17,000	16	35
1. Asia/Indonesia	52,000	17	39
6. East Africa/Madagascar	5,000	8	9
ACEP			
5. West Africa	27,000	3	5
4. Western Atlantic/Caribbean	48,000	3	6
3. Eastern Pacific	19,000	4	7

Source: Data from Saenger, Hegerl, and Davie 1983 and table 20.1.

western edge of the IWP region, the coasts of East Africa and Madagascar (area 6) support restricted areas of mangrove habitat and relatively low diversities of taxa. This low diversity may be related to the small area of suitable habitat and to local environmental conditions. More than half the mangrove habitat in area 6 is on the island of Madagascar. The eastern coast of Africa lacks large rivers with well-developed deltas, and much of the coast is arid and unsuitable for mangrove genera that occupy the upper zones in wetter climates. Diversity also decreases eastward from New Guinea into the Pacific Islands, presum-

ably as a result of the difficulty of long dispersal distance against prevailing ocean currents (Jokiel and Martinelli 1992). Species of *Bruguiera* and *Rhizophora* have been introduced successfully to Hawaii, which lacks native mangroves (Wester 1981). This suggests that diversity on the Pacific islands is indeed limited by colonization.

Local (i.e., hectare scale) diversity in mangrove habitat parallels regional diversity. Within the ACEP region, local diversity generally is 3–4 species, half the total number present in the region, but usually including all the species that co-occur geographically (Davis 1940; Chapman 1970, 1976). Within the IWP region, local diversity is more difficult to ascertain from published accounts, which tend to present floristic maps and idealized transects within localities. One such representation of a typical area on the Malayan west coast includes 6 genera and 11 species of predominant mangroves (Watson 1928); Macnae (1966) and Elsol and Saenger (1983) similarly depict several areas on the Queensland coast of Australia with 5–8 genera of exclusive mangrove taxa. Tomlinson (1986) indicates that certain localities on the coast of Queensland, Australia, may harbor up to 30 species of mangroves, most of them exclusive species. Transects from low to high water at several localities along the Endeavour River estuary in northeastern Australia revealed 7–15 species of mangroves per transect and a total of 25 species (Bunt et al. 1991). Thus, species richness in the

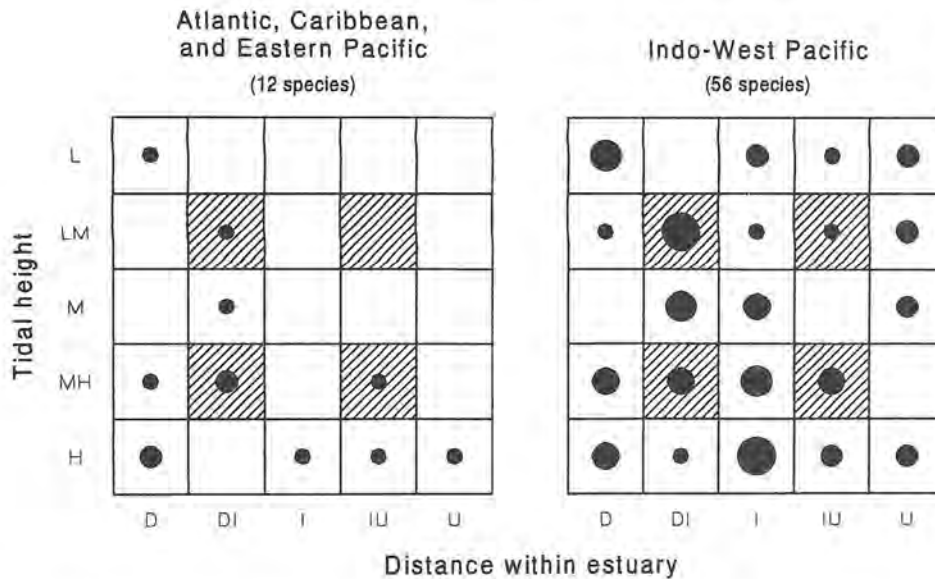


Figure 20.2 Distribution of mangrove taxa among categories of intertidal zone height (L, low; M, mid; H, high) and position within an estuary (D, downstream; I, intermediate; U, upstream) in the ACEP and IWP regions. Numbers of taxa per cell (1–6) are indicated by the sizes of the dots. Generalized taxa distributed in more than one category within each ecological axis are indicated by hatching. (Data from Duke 1993.)

IWP region exceeds that of the ACEP region by factors of 6 at the regional level and probably at least 2–3 at the local level.

Whether the greater diversity of IWP mangroves is accompanied by greater ecological specialization of taxa and greater zonation with respect to salinity and height in the tidal zone has not been well resolved. Zonation within the mangrove habitat and the tendency of stands to be dominated by a single species result in local coexistence of species being perceived over distances of tens or even hundreds of meters rather than on the scale of neighboring individuals (Macnae 1968; Chapman 1976; Hutchings and Saenger 1987). This dimension of heterogeneity appears to characterize the lower-diversity ACEP mangroves as well as the higher-diversity IWP mangroves (Davis 1940). Nonetheless, some zones of the IWP mangrove habitat may be occupied by mixed-species stands, particularly at mid-tidal levels (Macnae 1968; Elsol and Saenger 1983).

Duke (1993) characterized exclusive mangrove species and their hybrids on the basis of intertidal position and estuarine location. His tabulation allows one to determine whether ACEP and IWP mangroves occupy the same total niche space, and whether differences occur in the degree of specialization of taxa in the two regions. The intertidal zone was divided into three zones: L (lower, inundated more than 45 times per month), M (mid, 20–45 times), and H (high, fewer than 20 times). Distance up an estuary was divided arbitrarily into thirds: D (downstream), I (intermediate), and U (upstream). Each species of mangrove was cross-classified according to these two axes of the ecological space; each species was placed in one (e.g., L, M, or H) or two subdivisions (e.g., LM or MH) of each ecological axis. The number of species in each of the cross-tabulated categories in the ACEP and IWP regions is presented in figure 20.2.

The ACEP region lacks mangrove taxa in the lower intertidal upstream region of the ecological space (L-U, LM-U, L-IU, LM-IU). In the IWP region, this space is occupied by *Nypa fruticans*, *Rhizophora mucronata*, *Sonneratia*

apetala, *S. caseolaris*, *S. lanceolata*, and *Aegiceras corniculatum*. Suitable habitat presumably exists in the ACEP region; it is unclear why it is not filled. Evidently, the ACEP mangrove species have not expanded their niches to occupy this portion of the habitat, and terrestrial forms have not invaded.

In regions of low species richness, individual species often exhibit expanded ecological distributions, a phenomenon known as ecological release (MacArthur, Recher, and Cody 1966; Cox and Ricklefs 1977). Accordingly, one would predict that a larger proportion of species would occupy two, rather than one, of the habitat categories in the ACEP region compared with the IWP region. The proportions of species that Duke (1993) classified as occupying two categories of both tidal height and distance upriver (ACEP: 4 of 12; IWP: 13 of 56) do not differ significantly between the regions ($\chi^2 = 0.54, P > .10$). The same is true if one considers taxa specialized to just one category on both ecological axes. Thus, ACEP mangrove species do not exhibit increased niche breadth. This is consistent with the greater local diversity of mangrove species in the IWP region. Evidently, species have been added to the mangrove association in part by the invasion of niche space already occupied by other taxa. That is, the mangrove habitat does not appear to be saturated by species.

Regional species richness of other taxonomic groups ecologically associated with, but not exclusive to, mangrove vegetation also tends to be higher in the IWP region than in the ACEP region. Some of these associated taxa are marine, including numerous invertebrates and fishes, while others, particularly various plant taxa, have terrestrial affinities. Saenger, Hegerl, and Davie (1983) tabulated the number of species of mangrove-associated biota in several regions. Their results are excerpted in table 20.3 for the three areas that have been well surveyed: 1 (Asia/Indonesia), 2 (Australia/New Guinea), and 4 (western Atlantic/Caribbean). The details of this table undoubtedly reflect the varying degrees of attention that specialists have paid to each taxonomic group in each region. Of the

Table 20.3. Species Diversity of Plants and Animals Associated with Mangrove Vegetation

Taxonomic group	Area 1 (IWP)	Area 2 (IWP)	Area 4 (ACEP)
Monocotyledons	73	42	20
Dicotyledons	110	80	28
Total flowering plants	183	122	48
Algae	65	93	105
Non-polychaete worms	13	74	13
Polychaetes	11	35	33
Crustaceans	229	128	87
Mollusks	211	145	124
Echinoderms	1	10	29
Ascidians	0	8	30
Fishes	283	156	212
Total marine animals	748	556	528

Source: Data from Saenger, Hegerl, and Davie (1983).

three areas, the Asian/Indonesian part of the IWP region (area 1) is probably the most poorly known. Indeed, although more species have been reported from Asian/Indonesian mangroves (area 1) than from Australian mangroves (area 2) among herbaceous plants, crustaceans, mollusks, and fish, several invertebrate groups appear to be underreported. The data in table 20.3 reveal a nearly threefold or fourfold greater species richness of higher plants in the IWP region than in the ACEP region (122 or 183 versus 48). Among marine animals and marine algae, numbers of species in regions 2 and 4 are similar (556 versus 528 and 93 versus 105, respectively). Thus, the global diversity anomaly in mangrove habitat applies quite generally to elements of the flora derived from terrestrial habitats, but perhaps not so strikingly to the marine biota.

GEOGRAPHY OF MANGROVES

Mangroves are confined primarily to tropical latitudes (see fig. 20.1), although *Avicennia* occurs at high latitudes in some temperate areas of moderate climate, such as southern Australia and northern New Zealand (Chapman 1976; Wells 1983; Woodroffe and Grindrod 1991). The distributional limits of mangrove vegetation coincide approximately with the 24° C isotherm of mean sea surface temperature during the warmest month (Hutchings and Saenger 1987), the 15° C isotherm in the coldest month (Woodroffe and Grindrod 1991), and a variety of other climate indices. Regardless of the particular criterion, barriers to dispersal between the ACEP and IWP regions are presently maintained by the cool coastal environment of southern and southwestern Africa (Briggs 1974); within tropical latitudes across the central Pacific Ocean, dispersal is limited by distance (Chapman 1975). Within the ACEP region, the eastern Pacific Ocean (western coasts of Central and South America) has been isolated from the Caribbean and tropical Atlantic Ocean by the Panamanian Isthmus for the past three million years (Saito 1976; Keigwin 1978). Tomlinson (1986) does not recognize any taxonomic differences between the Pacific and Caribbean

Table 20.4. Geographical Distribution of Mangrove Genera

	Atlantic/Caribbean/ East Pacific		Indo-West Pacific
<i>Avicennia</i>	3 species		4–6 species
<i>Rhizophora</i>	2 + 1 hybrid		3 + 2 hybrids
<i>Laguncularia/Lumnitzera</i>	1 species		2 species
<i>Nypa</i>	Paleogene fossil		1 species
<i>Wetherellia</i>	Paleogene fossil		
<i>Pelliciera</i>	1 species		
Indo-West Pacific endemics			14 genera 32 species
Total	4 genera 7 species		17 genera 40–42 species

sides of the Isthmus, although *Avicennia bicolor* is found only on the Pacific coast and *A. schaueriana* is restricted to the Lesser Antilles and Atlantic coast of South America. Duke (1993) discusses in more detail distribution anomalies within the IWP region, which indicate biogeographical subdivision.

The present distributions of mangrove taxa can be divided broadly into three types with respect to their occurrence in the ACEP and IWP regions: cosmopolitan, endemic to ACEP, and endemic to IWP (table 20.4). Only two genera are cosmopolitan: *Avicennia* and *Rhizophora*. The mangrove palm *Nypa*, currently widely distributed in the IWP region, is known from the fossil record of the early Tertiary in the ACEP region, including western Europe (fig. 20.3; see below), and has been reintroduced to Panama (Duke 1991a). According to Tomlinson (1986), *Laguncularia* (ACEP) and *Lumnitzera* (IWP) are sister taxa, suggesting a cosmopolitan distribution of their common ancestor. Endemic IWP genera can be further subdivided according to presence (6 genera) or absence (6 genera) in Madagascar and East Africa.

Within the cosmopolitan genera *Avicennia* and *Rhizophora*, each species is endemic to either the IWP or the ACEP region, although Tomlinson (1986) and Ellison (1991) suggest that the IWP species *Rhizophora samoensis* is the same as the widespread ACEP species *R. mangle*, perhaps having colonized the IWP region from the eastern Pacific.

Only one mangrove clade is, at present, restricted to the ACEP region, the monotypic family Pellicieraceae³ (*Pelliciera rhizophorae*), although Gentry (1982) would include six others with distributions restricted, like that of *Pelliciera*, to the Pacific coast of the Americas.

In contrast to the low level of endemism of mangroves in the ACEP region (2 genera of exclusive mangroves including 2 species), 13 genera in 11 families, including 31 species, are restricted to the IWP region; these endemic IWP taxa represent 72% of the entire IWP exclusive mangrove flora at the genus level. With the exception of *Cerriops* and *Bruguiera* (*Paleobuguiera*) in the Eocene of England, none of these genera is known from the fossil record of the ACEP region (see below).

3. The name is given as Pellicieraceae (genus *Pelliciera*) in Willis (1966).

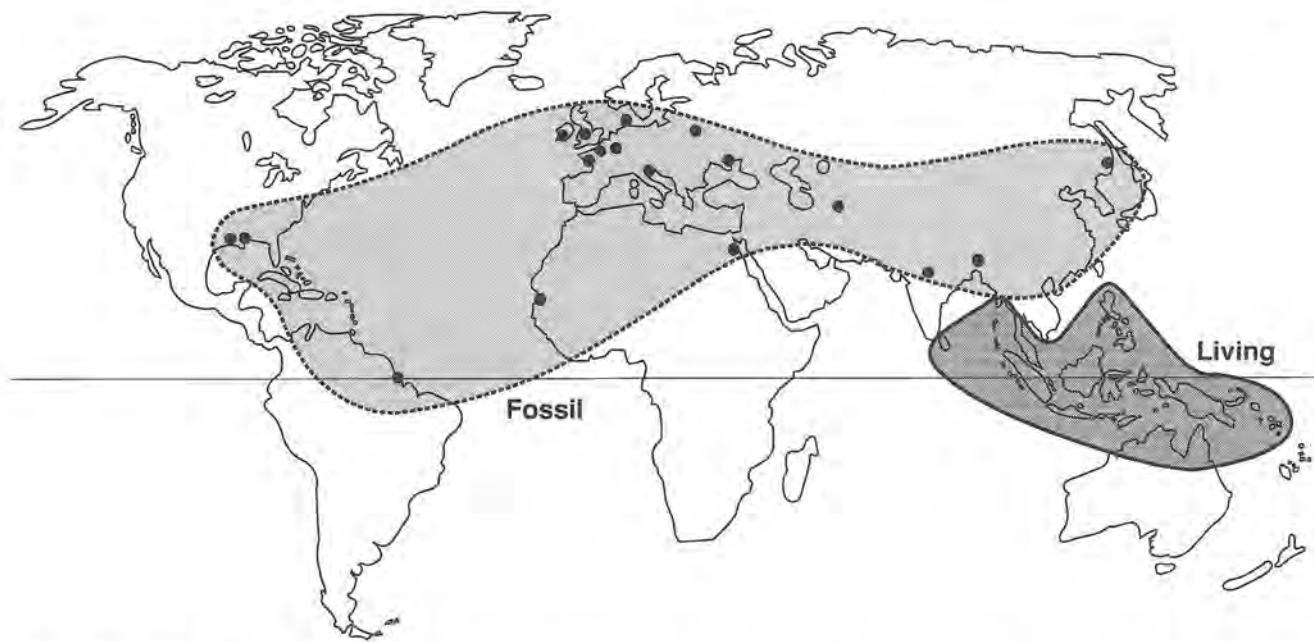


Figure 20.3 Fossil (symbols with dashed line) and contemporary (continuous line) distributions of the mangrove palm *Nypa*. (After Croizat 1968.)

THE FOSSIL RECORD OF MANGROVES

The mangrove habitat—protected, intertidal soft sediments within frost-free regions—presumably has existed for a very long time. According to Tomlinson (1986), fossil evidence suggests the continuous presence of mangrove vegetation since the end of the Paleozoic and certainly predating the origin of angiosperms. Croizat (1964) and others have even suggested that mangrove taxa may have left terrestrial descendants following uplift of mangrove habitat; certainly *Sonneratia* and *Pemphis* have sister taxa with restricted distributions at high elevations in Indomalaysia and Madagascar, respectively. Mephram and Mephram (1985) report the presence of many “exclusive” mangrove taxa at upland sites in various parts of the IWP region, including an inland stand of *Bruguiera* on Christmas Island in the Indian Ocean, which lacks shoreward stands of mangrove (Woodroffe and Grindrod 1991).

The presence of modern mangrove taxa in the fossil record dates back to the late Cretaceous (*Nypa*; Muller 1964), with dicotyledonous taxa (*Rhizophora*, *Pelliciera*, *Sonneratiaceae*) known from the early Eocene, at least 30 mya (Muller 1981). In general, the record is not particularly good. Mangroves are a restricted vegetation form difficult to recognize in the fossil record, except where remains of modern mangrove taxa are present; reproductive structures do not distinguish modern mangrove taxa from those of terrestrial habitats. Even when flowers, fruits, pollen, or wood can be assigned to a modern, exclusive mangrove genus, one cannot assume that the genus has been an exclusive mangrove taxon lacking terrestrial representatives in the past: the contemporary genera *Heritiera*, *Excoecaria*, *Pemphis*, and *Xylocarpus* include both terrestrial and mangrove species. However, a convincing

case for an extinct mangrove taxon has been made for *Wetherellia* and *Paleowetherellia* (possibly Euphorbiaceae), which are recorded from marine deposits in the Eocene of Maryland, Germany, and England (in association with *Nypa*) and the late Cretaceous and Paleocene of Egypt (Mazer and Tiffney 1982). The distribution of *Wetherellia* and *Paleowetherellia* is clearly Tethyan, but the absence of associations with the contemporaneous *Pelliciera* and *Rhizophora* is puzzling.

Many mangrove genera (e.g., *Aegiceras*, *Heritiera*, *Excoecaria*, *Osbornia*) apparently have not been reported from the fossil record because of poor sampling, difficulty of recognizing their fossil remains, or absence of the taxa from areas of fossilization. Considerable confusion has arisen because of the misidentification of some fossil remains, notably, claims of *Rhizophora* and *Bruguiera* pollen in the Paleogene of Europe (Muller 1981; but see Wilkinson 1981, 1983 for macrofossil evidence of *Ceriops* and *Paleobruguiera* [Rhizophoraceae]). Finally, many interpretations of the present distribution of mangroves incorporate tectonic conditions or events that predate the oldest fossils. Among these conditions is the availability of the Tethys connection between the IWP and ACEP regions, which closed 30–35 mya. We shall discuss implications of the fossil record below.

THE ORIGIN OF THE IWP-ACEP DIVERSITY ANOMALY

Diversity anomalies may arise historically from region-specific differences in the origin of clades, rates of diversification within clades, propensity for dispersal between regions, extinction, or some combination of these.

Extinction and Range Contractions

Differential extinction may cause disparity in species richness between regions, as it has contributed to the depauperization of the woody flora of temperate Europe (Latham and Ricklefs, chap. 26). However, the fossil record provides little evidence that extinction has been responsible for the low species richness of ACEP mangroves. *Nypa*, and possibly the Paleogene *Wetherellia*, are the only mangrove taxa that have disappeared from the ACEP region, although the distribution of the ACEP genus *Pelliciera* has been severely restricted as well. Furthermore, *Ceriops* and *Paleobruquiera* (Rhizophoraceae) are known from the Eocene of southern England (Tethyan), but not from the Caribbean. Possibly these arrived at the doorway to the ACEP region but did not extend their ranges fully into it. *Wetherellia* appeared along the eastern coast of North America but apparently failed to enter the Caribbean.

No extinctions of mangrove taxa have been recorded from the IWP region. However, regional extinctions of mangrove taxa cannot be identified as such without contemporary representation of the taxa elsewhere. Thus, regional (= global) extinctions may have occurred of endemic taxa that were either not recorded in the fossil record or not recognized as mangroves.

Fossils do reveal substantial range contractions in the past in a few cases: (1) the disappearance of *Nypa* from an extensive distribution in the ACEP region in the early Tertiary (Croizat 1964, 1968; Daghljan 1981; Tralau 1964); (2) the contraction of mangrove vegetation that once occurred at high latitudes in central Europe (*Nypa*, *Ceriops*, *Paleobruquiera*: Daghljan 1981; Wilkinson 1981, 1983), in the Sahara of Egypt (Kräusel 1939), in southeastern Australia (*Nypa*, *Sonneratia*, Rhizophoraceae: Churchill 1973), on the Gulf Coast of North America (*Nypa*: Westgate and Gee 1990), and on the east coast of North America (*Wetherellia*: Mazer and Tiffney 1982); (3) contraction of the ACEP genus *Pelliciera* from its formerly widespread distribution to relictual populations (Graham 1977). The latitudinal contraction of mangroves may be explained by the general cooling of the earth, particularly at high latitudes, since the mid-Tertiary (Savin 1977; Keigwin 1980).

Pelliciera was widespread in the ACEP region from the Eocene (Panama, Greater Antilles) to the early Miocene, at which time it apparently disappeared from the northern parts of its distribution in the Greater Antilles and the Isthmus of Tehuantepec in Mexico (Graham 1977). It persisted on the northern coast of South America and Brazil through the Miocene, but is not reported thereafter, possibly owing to a paucity of suitable sediments (Graham 1977). The palm *Nypa* similarly disappeared from the Caribbean fossil record at the end of the Miocene. According to Graham (1977), *Rhizophora* pollen constitutes a minor part of *Pelliciera* associations in the Eocene of Panama and Jamaica, becoming abundant only during the Oligocene/Miocene time.

At present, *Pelliciera* occurs in wet refuges on the west coast of Central America and northern South America from Costa Rica to Ecuador, with a few relictual populations on the Caribbean coasts of Colombia, Panama, and

Nicaragua (Calderon 1983; Winograd 1983; Jiménez 1984; Roth and Grijalva 1991). Graham (1977) suggested that the range contraction of *Pelliciera* may have resulted from a variety of factors, including sea level fluctuations, cooling climates, and competition from *Rhizophora*. Jiménez (1984) emphasized *Pelliciera*'s intolerance of hypersaline conditions (soil salinity greater >37%, i.e., approximately that of seawater) and related its decline to drying conditions beginning in the Caribbean basin during the Miocene (references in Jiménez 1984). Today, *Pelliciera* occurs only under wet climate regimes (where abundant rainfall prevents mangrove soils from drying and prevents salinities from rising about the level of seawater) and in estuaries (e.g., the Caribbean coast of northern Colombia). The idea that drying climates caused the range contraction of *Pelliciera* is consistent with the disappearance from the region of *Nypa*, a species that occurs primarily in brackish estuaries. The distribution of *Pelliciera* prior to the Neogene also emphasizes the widespread presence of mangrove habitat adjacent to areas of wet tropical forest during the Paleogene, as well as the apparent absence of other mangrove taxa from the fossil record of the ACEP region.

Dispersal

Contemporary exclusive mangrove taxa disperse via floating propagules, whether fruits, seeds, or precociously germinated seedlings (Saenger 1982). Three connections between the ACEP and IWP regions may have been available at various times during the Cenozoic period: the Pacific Ocean, the Tethys Sea, and southern Africa. The IWP has experienced a change in configuration during the last 100 million years owing to the northward movements of the Indian and Australian landmasses, but the region has had a geographical continuity throughout the Phanerozoic. In contrast, the ACEP region as we know it today developed with the breakup of Pangaea beginning during the late Mesozoic. The opening of the Atlantic Ocean undoubtedly predates the origin of modern taxa (genera and species) of mangroves, but earliest appearances in the fossil record are relatively uninformative about the origins of most taxa. Prior to the development of the Atlantic Ocean, the ACEP region was restricted to the eastern Pacific Ocean, that is, the western coast of Pangaea, which presently supports a depauperate sample of IWP taxa of corals, mollusks, and fishes that apparently dispersed eastward across the Pacific Ocean (Newton 1988). Because of this Pacific component to the ACEP region, however, its biota potentially is as old as that of the IWP region. This fact takes on significance in light of Gentry's (1982) suggestion of high mangrove diversity in the Choco region of western Columbia.

Dispersal has always been possible between the IWP and ACEP regions across the Pacific Ocean, but movement of propagules between the west coast of tropical America and the nearest large islands in the western Pacific Ocean requires several months at present-day current velocities of about 1 knot. Probably only *Rhizophora* propagules remain viable long enough to make this journey (Rabinowitz 1978; Clarke and Myerscough 1991). Throughout the Tertiary, currents have been favorable

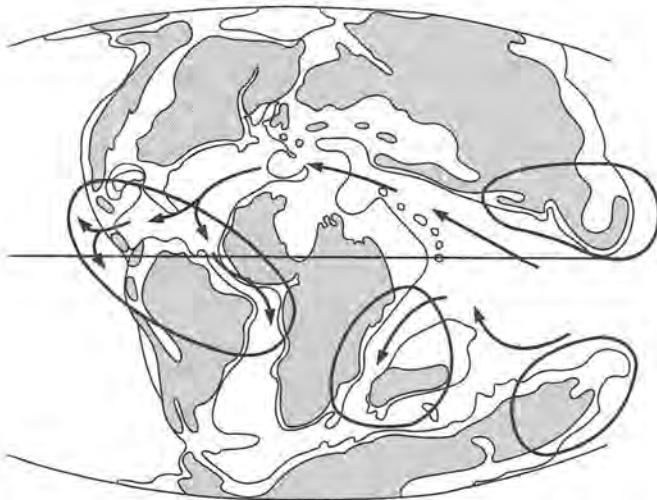


Figure 20.4 Map of the earth during the Paleocene-early Eocene showing the distribution of present-day mangroves. Arrows indicate ocean currents. Shaded areas indicate land masses; lines, continental shelves.

only for westward dispersal across the Pacific within tropical latitudes (Haq 1981; but see Newton 1988). The absence of localized eastern Pacific populations of IWP taxa suggests that mangrove taxa have not dispersed from east (IWP) to west; the presence of *Rhizophora samoensis* (= *R. mangle*) on New Caledonia, the new Hebrides, Tonga, and Samoa provides the only mangrove example of dispersal from west to east (Ellison 1991). We tentatively conclude, in agreement with Tomlinson (1986), Mepham (1983b), and others, that the Pacific is not now, and has not been in the past, an important dispersal route or center of evolution (in the sense of Croizat) for mangrove vegetation. However, Germeraad, Hopping, and Muller (1968) favored a trans-Pacific dispersal route for *Rhizophora* between the IWP and ACEP regions based on the appearance of *Rhizophora*-type pollen in the Caribbean during the late Eocene, possibly after the closure of the Tethys connection, and its later (Miocene) appearance in western Africa (Nigeria).

The second potential route of exchange between the ACEP and IWP regions was through the Tethys Sea, which connected the Indian Ocean to the developing Atlantic Ocean through the Mediterranean region during the Cretaceous and early Tertiary (fig. 20.4). The connection was closed off about 30–35 mya, during the Eocene. The presence of tropical elements in the European Paleogene fossil record (e.g., Reid and Chandler 1933; Chandler 1961), and the presence of mangrove genera in Tethyan and European deposits of Eocene age (Kräusel 1939; Prakash 1960; Tralau 1964; Haseldonckx 1972; Wilkinson 1981, 1983), suggest that the Tethyan region contained suitable mangrove habitat.

The only other marine connection between the IWP and ACEP regions is around the southern end of the African continent. Mangrove habitat is abundant on Madagascar and extends sporadically down the eastern (Indian Ocean) coast of Africa to Natal (Palmer and Pitman 1972; Moll and Werger 1978; Ward and Steinke 1982; Woodroffe and Grindrod 1991). At present, however, the south-

ern and western coasts of southern Africa are dry, cold (due to upwelling currents: Schulze and McGee 1978), and devoid of extensive, gently sloping coasts. Mangroves currently extend down the Atlantic coast of Africa, which is part of the ACEP region, only to a latitude of 12° S (Chapman 1976). The present situation does not represent conditions during the early Tertiary, when the oceans surrounding southern Africa were much warmer and may have provided a dispersal route for mangrove vegetation; Mepham (1983a) has argued persuasively for a southern, high-latitude dispersal route for mangrove taxa between southern Africa and Australia prior to the Eocene.

Regardless of the relative likelihood of any particular corridor, the continent of Africa provides a prominent biogeographical connection between ACEP and IWP mangroves, a connection that is also shared by the distributions of many terrestrial taxa (Croizat 1964). The apparent connection between the ACEP and IWP regions may be referable to the northern African shores of the Tethys Sea, as the continent of Africa has been intact through the whole of the evolution of contemporary mangrove taxa and an overland connection is out of the question.

With respect to the possibility of mangrove dispersal, we conclude that the distribution of mangrove habitat could have been continuous, or nearly so, on the scale of dispersal distances of propagules, between the ACEP and IWP regions during most of the Paleogene. Furthermore, dispersal through the Tethyan region by ocean currents was predominantly from east to west (Specht 1981a). Finally, the two regions have been isolated throughout the past 30–35 million years, as both the Tethyan connection and southern Africa would have been unavailable for mangrove dispersal.

Origin of Mangrove Clades

Clades occupying the mangrove habitat arose independently in at least 15 plant families. This count is based upon the premise that the ancestral habitat for modern mangrove clades was terrestrial, which is supported by the fact that most mangrove taxa exist within larger, otherwise terrestrial clades. Four of the 15 mangrove clades are or were cosmopolitan, 1 is restricted to the ACEP region, and 10 are restricted to the IWP region.

The fossil record often reveals that contemporary distribution may not coincide with or even include past geographical distribution. For example, the earliest Bombacaceae appear in the late Cretaceous (80 mya) fossil record of New Jersey, but the family presently occurs only in tropical regions of South and Central America, Africa, and Southeast Asia; similarly, *Symplocos* (family Symplocaceae) was first recorded from the late Cretaceous of western North America, and later was widespread across all of Laurasia, but presently occurs only in southeastern North America, South America, and eastern Asia to Australia (Kruttsch 1989). Similar examples occur in the Juglandaceae (Manchester 1989), and also include *Nyssa* (see fig. 20.3).

In the case of clades in mangrove habitat, the geographical distributions of fossils support the generaliza-

tion that present distributions include the area of origin.⁴ When sister taxa are restricted to the same region, i.e., have shared geographical distributions, one can surmise either that the ancestral taxon had a similar distribution or that the ranges of the sister taxa have changed in parallel, perhaps even moving from the place of their origin. The latter scenario is unlikely in the case of mangroves, whose sister taxa now occupy a substantially different, terrestrial habitat, which may be influenced by different factors in the physical environment. Parsimony would lead one to conclude that the common geographical distribution of sister taxa includes, in a very general sense, the place of the origin of the derived clade.

The distributions of mangrove taxa and their terrestrial relatives clearly indicate the place of mangrove origins in many cases, including *Camptostemon*, *Osbornia*, and *Sonneratia*, which are discussed below. For several taxa, however, one cannot identify sister taxa of comparable taxonomic level owing to the distinctiveness of the mangrove taxon (e.g., *Nypa*, *Aegiceras*, *Aegialitis*, *Avicennia*). Additionally, when a sister taxon has a cosmopolitan distribution, one cannot identify the place of origin without additional historical or phylogenetic information. Of the three cosmopolitan mangrove clades, the subfamily Rhizophoraceae belongs to a larger cosmopolitan family (Rhizophoraceae: 15 genera, 135 species; Juncosa and Tomlinson 1988a) with primarily Old World genera (including non-mangrove forms), but also including the cosmopolitan terrestrial genus *Cassipourea* (55 spp.), which is widespread in tropical America and the West Indies as well as in southern Africa, Madagascar, and Sri Lanka. The history of the Rhizophoraceae will be discussed at greater length below.

The *Laguncularia/Lumnitzera/Macropteranthes* clade is part of a larger, pantropical, woody family (Combretaceae) having 20 genera and over 500 species (Tomlinson 1986). The largest genera in the family (*Terminalia*, *Combretum*, *Quisqualis*) are pantropical in distribution. The terrestrial *Macropteranthes* (4 spp.) is restricted to tropical northern Australia. The ACEP nonexclusive mangrove *Conocarpus* also belongs to the Combretaceae. Thus, the origins of these mangrove taxa cannot be placed unambiguously.

The cosmopolitan *Avicennia* is usually placed in its own family (Avicenniaceae), although it has been included in the Verbenaceae. Willis (1966) suggests a relationship to the Salvadoraceae, whose members inhabit hot, dry regions, often coastal or saline, and whose largest genera (*Salvadora*, *Azima*, *Dobera*) are Old World groups centered around the Indian Ocean. The earliest fossil pollen records of *Avicennia* are from the IWP: the Eocene of Australia (probable), the lower Miocene of the Marshall Islands, and the upper Miocene of northwestern Borneo. The earliest ACEP record is from the Pliocene of Guyana

(Muller 1981); such a late arrival in the West is inconsistent with the much earlier closure of the Tethys corridor between the IWP and ACEP regions, but supports a trans-Pacific connection or southern African connection.

Most of the IWP endemics are closely allied to taxa having IWP-East African-Madagascan distributions. The three genera having a single mangrove species (*Exocoecaria*, *Xylocarpus*, *Heritiera*) are presently confined to the IWP region. Seven exclusive mangrove genera restricted to the IWP region show varying degrees of affinity to IWP terrestrial taxa, as illustrated below.

Camptostemon (Bombacaceae, cosmopolitan) is placed by Tomlinson (1986) in the tribe Durioneae, whose principal genus *Durio* consists of twenty-seven species restricted to Burma and western Malaysia. Pollen of *Durio* is first recorded from the Oligocene-Miocene of northwestern Borneo, and that of *Camptostemon* from the lower Miocene of Borneo and possibly the upper Miocene of Papua (Muller 1981).

Osbornia (Myrtaceae, cosmopolitan) is quite isolated taxonomically but probably belongs to the Old World subfamily Leptospermoideae (Tomlinson 1986).

Sonneratia (Sonneratiaceae) has affinities with the cosmopolitan family Lythraceae. The only other genus in the Sonneratiaceae is *Duabanga*, which contains two allopatric terrestrial species restricted to Indomalaysia (Mahabale and Deshpande 1959; Willis 1966; Croizat 1968). *Sonneratia* is the only mangrove genus for which the pollen record reveals an intermediate form relating it to a taxon that is presently restricted to terrestrial habitats. The earliest pollen records of *Sonneratia* are from the lower and middle Miocene of Borneo (Muller 1981). A Lythraceae/Sonneratiaceae type of pollen (*Florschuetzia trilobata*) is known from Oligocene and Miocene coastal sediments of northwestern Borneo and possibly the Eocene of western Malaysia. This pollen is regarded as ancestral to that of Sonneratiaceae (Germeraad, Hopping, and Muller 1968) and disappears from the fossil record by the end of the Miocene, suggesting that it may be a transitional form connecting terrestrial and mangrove taxa.

Aegialitis belongs to the cosmopolitan family Plumbaginaceae and is probably closest to the cosmopolitan *Plumbago* (Willis 1966), which typically inhabits salt steppes and seacoasts. *Aegialitis* is first recorded in the pollen record from the middle Miocene of Borneo, where it no longer occurs.

Aegiceras (Myrsinaceae, cosmopolitan) is placed in the subfamily Myrsinoideae, tribe Ardisiæae, which includes the genera *Ardisia* (400 tropical species, cosmopolitan, including one mangrove associate in Southeast Asia) and *Tapeinosperma* (40 species in New Guinea, Queensland, New Hebrides, New Caledonia, and Fiji).

Scyphiphora (Rubiaceae, cosmopolitan) probably belongs to the tribe Gardeniæae, which contains both Old World and New World genera. The largest (*Gardenia*) is restricted to the Paleotropics.

Pemphis acidula (Lythraceae, cosmopolitan) shows no clear relationships within the family. A non-mangrove congener, *P. madagascariensis*, is restricted to the mountains of southwestern Madagascar.

4. However, Mephm (1983a) emphasizes the observation that several mangrove genera distributed widely during the Eocene (*Avicennia*, *Rhizophora*, *Sonneratia*) did not appear in the fossil record of Borneo until the Oligocene or Miocene (Muller 1964), and suggests that the present concentration of mangrove taxa in Southeast Asia/Malaysia is relictual.

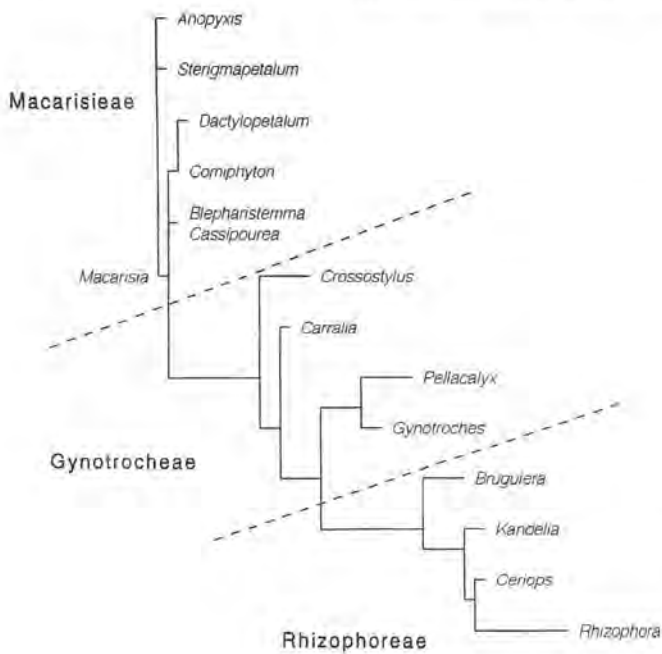


Figure 20.5 Cladistic phylogenetic tree of the Rhizophoraceae. Branch lengths are proportional to the number of character stage changes. The three tribes of the Rhizophoraceae are separated by dashed lines. (After Juncosa and Tomlinson 1988b.)

In summary, distributions of related taxa are either consistent with the origin of IWP endemic mangrove taxa within the IWP region (*Exocoecaria*, *Xylocarpus*, *Heritiera*, *Camptostemon*, *Osbornia*, *Sonneratia*) or uninformative (*Aegialitis*, *Aegiceras*, *Scyphiphora*, *Pemphis*). The pollen records of *Camptostemon*, *Sonneratia*, and *Aegialitis* are also consistent with IWP origins.

History of the Rhizophoraceae

Muller (1981) summarized the earliest records of *Rhizophora*-type fossil pollen: upper Eocene of the Caribbean, Brazil, and India; lower Oligocene of Australia (Queensland); Oligocene/Miocene of Mexico; Miocene of Borneo, Nigeria, and Senegal. Modern species of *Rhizophora* apparently were differentiated by the end of the Miocene. Pollen records of the IWP genera of Rhizophoraceae, *Bruguiera* and *Ceriops*, from the upper Miocene of the Marshall Islands require confirmation.⁵ Muller (1981) rejected claims of *Bruguiera* pollen from the Oligocene of England, and of *Rhizophora* pollen from the Paleocene and early Eocene of western Europe. The evidence for mangrove vegetation in western Europe consists of Eocene records of fruits of *Nypa* and hypocotyls of *Ceriops* and *Paleobruigiara*.

Juncosa and Tomlinson (1988b) have recently produced a cladogram of the genera of Rhizophoraceae, based on 45 characters, which is reproduced in fig. 20.5.

5. According to Tomlinson, Primack, and Bunt (1979), other than *Rhizophora*, members of the Rhizophoreae are animal-pollinated and do not produce abundant wind-borne pollen.

The subfamilies Macarisieae, Gynotrocheae, and Rhizophoreae are well differentiated but are paraphyletic. The basal taxa of the Macarisieae have undergone relatively little evolutionary change with respect to the characters used. This cladogram is supported by another based on 16 seed characters (Tobe and Raven 1988), except that *Crossostylis* is located closer to the base of the Gynotrocheae, and the genera of the Macarisieae are arranged differently. A phenetic analysis based on pollen characters places, incorrectly it would seem, the Macarisieae between the Gynotrocheae and Rhizophoreae (Vezev et al. 1988).

Of the terrestrial taxa of the Rhizophoraceae, the basal taxa of the Macarisieae occur in Madagascar (*Macarisia*, 7 species), West Africa (*Anopyxis*, 2 species), and northern South America (*Sterigmapetalum*, 7 species). Generic diversity in the group is concentrated in West Africa and Madagascar. The Gynotrocheae occupy primarily Southeast Asia and islands to the east, as far as Fiji. The basal taxon *Carallia* extends west to India and Madagascar, providing the only contemporary geographical connection between the Gynotrocheae and the ancestral Macarisieae (fig. 20.6). The Rhizophoreae overlap the distribution of *Carallia* extensively, with the most highly derived genus, *Rhizophora*, extending into the ACEP region.

The cladogram and modern geographical distributions of the Rhizophoraceae suggest a scenario for the history of the family, which begins with the distribution of the subfamily Macarisieae in the upper Cretaceous in a broad belt extending across much of Gondwanaland (fig. 20.7). The Gynotrocheae, represented by the basal genus *Carallia*, possibly originated from Madagascar-Indian components of the Macarisieae (presently *Macarisia*, *Dactylopetalum*, and *Cassipourea*, with *Macarisia* being closest to the base). The connection between the Gondwanan distribution of the Gynotrocheae may have been provided by the drifting of the Indian subcontinent to its present position, leaving a remnant of *Carallia* behind on Madagascar. The origin of the Rhizophoreae from the Gynotrocheae might have occurred anywhere within the range of the basal *Carallia*, but Indochina/Malesia is strongly implicated by the high diversity of Rhizophoreae there. Subsequent spread of genera to the western part of the Indian Ocean, and of *Rhizophora* to the ACEP region, would have been accomplished by aquatic dispersal, either through the Tethys connection or eastward across the Pacific, prior to the end of the Eocene, by which time *Rhizophora*-type pollen appears in the ACEP region.

Proliferation of Mangrove Taxa

Once taxa have become established within mangrove habitat, they may speciate and diversify. The total number of species per clade is directly related to the taxonomic level of endemism of the clade in mangrove habitat (fig. 20.8). Similarly, the number of species per genus is related to the extent of geographical distribution (fig. 20.9). The latter relationship arises both from the presence of allopatric populations within a broad geographical distribution and from the presence of sympatric species. For example, four species of *Avicennia* co-occur in Malaysia, two in various parts of the ACEP region. Considerable

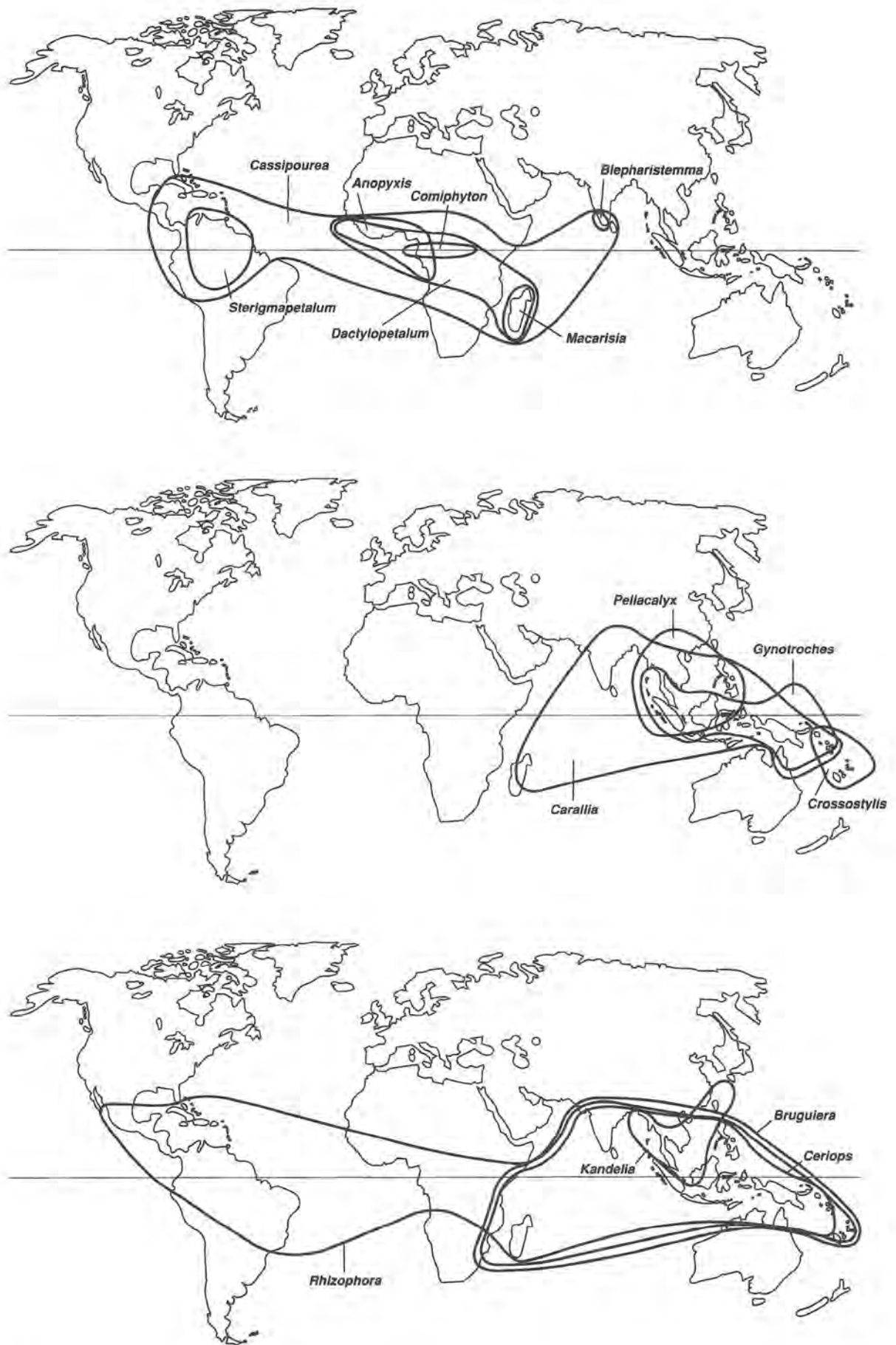


Figure 20.6 Distributions of the three tribes of the Rhizophoraceae: the Macarisiae (top), the Gynotrocheae (center), and the Rhizophoreae (bottom). The Macarisiae are the most primitive and the Rhizophoreae the most derived. (After Juncosa and Tomlinson 1988a.)

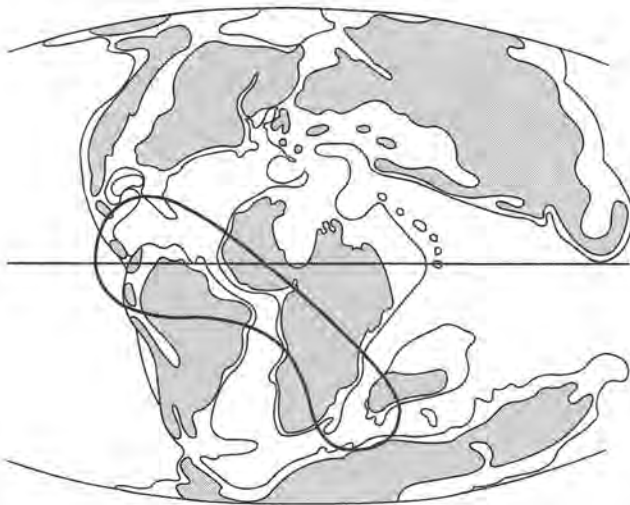


Figure 20.7 Contemporary distribution of the tribe Macariseae superimposed on a map of the earth during the Paleocene–early Eocene. Shaded areas represent land masses; lines, continental shelves.

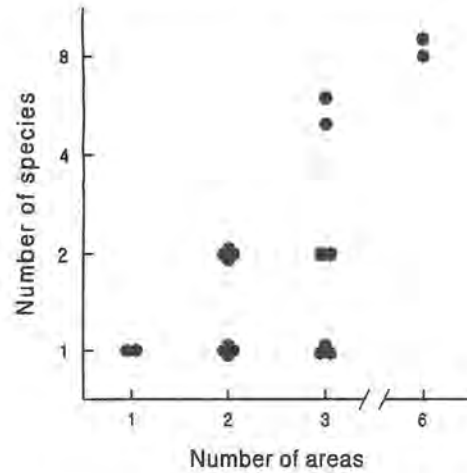


Figure 20.9 Number of species per genus of mangrove trees as a function of the number of areas (see Fig. 20.1) occupied. Also included are symbols representing the number of species of *Rhizophora* and *Avicennia* solely within the ACEP and IWP regions. (Data from table 20.1.)

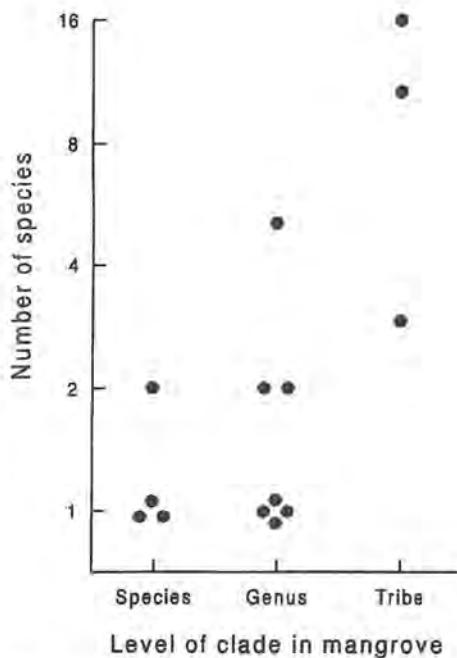


Figure 20.8 Number of species per clade of mangrove trees as a function of the taxonomic level of the clade. Each triangle represents a single clade. (Data from table 20.1.) The Rhizophoreae are considered a single mangrove clade; *Laguncularia* and *Lumnitzera* are placed in a single clade at the tribe level; *Xylocarpus* is considered to be a single species. (Tomlinson 1986.)

sympatry of species also exists within *Rhizophora*, *Bruguiera*, *Ceriops*, and *Sonneratia*. For example, *Sonneratia* contains two wide-ranging IWP species that include the ranges of three allopatric Austro-Malaysian species (fig. 20.10).

We presume that new taxa arise by allopatric speciation within mangrove habitat because of the unlikelihood

of sister taxa arising independently by parallel evolution from a more distantly related ancestor. Geographically separated sister taxa are known from *Bruguiera hainsii*, *Pemphis acidula*, *Aegialitis*, and *Camptostemon*, with most of the disjunctions occurring within Malaysia. These may represent cases of incipient or completed allopatric speciation. Allopatric models of isolation followed by secondary sympatry suggest reversible tectonic movements or cycles in climate that caused distributions to expand and contract, as might have occurred in the late Pliocene and Pleistocene (e.g., Prance 1982; Woodroffe and Grindrod 1991). Distributions of species boundaries of mangrove taxa within Malesia present a very complex picture (fig. 20.11), which suggests considerable independence of the factors affecting the distributions of each species.

Both *Avicennia* and *Rhizophora* have many species in the ACEP and IWP regions, but whether sister taxa within either genus occur within or between regions is not clear. Neither genus appears to have differentiated across the Panamanian Isthmus; *Avicennia schaueriana* and *A. bicolor* occur on opposite sides of the isthmus, but these probably are not sister taxa. *Rhizophora mangle* and *R. × harrisonii* are undifferentiated across the isthmus (Tomlinson 1986). Until phylogenetic relationships have been worked out in more detail, the geography of speciation in mangrove taxa will remain poorly understood.

CONCLUSION

We envision the origin of the ACEP-IWP diversity anomaly as the result of differences between the regions in the origin of mangrove clades and their subsequent diversification within the mangrove habitat. Extinction does not appear to have played a major role in the generation of the diversity anomaly, although the fossil record documents contractions of the ranges of taxa within each region, the extinction of *Nypa* and possibly *Wetherellia* in

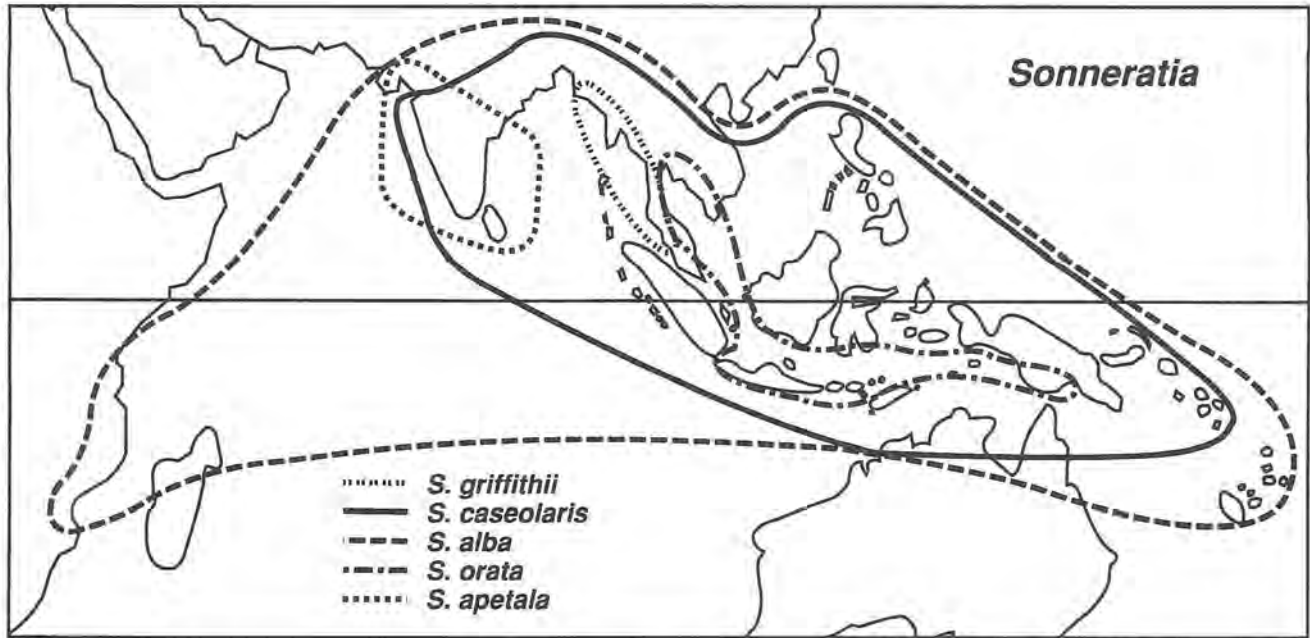


Figure 20.10 Distributions of species of the genus *Sonneratia*. (After Chapman 1970.)

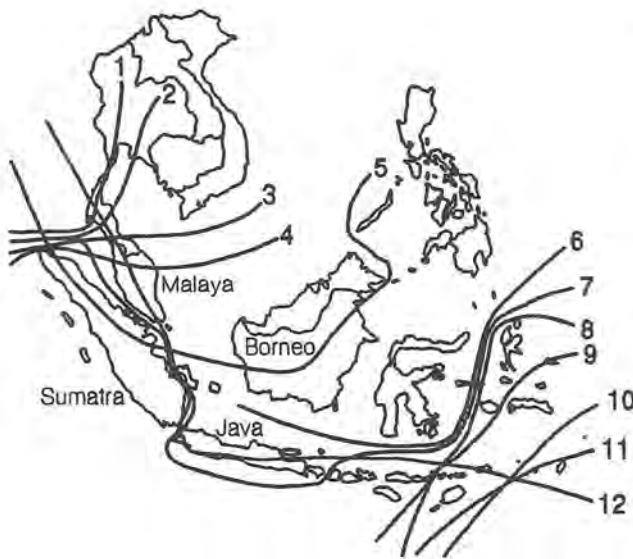


Figure 20.11 Limits to distributions of several mangrove species in Malasia: 1, *Aegialites rotundifolia* (Van Steenis 1949); 2, *Sonneratia griffithii* and *S. ovata* (Chapman 1970); 3, *Rhizophora stylosa* (Chapman 1970); 4, *Lumnitzera* spp. (Excell 1954); 5, *Kandelia candel* (Ding Hou 1958); 6, *Camptostemon philippinensis* and *C. schultzei* (Chapman 1976); 7, *Ceriops decandra* (Ding Hou 1958); 8, *Avicennia eucalyptifolia* (Chapman 1976); 9, *Aegialites annulata* (Van Steenis 1949); 10, *Rhizophora apiculata* (Chapman 1970); 11, *Lumnitzera* spp. (Excell 1954); 12, *Sonneratia ovata* (Chapman 1970).

the ACEP region, and the possibility that Southeast Asia/Malaysia is more a refugium than a center of origin. Although one cannot pinpoint the location of origin of cosmopolitan mangrove taxa (Mephram 1983a), origins since the closure of the Tethys Sea appear to have been restricted to the Indo–West Pacific region and more specifically to southeastern Asia. This raises the question of why entry into the mangrove zone and subsequent diversification did not happen more frequently in the ACEP region. It also raises the question of why clades arising prior to the closure of the Tethys connection, such as *Ceriops* and *Bruguiera*, did not extend into the heart of the ACEP region, or, if they did, why they disappeared without leaving a fossil record.

Presumably the terrestrial–mangrove transition is most likely in wet climates where a gradual transition in soil salinity exists between terrestrial and mangrove habitats, without the high salinity of the upper intertidal zone typical of arid regions (Hutchings and Saenger 1987). Southeast Asia and Malaysia are unique within the tropics in the continuous presence of extensive wet habitat since the end of the Cretaceous. Palynological and geological evidence suggests that most of the African and New World tropics were dry during the late Cretaceous (see Horrell 1990). Tropical latitudes became wetter during the early Tertiary, but the extinction of *Nypa* and the range contraction of *Pelliciera* since the Miocene suggest a marked drying trend in the ACEP region during the Neogene, at which time the ACEP and IWP regions were isolated from each other. Perhaps, then, contact between wet terrestrial vegetation and mangrove habitat was much reduced during this period, at which time diversity continued to increase in the Asian mangroves through invasion of new clades and autochthonous production of new taxa. Pre-

dictably, many more nonexclusive taxa of trees invade mangrove habitat from terrestrial habitats in the IWP region, especially Malaysia, than in the ACEP region (Saenger, Hegerl, and Davie 1983; Mepham 1983b; Mepham and Mepham 1985).

Mangrove taxa suggest a scenario for the development of diversity patterns in which elements of a diverse biota invade a stressful environment and require substantial

evolutionary modification to make the transition. Farrell and Mitter (chap. 23) and Latham and Ricklefs (chap. 26) suggest a similar scenario for latitudinal gradients of diversity in terrestrial insects and forest trees. We suggest that invasion of novel environments by clades may be responsible for a component of the general relationship observed between diversity and habitat or other environmental characteristics.