Global Ecology and Biogeography (1999) **8**, 95–115

RESEARCH ARTICLE

Origins of mangrove ecosystems and the mangrove biodiversity anomaly

AARON M. ELLISON[1]*, ELIZABETH J. FARNSWORTH[2]† and RACHEL E. MERKT[1]‡
[1]*Department of Biological Sciences, Mount Holyoke College, 50 College Street, South Hadley, MA 01075–6418, U.S.A., and* [2]*The Nature Conservancy, 55 High Street, Middletown, CT 06457, U.S.A.*

ABSTRACT

1. Mangrove species richness declines dramatically from a maximum in the Indo-West Pacific (IWP) to a minimum in the Caribbean and Western Atlantic. Explaining this 'anomalous' biogeographic pattern has been a focus of discussion for most of this century.
2. Two hypotheses have been put forward to explain the mangrove biodiversity anomaly. The 'centre-of-origin hypothesis' asserts that all mangrove taxa originated in the IWP and subsequently dispersed to other parts of the world. The 'vicariance hypothesis' asserts that mangrove taxa evolved around the Tethys Sea during the Late Cretaceous, and regional species diversity resulted from *in situ* diversification after continental drift.
3. Five lines of evidence are used to test between these two hypotheses. First, we review the mangrove fossil record. Second, we compare modern and fossil distributions of mangroves and eight genera of gastropods that show high fidelity to the mangrove environment. Third, we describe species-area relationships of mangroves and associated gastropods with respect to area of available habitat. Fourth, we analyse patterns of nestedness of individual plant and gastropod communities in mangrove forests. Fifth, we analyse patterns of nestedness of individual plant and gastropod species.
4. All five lines of evidence support the vicariance hypothesis. The first occurrences in the fossil record of most mangrove genera and many genera of gastropods associated with mangrove forests appear around the Tethys Sea from the Late Cretaceous through the Early Tertiary. Globally, species richness in any given mangrove forest is tightly correlated with available area. Patterns of nestedness at the community and species-level both point towards three independent regions of diversification of mangrove ecosystems: South-east Asia, the Caribbean and Eastern Pacific, and the Indian Ocean region.

Key words. Centre of origin, diversity, fossil record, gastropods, mangroves, nestedness, species-area relationship, vicariance.

INTRODUCTION

Mangrove forests occur world-wide on tropical, sheltered shores (Chapman, 1976; Tomlinson, 1986). These forests consist of a group of about seventy taxonomically diverse, tree, shrub, and fern species (in twenty-seven genera, twenty families, and nine orders) that share a suite of convergent adaptations to saline, anoxic habitats (e.g. Tomlinson, 1986; Stewart & Popp, 1987; Ball, 1988; Duke *et al.,* 1998). These well-studied adaptations – aerial root systems, succulent, sclerophyllous leaves, and viviparous seedlings – together constitute one of the most convincing cases for convergent evolution among diverse taxa in response to similar environmental constraints (e.g. Tomlinson, 1986; Farnsworth & Farrant, 1998). Several investigators have predicted that species diversity in habitats with similar physical and environmental characteristics that occur in different parts of the world

---

* Corresponding author. E-mail: aellison@MtHolyoke.edu.
† Current address: Department of Biological Sciences, Smith College, Northampton, MA 01063, USA.
‡ Current address: Department of Marine Science, University of South Florida, Saint Petersburg, FL 33620, USA.

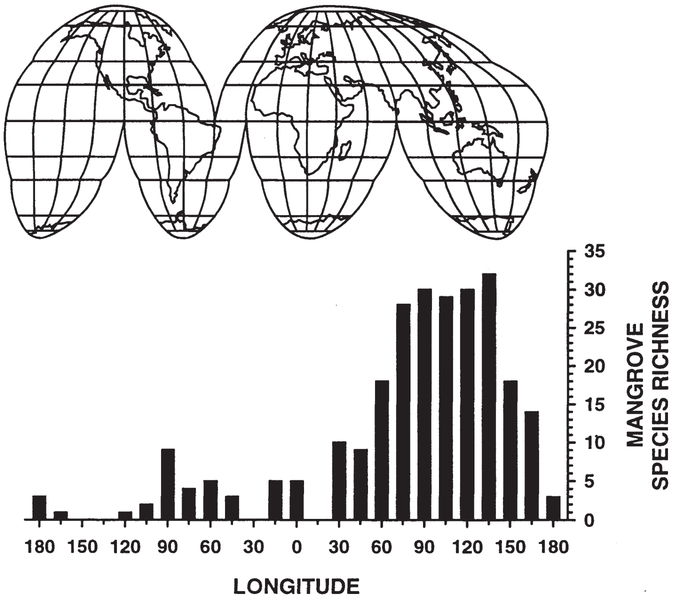

Fig. 1. Species richness of mangroves as a function of longitude (in 15° increments). Data compiled from Chapman (1976), Tomlinson (1986), Duke (1992), Ricklefs & Latham (1993), and Duke *et al.* (1998).

should support similar numbers of species, provided that these local communities have developed independently (Recher, 1969; Cody, 1975; Orians & Paine, 1983; Ricklefs, 1987). However, species richness of trees, shrubs, and ferns in mangrove forests is an order of magnitude higher in the Indo-West Pacific (IWP) than it is in the Atlantic, Caribbean and Eastern Pacific (ACEP) region (Fig. 1). This 'anomalous' (*sensu* Ricklefs & Latham, 1993) IWP-to-ACEP decline in species richness has been a focus of discussion for much of the twentieth century (e.g. Schimper, 1903; van Steenis, 1962; Aubréville, 1964; Chapman, 1976; McCoy & Heck, 1976; Mepham, 1983; Tomlinson, 1986; Ricklefs & Latham, 1993; Duke, 1995; Duke *et al.*, 1998). In this paper, we propose an explanation for this diversity anomaly based on a thorough review of the mangrove fossil record, correlated distributions of mangrove-associated invertebrates, and statistical analyses of biogeographic patterns of mangrove flora and fauna.

Two general hypotheses have been suggested to explain the modern distribution of mangrove forests and the IWP-to-ACEP decline in species richness (summarized from Tomlinson, 1986; Ricklefs & Latham, 1993). There is general agreement that mangrove ecosystems first appeared in the Late Cretaceous – Early Tertiary on the shores of the Tethys Sea, although most extant mangrove genera do not extend all the way back through the Tertiary. Van Steenis (1962) suggested that modern genera arose on the eastern shores of the Tethys Sea, diversified in what is now the IWP, and dispersed eastward across the Pacific Ocean into the ACEP region prior to the closure of the Panamanian isthmus ≈3 million years ago (Mya). Tomlinson (1986), supporting earlier interpretations of Aubréville (1964) and Chapman (1976), suggested that mangroves colonized the ACEP by moving from the eastern Tethys westward into the Atlantic (see also Dodd *et al.*, 1998; Duke *et al.*, 1998). The modern elaboration of this 'centre-of-origin hypothesis' is that 'throughout most of the Tertiary, conditions for the invasion of mangrove habitat occurred primarily in south-east Asia/Malaysia and, to a lesser extent, East Africa/Madagascar' (Ricklefs & Latham, 1993: 215–216), restricting most mangrove taxa to the IWP because of poor dispersal abilities and the closure of the Tethys connection to the Atlantic by the mid-Tertiary. Ricklefs & Latham (1993) allowed for the possibility that south-east Asia/Malaysia may be more of a refugium for mangroves than a centre of origin, but concluded from a brief review of the mangrove fossil record that there was inadequate information to resolve this issue.

In contrast, McCoy & Heck (1976) argued that the peak of mangrove species richness does not correspond to the centre of origin of mangrove ecosystems. Rather, they hypothesized that most modern mangrove genera arose on the shores of the Tethys Sea, and that subsequent continental drift resulted in disjunct distributions of species within genera. *In situ* diversification of these genera since the late Tertiary then led to the modern-day mangrove diversity anomaly. Tomlinson (1986) pointed out that this 'vicariance hypothesis' was based on analysis of the distribution of mangrove genera, while analysis of diversity patterns at the species level raised additional problems. He concluded that a consistently applicable hypothesis accounting for the distribution of modern mangrove species was yet to be developed. Similarly, Duke (Duke, 1995; Duke *et al*., 1998) asserted the importance of tectonic events and continental drift in influencing the present-day distribution of mangrove species, but found little evidence that these forces could explain discontinuous distributions of seven widely occurring ACEP species. Our analyses support McCoy & Heck's (1976) vicariance hypothesis, and because our analysis is conducted at both generic and species levels, we provide a consistent account of the importance of vicariance in the development of modern-day mangrove assemblages. We use the approach suggested by McCoy & Heck (1976), with additional analyses of global patterns of geographical nestedness of whole assemblages and individual species, to distinguish between these two hypotheses.

METHODS

McCoy & Heck (1976) suggested three lines of investigation that could lead to inferential tests between the centre-of-origin and the vicariance hypotheses (Table 1). First, a more detailed study of the mangrove fossil record is needed. The centre-of-origin hypothesis would be supported if the oldest mangrove fossils were to be found in the IWP (the eastern Tethys), with later occurrences paralleling predicted dispersal routes. Alternatively, the vicariance hypothesis would be supported if the oldest mangrove fossils were found uniformly around the Tethys (and elsewhere), with later occurrences illustrating independent origins of mangrove taxa coincident with available area for colonization and diversification. Because there are no comprehensive compilations of the fossil record of mangroves in the literature (summaries in McCoy & Heck, 1976, Plaziat *et al.,* 1983, Tomlinson, 1986 and Ricklefs & Latham, 1993 include $<10\%$ of known occurrences), we begin our analysis with a thorough review of the mangrove fossil record and relate it to continental positions during the Tertiary.

Second, McCoy & Heck suggested that the relationship between mangrove species richness and area of available habitat should be examined carefully, to determine if areas with relatively large mangrove habitat, as well as geographical isolation leading to rapid reproductive isolation and potential speciation, in fact have higher species richness of both mangroves and closely associated fauna. The two hypotheses, centre-of-origin and vicariance, yield different predictions regarding the relationship of mangroves and available area. If mangrove ecosystems originated in a single centre of origin, then species richness of extant mangrove forests should be negatively correlated with distance from that centre of origin, not available area (unless available area is also tightly correlated with distance from the centre of origin). In contrast, if mangroves speciated *in situ*, then species richness should be positively correlated with available area, after removal of any covariance between distance from the proposed centre of origin and available area. While Ricklefs & Latham (1993) estimated that similar areas of mangrove habitat occur in the IWP and ACEP (using data from Saenger *et al.,* 1983), more recent data (Spalding *et al.,* 1997) suggest different conclusions and necessitate a re-evaluation of the species-area relationship for mangroves. We conduct this re-evaluation.

Third, distributions of faunal taxa that are closely associated with mangroves should show patterns either concordant or discordant with mangroves, depending on whether or not the fauna shared a common location of origin with the mangroves. McCoy & Heck (1976) used the parallel diversity anomalies of coral reefs and seagrass beds, both of which occur adjacent to mangrove forests, to argue for the vicariance hypothesis, but did not examine mangrove-associated fauna. If mangroves and their associated fauna diversified at similar rates or moved in roughly parallel ways, we would expect to see similarities between the diversity anomalies of both groups. We analyse modern and fossil distributions of eight gastropod genera in

Table 1. Predictions of the centre-of-origin and vicariance hypotheses as explanations for the mangrove diversity anomaly

Centre-of-origin	Vicariance
Earliest mangrove fossils in IWP; later occurrences parallel hypothesized dispersal tracks	Earliest mangrove fossils widespread, perhaps geographically restricted to Tethys. Later occurrences represent independent origins of mangrove taxa coincident with available habitat area.
Mangrove fauna independent of, or weakly dependent on, mangrove flora	Mangrove fauna show similar diversity anomalies
Generic ages of mangrove flora and fauna discordant or weakly concordant	Generic ages of mangrove flora and fauna regionally concordant
Loose species richness – available area relationship	Tight species richness – available area relationship
Significant nestedness of species due to colonization	Significant nestedness of species due to extinction *or* few nested patterns

three unrelated families that show a high degree of fidelity to mangrove ecosystems, and examine the likelihood that these groups colonized geographical regions in parallel. We also analyse species-available area relationships for these gastropods. Available phylogenies of mangroves and associated gastropods are discussed, but there are no data on rates of evolution in these groups.

In addition to using the three approaches suggested by McCoy & Heck (1976), we also examine species distributions of mangrove flora and associated fauna for patterns of geographical nestedness. Significant geographical nestedness of species could result from either a centre of origin followed by colonization of farther-flung areas by a subset of the species (Darlington, 1957; Cook & Quinn, 1995), or from *in situ* extinctions of taxa following vicariance events (Patterson, 1990). In conjunction with fossil data, we use nestedness statistics to infer the relative importance of colonization or extinction events in determining overall nested (or non-nested) distribution patterns of mangrove flora and fauna.

Atmar & Patterson (1993) developed a test statistic, the 'matrix nestedness temperature' to assess community-wide nestedness. Given a site × species matrix, where cell entries are 1 if the species is present at a site and 0 if it is absent, one first maximally packs the matrix by ordering sites (rows) from most speciose to least speciose, and by ordering species (columns) from those which occur at the most sites to those which occur at the fewest sites. Such a matrix is said to be perfectly nested if the joint pattern of species presence and site richness forms a triangle, with all presences above the top-right-to-lower-left diagonal and all absences below this diagonal of the matrix. Most communities show some divergence from perfect nestedness, and Atmar & Patterson's (1993) nestedness temperature measures this divergence on a scale from 0 (perfectly nested) to 100 (totally random); this scale is analogous to systems that are ordered (cold) or maximally entropic (hot). Atmar & Patterson (1993, 1995) provide details on computing matrix nestedness temperatures. Statistical significance of the matrix temperature is estimated using Monte Carlo techniques (Atmar & Patterson, 1995). All calculations were done using software developed by Atmar & Patterson (1995).

We analysed each community type – mangroves, all gastropods, each individual gastropod genus – for overall nestedness in order to address the question: are *entire communities* nested with respect to distance from the observed peak location of mangrove or gastropod species richness? While measures of overall nestedness have been developed principally for comparisons among islands within archipelagos, or for island-mainland comparisons (Atmar & Patterson, 1993), we used longitude as our metric of location. In other words, instead of constructing a site × species matrix, we constructed a longitude × species matrix. Because packing the matrix prior to computation of the nestedness temperature does not preserve the ordering of sites by their distance from the location of maximal species richness, examination of the new ordering of sites provides additional information on potentially related sites.

Simberloff & Martin (1991) argued that nestedness should be the rule, not the exception, in island assemblages, and this expectation has been born out both in island and in mainland communities (e.g. Worthen *et al.,* 1996; Wright *et al*., 1998). Consequently, community-level nestedness statistics may not be completely informative (Simberloff & Martin, 1991; but see Worthen, 1996). Simberloff & Martin (1991) suggested testing for geographical nestedness of individual species as a further check on patterns of community-wide nestedness identified with composite statistics such as those of Atmar & Patterson (1993, 1995). We therefore analysed each species individually to determine which species show non-nested distributions with respect to longitude. Following Simberloff & Martin (1991), we used the Wilcoxon-Mann–Whitney rank sum test to examine each species for deviation from expectation of nestedness. Each species was ordered with respect to distance (degrees of longitude) from the location of peak species richness of mangrove flora or fauna. If a given species has a nested distribution, the vector of its presences and absences should be a string of presences followed by a string of absences (e.g. [1, 1, 1, . . ., 1, 0, 0, 0, . . ., 0]). Deviations from nestedness results in a less predictable vector of presences and absences (e.g. [1, 0, 1, 1, 0, 0, 0, 1, 0, 1, 1, . . .,]). We used StatXact (v. 3.0) to compute exact *P*-values for the Wilcoxon-Mann–Whitney rank sum test (Cytel Software Corp. 1995).

RESULTS

Biogeography of mangroves

Modern distribution of mangroves

The distribution patterns of modern mangrove species have been reviewed extensively (e.g. van Steenis, 1962; Chapman, 1976; Tomlinson, 1986; Ricklefs & Latham, 1993; Duke *et al*., 1998). Rather than recapitulate these reviews, we draw attention to several key details. All mangroves are restricted to tropical climates where the average monthly minimum air temperature is ≥ 20 °C (Chapman, 1976). The winter 20 °C seawater isotherm generally limits the poleward extension of mangroves, although prevailing warm currents and broader tolerance of environmental extremes allow the extension of *Avicennia marina* (Forsk.) Vierh. southward to the north island of New Zealand (Duke *et al*., 1998). Overall species richness of mangroves declines from a peak of about thirty species (per 15° longitude) in South-east Asia to < 5 in the Caribbean (Fig. 1). This distribution is unimodal ($P[H_0$: distribution is unimodal$] = 0.16$, using the test for multimodality described by Efron & Tibshirani, 1993), with a peak of species richness at 99°E.

Only the mangrove fern, *Acrostichum aureum* L., occurs in both the eastern and western hemispheres. Three genera (*Acrostichum, Avicennia, Rhizophora*) occur in both hemispheres, and all ACEP families except the Pelliceriaceae can also be found in the IWP. *Bruguiera gymnorrhiza* (L.) Lamk. has the broadest distribution, ranging from East Africa to Samoa (Chapman, 1976; Tomlinson, 1986). *Rhizophora mangle* L. ranges from West Africa to the Pacific coast of South America, and if not distinct from *R. samoensis* (Hochr.) Salvoza (Tomlinson, 1986), would extend westward to New Caledonia and Fiji. Neotropical endemics include *Avicennia bicolor* Standley (Pacific Costa Rica to Columbia), *Avicennia schaueriana* Stapf & Leechman ex Moldenke (Lesser Antilles to Guyana) and *Pelliceria rhizophorae* Triana & Planchon (Nicaragua to Columbia). As a proportion of the total mangrove flora, palaeotropical endemics are more numerous, particularly in the genus *Avicennia* (Duke, 1991). Other notable palaeotropical species with restricted or discontinuous distributions include *Bruguiera hainesii* C. G. Rogers (discontinuous between western Malaysia and New Guinea), *Aegialitis rotundifolia* Roxburgh, *Heritiera fomes* Buch.-Ham., and *Sonneratia griffithi* Kurz (endemic to the Bay of Bengal from eastern India southward to Burma), and *Pemphis acidula* Forst. (recorded from East Africa and eastern Malaysia, but not found in between) (Tomlinson, 1986).

The fossil record of mangroves

The fossil record of mangroves, consisting of both macrofossils (leaves, wood, flowers, and fruit) and microfossils (pollen grains) is surprisingly rich (*contra* Plaziat *et al*., 1983; Ricklefs & Latham, 1993). The data are summarized in Table 2, and temporal patterns in mangrove fossil distribution throughout the Tertiary are illustrated in Fig. 2. These data illustrate that few mangrove genera arose in the IWP, moreover, they were not generally restricted to the eastern shores of the Tethys. Rather, most genera evolved in the Late Cretaceous/Early Tertiary around the Tethys Sea, and were widely distributed by the Late Eocene (Fig. 2). Because all mangrove genera had evolved by the end of the Tertiary, and continental positions have not changed appreciably during the Quaternary, we focus

Table 2. The fossil record of mangroves. Genera marked with an asterisk (*) are represented by macrofossils (leaves, wood, flowers, fruits). Unmarked genera are represented by fossil pollen

Epoch	Genus	Location	Reference
Upper Cretaceous	*Nypa*	Bengal Basin	Thanikaimoni (1987)
		Borneo	Germeraad *et al.* (1968)
		Sarawak	Germeraad *et al.* (1968)
		Nigeria	Germeraad *et al.* (1968)
		Cameroon	Salard-Cheboldaeff (1981)
		Venezuela	Germeraad *et al.* (1968)
	*Palaeowetherellia**	Egypt	Mazer & Tiffney (1982)
Palaeocene	*Nypa**	Brazil	Dolianiti (1955)
		S. Australia	Cookson & Eisenack (1967)
		India	Thanikaimoni (1987)
		Cameroon	Salard-Cheboldaeff (1981)
	Rhizophora	India	Thanikaimoni (1987)
	Sonneratia	France	Graus-Cavagnetto *et al.* (1988)
Lower Eocene	*Nypa**	India	Prakash (1960); Thanikaimoni (1987)
		S. Australia	Stover & Partridge (1973); Kemp (1978)
		Cameroon	Salard-Cheboldaeff (1981)
		France	Haseldonckx (1973); Cavagnetto *et al.* (1980); Gruas-Cavagnetto *et al.* (1988)
		Spain	Haseldonckx (1973)
	Rhizophora	India	Prakash (1960)
		France	Gruas-Cavagnetto *et al.* (1988)
	Bruguiera	France	Cavagnetto *et al.* (1980)
	*Sonneratia**	India	Prakash (1960); Thanikaimoni (1987)
	Avicennia	France	Gruas-Cavagnetto *et al.* (1988)
	Pelliceria	France	Gruas-Cavagnetto *et al.* (1988)
		Cameroon	Salard-Cheboldaeff (1981)
		Texas	Elsik (1974)
	*Wetherellia**	London	Mazer & Tiffney (1982)
		Virginia	Mazer & Tiffney (1982)
		Germany	Mazer & Tiffney (1982)
	*Palaeowetherellia**	London	Mazer & Tiffney (1982)
		Virginia	Mazer & Tiffney (1982)
	Acrostichum	France	Cavagnetto *et al.* (1980)
Middle Eocene	*Nypa**	Borneo	Lakhanpal (1952); Muller (1964); Brande & Prakash (1986)
		London	Chandler (1951); Collinson & Hooker (1987)
		Belgium	Collinson & Hooker (1987)
		Egypt	Lakhanpal (1952)
		Texas	Westage & Gee (1990)
		Ukraine	Lakhanpal (1952)
		S. Australia	Stover & Partridge (1973)
	Brownlowia	Borneo	Muller (1964); Brande & Prakash (1986)
	Rhizophora	Borneo	Muller (1964); Brande & Prakash (1986)
		Senegal	Medus (1975)
		Gabon	Medus (1975)
		Panamá	Graham (1985)
		Surinam	Medus (1975)
	*Palaeobruguiera**	London	Chandler (1951); Collinson & Hooker (1987)
	*Ceriops**	London	Chandler (1951); Collinson & Hooker (1987)
	*Kandelia**	Alaska	Wolfe (1972, 1977)
	Pelliciera	Jamaica	Graham (1993, 1994)
		Panamá	Graham (1985)

[*continued*]

Table 2. *Continued*

Epoch	Genus	Location	Reference
	Lumnitzera	Sumatra	Brande & Prakash (1986)
	Acrostichum	London	Collinson & Hooker (1987)
		Texas	Westage & Gee (1990)
	*(Palaeo)Wetherellia**	London	Collinson & Hooker (1987)
	Barringtonia	Alaska	Wolfe (1972, 1977)
	*Sonneratia**	Libya	Muller (1978)
Upper Eocene	*Nypa**	India	Thanikaimoni (1987)
		W. Australia	Churchill (1973)
		Hungary	Kedves (1969)
	Rhizophora	India	Thanikaimoni (1987)
		W. Australia	Churchill (1973)
		Hungary	Kedves (1969)
	*Bruguiera**	S. England	Chandler (1964)
	Sonneratia	India	Thanikaimoni (1987)
	Avicennia	W. Australia	Churchill (1973)
	Barringtonia	Hungary	Kedves (1969)
	*Acrostichum**	S. England	Chandler (1964)
Oligocene	*Nypa*	Borneo	Muller (1964)
	Brownlowia	Borneo	Muller (1964)
	Rhizophora	Borneo	Muller (1964)
		New Guinea	Kuyl *et al.* (1955)
		Senegal	Medus (1975)
		Nigeria	Kuyl *et al.* (1955)
		Br. Guiana	van der Hammen & Wymstra (1964); Wijmstra (1968)
		México	Langenhem *et al.* (1967)
		Puerto Rico	Graham & Jarzen (1969)
	Bruguiera	Isle of Wight	Machin (1971)
	Pelliciera	Br. Guiana	van der Hammen & Wymstra (1964); Wijmstra (1968)
		México	Langenheim *et al.* (1967)
		Puerto Rico	Graham & Jarzen (1969)
Lower Miocene	*Avicennia*	Mediterranean	Thanikaimoni (1987)
	Nypa	Borneo	Muller (1964)
	Brownlowia	Borneo	Muller (1964)
	Rhizophora	Borneo	Muller (1964)
		New Guinea	Kuyl *et al.* (1955)
		Nigeria	Kuyl *et al.* (1955)
		British Guiana	van der Hammen & Wymstra (1964)
		Venezuela	Kuyl *et al.* (1955)
	Sonneratia	Borneo	Muller (1964)
Middle Miocene	*Nypa*	India	Lakhanpal (1952); Thanikaimoni (1987)
	Rhizophora	Burma	Thanikaimoni (1987)
		India	Thanikaimoni (1987)
		Senegal	Medus (1975)
		Pacific Islands†	Leopold (1969)
		Costa Rica	Graham (1987)
		Panamá	Graham (1988a, 1988b, 1989)
	Sonneratia	Burma	Thanikaimoni (1987)
		Java	Brande & Prakash (1986)
		India	Thanikaimoni (1987)
		Japan	Thanikaimoni (1987)
		Pacific Islands†	Leopold (1969)
	Avicennia	Pacific Islands†	Leopold (1969)

[*continued*]

Table 2. *Continued*

Epoch	Genus	Location	Reference
	Bruguiera	Japan	Thanikaimoni (1987)
		Pacific Islands†	Leopold (1969)
	Ceriops	Pacific Islands†	Leopold (1969)
	Pelliciera	Brazil	Wijmstra (1968)
		Venezuela	Wijmstra (1968)
		Columbia	Wijmstra (1968)
		Panamá	Graham (1988a, 1988b, 1989)
	Excoecaria	Japan	Thanikaimoni (1987)
Upper Miocene	*Nypa*	Borneo	Muller (1964)
	Brownlowia	Borneo	Muller (1964)
	Rhizophora	Borneo	Muller (1964)
		New Guinea	Kuyl *et al.* (1955)
		Nigeria	Kuyl *et al.* (1955)
		Venezuela	Kuyl *et al.* (1955)
		Panamá	Graham (1991a, 1991b, 1991c)
		Mexico	Graham (1976)
	Sonneratia	Borneo	Muller (1964)
	Avicennia	Borneo	Muller (1964)
		Mexico	Graham (1976)
Pliocene	*Nypa*	Borneo	Muller (1964)
	Rhizophora	Borneo	Muller (1964)
		New Guinea	Kuyl *et al.* (1955)
		Nigeria	Kuyl *et al.* (1955)
		Venezuela	Kuyl *et al.* (1955)
		Guatemala	Graham (1998)
	Pelliceria	Costa Rica	Graham & Dilcher (1998)
	Brownlowia	Borneo	Muller (1964)
	Sonneratia	Borneo	Muller (1964)
	Avicennia	Borneo	Muller (1964)
		British Guiana	van der Hammen & Wymstra (1964)
	Acrostichum	Guatemala	Graham (1998)

† Pacific Islands refers to Eniwetok Atoll, Bikini Atoll and the Marshall islands.

our attention on the Tertiary fossil record of mangroves.

Fossil record of modern mangrove genera

The mangrove palm *Nypa* is the earliest of the modern mangrove genera to appear in the fossil record. Late Cretaceous and Palaeocene records of *Nypa* are uncommon (Table 2). Late Cretaceous (Maastrichtian) records of *Nypa* are all fossil pollen (Germeraad *et al.*, 1968; Salard-Cheboldaeff, 1981; Thanikaimoni, 1987). In the Maastrichtian of Cameroon, *Nypa*-type pollen comprises 20–25% of all pollen preserved in the samples studied by Salard-Cheboldaeff (1981), indicating widespread swamp development. Dolianiti (1955) reported *Nypa* fruits from the Palaeocene of Pernambuco, Brazil. Fossil fruits and seeds of *Nypa* are widespread in Eocene deposits throughout Eurasia (southern England, Belgium, France, northern Italy, southern Poland, northern Hungary, western Russia, Borneo), Africa (western Senegal, Egypt), and the Americas (Texas, Brazil) (Tralau, 1964; Table 2). On morphological grounds, Tralau (1964) assigned all known fossil fruits and pollen to *Nypa* aff. *fruticans*, as they 'appear to be identical with the fruits and seeds of the only living species of *Nypa*' (Tralau, 1964: 21), *N. fruticans* (Thunb.) Wurmb. *Nypa* disappears from South America, Africa, and Australia by the Mid- to Late Eocene, an event associated with increased aridity and seasonality (Germeraad *et al.,* 1968; Stover & Partridge, 1973). Fossil occurrences of *Nypa* since the Miocene are restricted to South-east Asia (Table 2).

Four exclusively mangrove genera – *Bruguiera, Ceriops, Kandelia, Rhizophora* – occur in the family

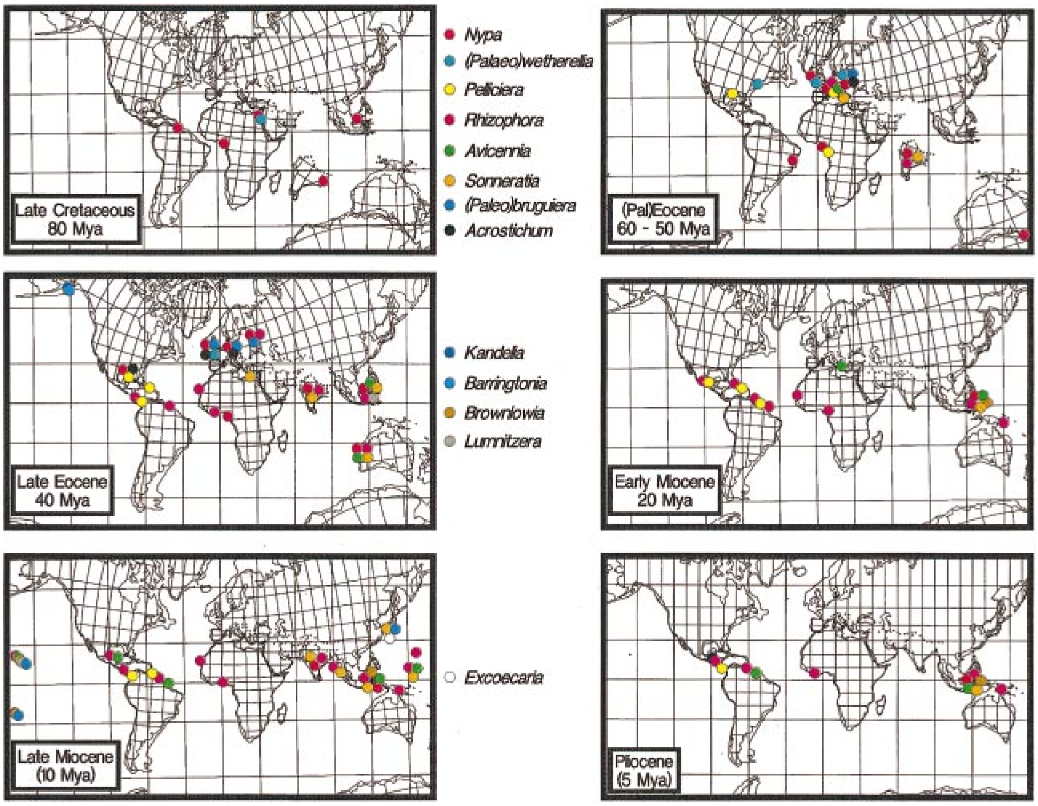

Fig. 2. Tertiary distribution of mangroves, superimposed on contemporaneous positions of the continental land masses. Data sources given in Table 2. Maps of continental positions redrawn from Smith & Briden (1977).

Rhizophoraceae, and this family is represented in all modern mangrove forests. Fossil fruits of *Bruguiera* (and its extinct relative, *Palaeobruguiera*) and *Ceriops* occur in the Middle Eocene London Clays (Chandler, 1951; Collinson, 1983; Collinson & Hooker, 1987). Cavagnetto *et al.* (1980) identified a 'fossil mangrove soil' (palaeosol) in the Ypresian (lower-most Eocene) Soissonaís lignite at Verzenay, France, in which *Brugueira*-type pollen occurred in the lowest horizon. *Nypa* pollen and *Acrostichum* spores were also present in this palaeosol, although the identification of fossil *Acrostichum* spores is considered difficult (Frederiksen, 1985). *Bruguiera* pollen persists into the Oligocene-aged beds of the Isle of Wight (Machin, 1971). *Ceriops* occurs throughout the Miocene of Guam, Fiji, and Eniwetok (Leopold, 1969). Its range has contracted in a westward direction by at least 20° of longitude since the Miocene (Leopold, 1969). *Kandelia* fruits (propagules) occur in the late Middle Eocene of Alaska, along with the fruits of the mangrove associate *Barringtonia* and numerous genera characteristic of modern Malaysian tropical lowland forests (Wolfe, 1972, 1977; Fig. 2). Pollen of *Rhizophora* is produced abundantly, and its morphological distinctiveness has led to its recognition as a guide fossil indicative of humid tropical lowlands and wetlands (Muller & Caratini, 1977; see also Germeraad *et al.*, 1968; Thanikaimoni, 1987). However, it is virtually impossible to distinguish among *Rhizophora* species on the basis of fossil pollen alone (Muller & Caratini, 1977). The earliest fossil occurrence of *Rhizophora* pollen is in the Palaeocene of India (Thanikaimoni, 1987), but it is abundant in the Eocene of Eurasia (France, Hungary, India, Borneo), Africa (Senegal, Gabon, Surinam), western Australia and the Americas (British Guiana, Panama) (Table 2). *Rhizophora* pollen continues to be abundant in fossil deposits world-wide throughout the Miocene (Table 2, Fig. 2). Muller &

Caratini (1977) suggested that *Rhizophora* did not differentiate into modern species prior to the Oligocene, and posited independent radiations in the ACEP during the Oligo-Miocene and in the IWP during the Miocene.

The ACEP endemic genus *Pelliceria* (Pelliceriaceae) was widespread from the Palaeocene through the Miocene; its range extended from the Gulf Coast of the USA to West Africa, and northwards into Europe (Graham, 1977, 1995; Frederiksen, 1985; Graham & Dilcher, 1998; Fig. 2). Like *Rhizophora*, the pollen of *Pelliceria* is very distinctive and easily recognized (Graham, 1977). This genus may have locally dominated its habitat; Elsik (1974) described it as 'characteristic' of the Lower to Middle Eocene of the Gulf Coast of Texas, and it was abundant in the Eocene desposits in Cameroon (Salard-Cheboldaeff, 1981). *Pelliceria* pollen is common in the Oligocene to Lower Miocene of British Guiana (van der Hammen & Wymstra, 1964), but disappears from there by the Pliocene. Graham (1977, 1995) documents similar dramatic range contractions of *Pelliceria* throughout the Caribbean during the Tertiary.

The IWP endemic genus, *Sonneratia*, appears to have colonized south-east Asia from the west on the northward migrating Indian subcontinent (Fig. 2). Muller (1978) reviewed the fossil record of this genus, and confirmed pollen records from the uppermost Eocene through the Miocene of south-east Asia and the Late Miocene of the Pacific Islands of Eniwetok, Palau, and Fiji. Fossil wood resembling modern *Sonneratia* is known from the Middle Eocene of Libya and India (Mahabalé & Deshpande, 1955; Ramanujam, 1956; Prakash, 1960; Muller, 1978; Table 2). Based on available data, Muller (1978) concluded that *Sonneratia* originated in the western Tethyan region in the Early Eocene, but that the modern floral and pollen characters did not evolve until the Oligocene. Muller (1978) considered that the modern species radiated in the IWP during the Late Oligocene and Early Miocene. This conclusion contrasts with the apparent occurrence of fossil pollen clearly assignable to *Sonneratia* from the Palaeocene of France (Gruas-Cavagnetto *et al.,* 1988). As with *Ceriops*, the range of *Sonneratia* throughout the Pacific has contracted dramatically in a westward direction since the Miocene (Leopold, 1969). The fossil record of *Sonneratia* species indicates that *S. alba* J. Smith is the youngest, yet it extends throughout the modern range of the genus. On the other hand, the oldest fossil species, *S. caseolaris* (L.) Engler has the narrowest modern distribution (Muller, 1978).

Avicennia pollen occurs rarely until the Miocene. The earliest reported occurrence is from the Early Eocene of France (Gruas-Cavagnetto *et al*., 1988), but by the Miocene it is widespread throughout the IWP (Leopold, 1969; Thanikaimoni, 1987; Table 2; Fig. 2). Records of *Avicennia* in the ACEP do not begin until the Late Miocene (van der Hammen & Wymstra, 1964). Other modern mangrove genera are similarly rare in the fossil record. *Lumnitzera* is known in the palaeobotanical record only from pollen of the Middle Eocene of Sumatra (Brande & Prakash, 1986), and *Excoecaria* occurs in the Middle Miocene of Japan (Thanikaimoni, 1987). Fossil spores of the mangrove fern genus *Acrostichum* occur in the Early Eocene of France (Cavagnetto *et al*., 1980), the Middle Eocene London Clay (Collinson & Hooker, 1987), throughout the middle Eocene Gulf Coast of Texas (Westage & Gee, 1990), and from the Early Eocene through the Pliocene in the Caribbean (Graham, 1995). Fossil leaves (pinnae) of *Acrostichum* were described from the Late Eocene of southern England (Chandler, 1964).

Fossil record of extinct 'mangroves'

Several fossil taxa are thought to have occurred in habitats that now support mangrove forests: tropical, coastal swamps. For example, Frederiksen (1985) considers the fossil palynomorphs within the *Brevitricopites* group (which includes *B. variabilis* González-Guzmán, *Retribrevitricopites triangulatus* van Hoeken-Klinkenberg*, R. catatumbus* González-Guzmán*,* and *R. increatus* González-Guzmán) to have inhabited the *Rhizophora* 'niche' from the Palaeocene to the mid-Eocene of Columbia (see also González-Guzmán, 1967; Graham, 1995). These Columbian strata also have abundant fossil pollen of the palm *Proxapertites operculatus* (van der Hammen) van der Hammen, which Frederiksen (1985) places near *Nypa*. Supporting evidence for the mangrove affinities of these taxa are the co-occurrence of *Nypa* with *Proxapertites* pollen in the Eocene of Cameroon (Salard-Cheboldaeff, 1981), and the co-occurrence of *Retribrevitricopites triangulatus* with *Rhizophora* pollen in the Eocene of Nigeria (Frederiksen, 1985).

Mazer & Tiffney (1982) discussed the ecology and systematics of *Wetherellia* and *Palaeowetherellia*. Fruits and seeds of *Wetherellia* co-occur with *Nypa* in the Early Eocene London Clay flora of southern England (Chandler, 1964), and this is the second-most abundant taxon after *Nypa*. The closely related *Palaeowetherellia* was described from the Eocene and possibly Late

Cretaceous deposits of northern Egypt (Chandler, 1954). In these cases, as in the North American Eocene sediments of southern Maryland and Virginia, both genera occur in what were coastal, sandy or muddy, depositional environments, which Mazer & Tiffney (1982: 322) consider 'coastal or mangrove environment[s].' There are no modern analogues to either of these genera. *Palaeowetherellia* and *Wetherellia* share many characteristics with modern Euphorbiaceae and Meliaceae; genera within both of these families occur in modern mangrove forests.

Species-area relationships of mangroves

Based on a combination of data derived from remote sensing and ground truthing, a GIS database of world mangrove vegetation has been constructed at the World Conservation Monitoring Centre (Spalding *et al*., 1997). Their estimate of mangrove area throughout the world (181,077 km^2) is both higher (by 7%) and less evenly distributed than the estimates of Saenger *et al*. (1983) that have previously been used to address mangrove species-area relationships (Ricklefs & Latham, 1993). Spalding *et al*. (1997) estimated the relative proportion of total global mangrove 'available area' in the different biogeographic regions to be: 52% in the IWP (of which 42% is in South and South-east Asia and 10% in Australasia), 27% for the Caribbean and Eastern Pacific, 16% for West Africa, and 5% for East Africa and the Middle East (Spalding *et al*., 1997; *contra* Ricklefs & Latham, 1993). The corresponding species richness values for these regions are 41 (65%) in the IWP, 8 (13%) in the Caribbean and Eastern Pacific, 5 (8%) in West Africa, and 9 (14%) in East Africa (data from Ricklefs & Latham, 1993; Duke *et al*., 1998). Despite a sample size of only four biogeographic regions, species richness and available area are significantly correlated ($r = 0.88$; $P = 0.05$). The areas of mangrove habitat in these regions are not significantly correlated with their distance from the IWP ($P > 0.25$). Estimates of available mangrove area in corresponding locations throughout the Tertiary could be used to test the prediction that mangrove species richness and available area have been similarly well-correlated throughout the development of this ecosystem.

Biogeography of mangrove-associated gastropods

While few animals are restricted completely to mangrove forests, a number of gastropod genera show high fidelity to this habitat (Berry, 1963; Vermeij, 1974; Cantera *et al.,* 1983; Plaziat, 1984, 1995; Reid, 1986; Cruz & Jiménez, 1994). That is, these gastropods occur throughout mangrove forests and in adjacent mud flats, and often exhibit species zonation across the intertidal zone that closely but inexactly parallels mangrove species zonation (e.g. Reid, 1985). In addition, fossils of several genera of gastropods have been used as indicators of palaeo-habitats favourable for the development of mangrove swamps, even when mangrove fossils themselves are lacking (Plaziat, 1975). We analysed the modern and Tertiary distributions of eight gastropod genera in three unrelated families: *Littoraria* (Prosobranchia: Littorinidae); *Cerithidea*, *Telescopium*, and *Terebralia* (Prosobranchia: Potamididae); and *Cassidula, Ellobium, Melampus,* and *Pythia* (Pulmonata: Ellobiidae).

Living gastropods

Overall, the global pattern of species richness of all eight of these gastropod genera combined is remarkably similar to that of mangroves (Fig. 3), and the correlation between gastropod richness and mangrove richness (grouped by 15° of longitude) is strong ($r = 0.81$; $P < 0.001$). Like that of mangroves, the distribution of gastropods could be considered anomalous (*sensu* Ricklefs & Latham, 1993); its peak of species richness is also in the IWP (Fig. 3). The distribution of these gastropods, however, is clearly bimodal ($P[H_0$: distribution is unimodal$] < 0.0001$), with modes in the Eastern Pacific of Central America (at 96°W) and in South-east Asia (at 99°E).

All twenty-seven species of mangrove-inhabiting Littorinidae are placed in the genus *Littoraria* (Reid, 1986). Their global pattern of species richness parallels that of mangroves almost exactly (Fig. 3), and the two are tightly correlated ($r = 0.93$; $P < 0.001$). Like that of mangroves, the distribution of *Littoraria* could be considered anomalous; its distribution is unimodal ($P = 0.12$), and its peak of species richness in the IWP is about 9° west of that of mangroves. *Littoraria* is divided into five subgenera, *Littoraria, Palustorina, Lamellitorina, Littorinopsis,* and *Bulimilittorina* (Reid, 1986, 1989). These subgenera are based on morphological and genetic characters, but show little correspondence with modern geography. Mangrove-associated littorines in the two most primitive subgenera, *Littoraria* and *Lamellilitorina*, occur throughout the modern range of mangroves, although all but one of the Eastern Pacific species are placed in the subgenus *Littoraria* (Reid, 1986, 1999). Eighteen of the nineteen mangrove associates in the two more derived subgenera, *Littorinopsis* and *Palustorina*, occur in the IWP, but the remaining species, *L.* (*Littoriniopsis*) *angulifera* (Lam.), occurs in both the Caribbean and the Eastern Atlantic. The most derived subgenus, *Bulimilittorina*, is represented by a single species, *Littoraria aberrans* Reid, which is endemic to the Pacific coasts of Costa Rica and Panama (Reid, 1999).

Within the Potamididae, the one modern species of *Telescopium*, *T. telescopium* (L.), occurs throughout the IWP (Houbrick, 1991), as does the widespread *Terebralia palustris* (L.) (Fig. 3). The two other species of *Terebralia, T. semistriata* (Mörch) and *T. sulcata* (Born), are more narrowly distributed. *T. semistriata* occurs only in Australian mangroves, from Queensland northward and westward to Carnavon, and on the south coast of Irian Jaya (Houbrick, 1991). *Terebralia sulcata* occurs throughout south-east Asia, northern and western Australia, and northward to Okinawa (Houbrick, 1991). The closely related genus *Cerithidea*, however, has higher species richness in the ACEP (peak at 108°W; Fig. 3) and its distribution is unimodal ($P = 0.29$). Three groups of species are identifiable, one in the ACEP, one in southern Africa, and one in south-east Asia. Four species, *C. californica mazatlantica* Carpenter*, C. montagnei* (Orbigny)*, C. pulchra* (C. B. Adams)*,* and *C. valida* (C. B. Adams), occur only on the western coast of Central and South America (Cruz & Jiménez, 1994), while one, *C. costata* (da Costa), occurs in the western Atlantic (Coomans, 1969). The southern African endemic, *C. decollata* (L.), occurs from Natal, South Africa, northward to Mozambique, and eastward into Madagascar and the Comoros (Brown, 1971; Vermeij, 1974). Four species occur in south-east Asia: *C. cingulata* Gmelin*, C. obtusa* Lamarck, *C. quadrata* Sowerby, and *C. rhizophorarum* A. Adams. Both *C. cingulata* and *C. obtusa* extend into the Central Pacific islands (Cantera *et al.,* 1983).

The Ellobiidae show similar disjunct distribution patterns (Fig. 3). The presumed ancestral subfamilies Pythinae (which includes *Cassidula* and *Pythia*) and Ellobiinae (*Ellobium*) are best represented in the IWP, while the derived Melampinae (*Melampus*) is primarily an ACEP group (Morton, 1955; Martins, 1996). The distribution of the genus *Cassidula* is unimodal ($P = 0.61$) with a peak richness at 99°E. One species (*C. labrella* (Deshayes)) is a southern African endemic (Brown, 1971), while three other species are restricted to the Central Pacific islands (Cantera *et al.*, 1983). The remaining four species of *Cassidula* occur throughout

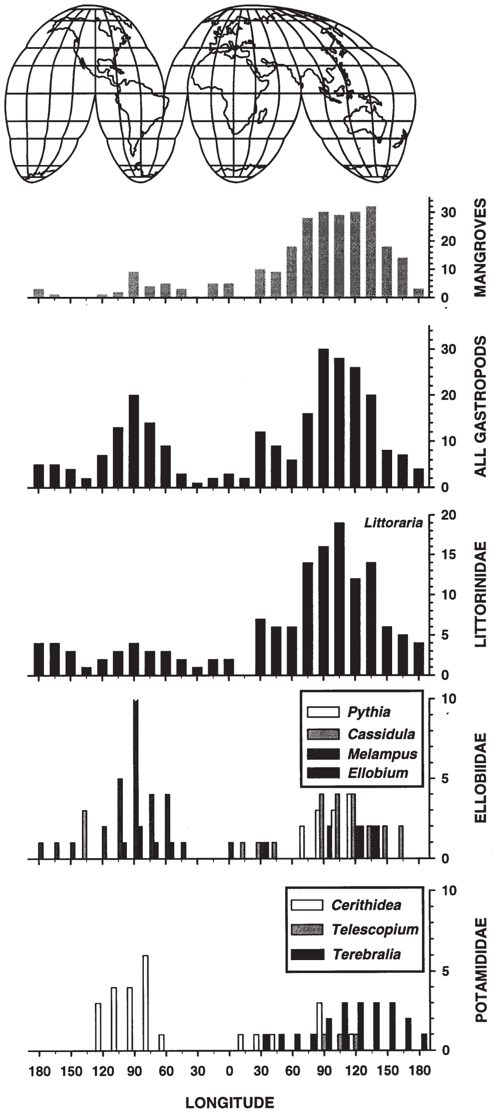

Fig. 3. Species richness of mangrove-inhabiting gastropods as a function of longitude (in 15° increments). Mangrove species richness shown in top bar chart for comparison. Data compiled from Smith (1940), Berry (1963), Macnae (1968), Coomans (1969), Brown (1971), Vermeij (1974), Marshall & Medway (1976), Bouchet (1977), Murty & Rao (1977), Way & Purchon (1981), Cantera *et al.* (1983), Plaziat (1984), Suárez & Castaing (1984)), Warmoes *et al.* (1990), Houbrick (1991), Deekae & Henrion (1993), and Cruz & Jiménez (1994).

Table 3. Fossil occurrences of mangrove-associated gastropods

Gastropod	Epoch	Location	Source
Ellobiidae			
Melampinae	Malm (late Jurassic)	Colorado, USA	Tracey *et al.* (1993)
Ellobium	Miocene	Yatuo Group, Japan	Oyama (1950)
Marinula	Pleistocene	Panama; Costa Rica	Dall (1912)
Melampus	Upper Cretaceous	Europe, N. America	Zilch (1959)
	Miocene	N. America	Zilch (1959)
Pythia	Eocene	Europe	Zilch (1959)
Littorinidae			
Littoraria	Lower & Middle Eocene	Paris, France	Reid (1989)
	Lower Miocene	Panamá	Reid (1989)
	Upper Miocene	France	Reid (1989)
	Pliocene	Florida	Reid (1989)
Potamididae			
Cerithidea	Oligocene	Georgia, USA	Dall (1915)
	Miocene	Yatuo Group, Japan	Oyama (1950)
	Miocene	Tampa, Florida, USA	Dall (1915)
Terebralia	Miocene	Italy	Sacco (1895)
	Miocene	Java	Martin (1899), Tesch (1920)
	Miocene	Pacific Islands	Ladd (1972)
	Miocene	Malaysia	Wissema (1947)
Telescopium	Miocene	Yatuo Group, Japan	Oyama (1950)

south-east Asia (Cantera *et al.*, 1983). The five species in the closely related genus *Pythia* occur only in south-east Asia (Cantera *et al.*, 1983). The distribution of *Ellobium* species is similar to that of *Cerithidea*, with unique assemblages in the ACEP (*E. dominicensis* (Férussac) and *E. stagnalis* (Oribgny)), East Africa (*E. gaziense* H. B. Preston), and south-east Asia (*E. aurismidae* (L.), *E. aurisjudae* (L.) and *E. chinense* (Pfeiffer)) (Vermeij, 1974; Cantera *et al.*, 1983; Martins, 1996). No modes (peaks in species richness) are identifiable for *Ellobium*. *Melampus* is strongly unimodal ($P = 0.37$), and its peak richness occurs in the ACEP (99°W). Twelve of the eighteen mangrove-inhabiting species of *Melampus* occur in the ACEP, one in West Africa (*M. liberianus* H. & A. Adams), one in East Africa (*M. semiaratus* (Conolly)), and the remaining four in south-east Asia (Cantera *et al.*, 1983; Martins, 1996).

The fossil record of mangrove-associated gastropods

The fossil record of estuarine gastropods is poor relative to that of mangroves. The same anoxic, acidic, peaty soils that encourage preservation of plant pollen and macrofossils rapidly dissolve the calcium carbonate of gastropod shells (Plaziat *et al.*, 1983). The few fossils of mangrove-associated gastropods that have been found are assignable to modern subfamilies, genera, and subgenera that live on mangrove trees and mudflats (Table 3). The Middle Eocene Casa Blanca group of south-west Texas (Westage & Gee, 1990), and the Middle Miocene Yatuo group in Japan (Oyama, 1950) each yielded rich fossil assemblages of both mangrove plants and gastropods.

The fossil record of *Telescopium* begins in the Upper Miocene, but its fossils have never been recorded outside its modern range in south-east Asia (Houbrick, 1991). In contrast, fossils assignable to the modern *Terebralia palustris* are known from the Miocene of Italy (Sacco, 1895) and Java (Martin, 1899; Tesch, 1920), and from the Pliocene of Timor and Java (Tesch, 1920). Similarly, *Terebralia sulcata* has a fossil record extending back into the Miocene, including occurrences in Eniwetok Atoll, the Marshall Islands, Java, and Malaysia (Martin, 1899; Wissema, 1947; Ladd, 1972), and Pliocene records throughout the IWP (Martin, 1899; Tesch, 1920; Wissema, 1947). The Australian endemic *Terebralia semistriata* is unknown in the fossil record, and Houbrick (1991) suggests that it is a recently evolved species. *Ceritihidea* occurs in Miocene deposits in Japan (Oyama, 1950) and Florida (Dall, 1915), and the Oligocene of Georgia (Dall, 1915).

Table 4. Nestedness of mangrove flora

All mangrove species combined			
Nestedness			
Matrix nestedness temperature[1]	11.3		
P(H$_0$: not nested)[2]	3×10^{-82}		
Outlier species[3]			
Taxon	Z-score	P	Modern range
Avicennia germinans (L.) Stearn	3.338	0.0001	ACEP
Conocarpus erectus L.	3.338	0.0001	ACEP
Rhizophora mangle L.	3.115	0.0002	ACEP
Laguncularia racemosa (L.) Gaertn.f.	2.691	0.0022	ACEP
R. × *harrisonii* Leechman*	2.360	0.0090	E. Pacific
R. racemosa Meyer	2.360	0.0090	E. Pacific
Pelliciera rhizophorae Triana & Planchon*	1.605	0.0441	ACEP
A. schaueriana Stapf & Leechman ex Moldenke*	1.605	0.0441	W. Indies
A. bicolor Standley*	1.605	0.0441	E. Pacific

[1] Matrix ‘temperature’ ranges from 0 to 100°, with small values being more nested than large values. See Atmar & Patterson (1993) for conceptual and mathematical details; calculations done using software developed by Atmar & Patterson (1995).

[2] Probability values based on 500 Monte Carlo randomizations of the site × species matrix (Atmar & Patterson 1993, 1995).

[3] Outlier species determined using Wilcoxon-Mann–Whitney rank-sum test following method of Simberloff & Martin (1991). P-values are exact (StatXact *v.* 3.0, Cytel Softwaref Corp. 1995).

* Modern-day endemic species

Species-area relationships of mangrove-associated gastropods

Like the relationship between mangrove species richness and area of habitat, the relationship between species richness of mangrove-associated gastropods and habitat area is strong ($r = 0.90$; $P < 0.05$). Forty-seven species (55%) of gastropods in the eight genera studied occur in the IWP, twenty (24%) in the Caribbean and Eastern Pacific, four (5%) in West Africa, and fourteen in East Africa (16%) (data compiled from sources listed in the legend of Fig. 3).

Nestedness of mangrove flora and fauna

Mangroves, all gastropods combined, and the genus *Littoraria* showed significant community-wide nested distributions with respect to longitude, while the other genera of gastropods were not nested with respect to longitude (Tables 4 and 5). As noted in the Methods, calculation of the community-wide nestedness temperature given in Tables 4 and 5 requires maximal packing of the longitude × species matrix. This packing did not preserve longitudinal ordering. Rather, sites from disparate parts of the globe were interspersed. For example, in the packed matrix, Sri Lanka lies between the Mariana Islands and Burma; India occurs seventeen rows below Sri Lanka, and the West Indies lie between Vanuatu and the Caroline Islands. Overall, in none of the significantly nested ‘communities’ do apparent geographical patterns emerge (full matrix rearrangements for all these groups are available on request from the senior author). Rather, this result suggests that speciation patterns in most of these regions has proceeded independently.

When we examined the nestedness of individual species (following Simberloff & Martin, 1991), clearer patterns emerged. For mangroves and *Littoraria*, all ACEP species deviated significantly from expectation: they were not nested with respect to the IWP. These species, indicated as ‘outlier species’ in Tables 4 and 5, included both modern-day geographically endemic species as well as those with more cosmopolitan distributions. For *Cerithidea* and *Melampus*, IWP species deviated significantly from expectation, while Pacific Island *Cassidula* species were aberrant. No *Ellobium* species deviated from expectation.

DISCUSSION

Implications of the fossil record

The fossil record of both mangroves and their associated gastropods begins in the Maastrichian (Upper Cretaceous) or Palaeocene, and strongly

Table 5. Nestedness of mangrove-associated gastropods. *Ellobium, Pythia, Terebralia*, and *Telescopium* were not analysed for nestedness or modality because of few species or restricted (IWP only) distributions. Sub-genera of *Littoraria* after Reid (1986, 1989). Statistical methods as in Table 4

Gastropod community statistics	All gastropods combined	*Littoraria*	*Cassidula*	*Melampus*	*Cerithidea*
Nestedness					
Matrix nestedness temperature	6.4	7.5	26.6	20.6	26.5
P(H_0: not nested)	6×10^{-45}	2×10^{-27}	0.29	0.81	0.62
Outlier species					
Taxon		*Z*-score	*P*	Modern range	
Littoraria (Littorinopsis) angulifera Lamarck		2.251	0.0035	Atlantic	
Littoraria (Littoraria) varia Sowerby		1.631	0.0441	E. Pacific	
Littoraria (Littoraria) fasciata Gray		1.631	0.0441	E. Pacific	
Littoraria (Littoraria) zebra Donovan		1.631	0.0441	E. Pacific	
Littoraria (Bulimilittorina) aberrans Philippi		1.631	0.0441	E. Pacific	
Littoraria (Littoraria) cingulifera Philippi		1.453	0.0883	W. Africa	
Littoraria (Littorinopsis) subvittata Reid		1.360	0.0887	Indian Ocean	
Cassidula labrella (Deshayes)		2.253	0.0014	South Africa	
Cassidula nucleus (Gmelin)		2.174	0.0087	Pacific Islands	
Melampus nuxcastanea (Kuroda)*		2.171	0.0087	Ryukyu Islands	
Melampus fasciatus (Deshayes)*		1.656	0.0455	Ryukyu Islands	
Melampus liberianus H. & A. Adams		1.600	0.0693	W. Africa	
Melampus semiaratus (Conolly)*		1.498	0.0909	Society Islands	
Cerithidea decollata (L.)*		1.861	0.0331	Madagascar	
Cerithidea cingulata (Gmelin)		1.559	0.0677	Indonesia	
Cerithidea quadrata Sowerby		1.559	0.0677	Indonesia	
Cerithidea obtusa (Lamarck)		1.559	0.0677	Indonesia	
Cerithidea rhizophorarum A. Adams		1.486	0.0724	IWP	

* Modern-day endemic species.

supports a Tethyan origin for both many extant mangrove taxa and the mangrove ecosystem. The earliest known mangrove fossils are Maastrichian pollen grains assignable to the extant palm genus *Nypa* (Germeraad *et al*., 1968), and Palaeocene/Eocene fruits and seeds in the extinct genera *Wetherellia* and *Palaeowetherellia* (Mazer & Tiffney, 1982). Distribution of fossil mangrove pollen, leaves, and fruits is pantropical by the Middle Eocene. Two genera now found only in the IWP – *Nypa* and *Kandelia* – occur in the Eocene neotropics (Germeraad *et al*., 1968; Wolfe, 1977). The modern neotropical endemic *Pelliceria* occurs in the Palaeocene of France (Gruas-Cavagnetto *et al*., 1988). The genus *Sonneratia*, which has a contemporary peak of species richness in Australia and South-east Asia first appears on the Palaeocene/Late Eocene island continent of India (Prakash, 1960). The IWP genus *Bruguiera* is common in the Eocene London Clays (Chandler, 1951; Collinson & Hooker, 1987). Graham (1977) suggested that the range reduction of *Pelliceria* at the Eocene/Oligocene boundary reflects a concurrent global cooling trend. This global cooling may also have resulted in the simultaneous loss of *Kandelia* and *Barringtonia* from the Gulf of Alaska (Wolfe, 1972), and of *Nypa*, *Pelliceria*, and *Rhizophora* from Europe (Graham, 1977; see also Plaziat, 1995). Global cooling would be expected to result in a reduction in the geographical range of mangroves because embryos of some viviparous mangrove species lack abscisic acid and associated 'stress' proteins that might have conferred cold tolerance (Farrant *et al*., 1996).

Reconstructions of palaeocirculation patterns posit that from the Middle Jurassic through the early Middle Miocene (150–20 Mya) the tropical equatorial current flowed east-to-west (Berggren & Hollister, 1977). In this scenario, the Tethys would have acted as a conduit through which marine flora and fauna were transported pantropically by prevailing currents. Given that many of the earliest mangrove fossils occur in the Eocene on the shores of the Tethys, we concur with Mepham (1983) that this equatorial current could have dispersed propagules of genera such as *Avicennia*, *Pelliceria*, and *Rhizophora* from the Tethys Sea, towards the Americas, and thence onward to what is now the IWP. Analysis of leaf chemical characteristics (aliphatic hydrocarbon and triterpenoid fraction of foliar waxes) of mangroves on both sides of the Atlantic further supports this hypothesis (Dodd *et al*., 1998).

Similarly, the two major gastropod families with high fidelity to modern mangrove ecosystems are also thought to have originated around the Tethys Sea (Reid, 1989, 1990 [Littorinidae]; Morton, 1955; Martins, 1996; [Ellobiidae]), and the fossil record lends support to this hypothesis. Both the Ellobiidae and the Littorinidae are thought to be of tropical origin (Morton, 1955; Reid, 1986, 1989, 1996; Martins, 1996). *Littoraria* (*Littorinopsis*) occurs in the Eocene of Europe, where it is contemporaneous with fossil finds of *Avicennia, Nypa, Pelliceria,* and *Rhizophora*. It similarly occurs in the Miocene of Panama, during which time mangroves were widely distributed in the Neotropics (Graham, 1995). The most ancestral Ellobiidae (*Ophicardelus*) occur in the mangroves of New Zealand and Australia (Morton, 1955). Ellobiid fossils (Melampinae, *Pedipes*, *Tralia*) representing modern neotropical subfamilies (Melampinae, Pedipinae) occur in neotropical Miocene deposits (Dall, 1912, 1915; Woodring, 1928; Gilbert, 1949; Gibson-Smith & Gibson-Smith, 1979, 1985; Tracey *et al.,* 1993), while the IWP *Ellobium* co-occurs with mangrove fossils in the Middle Miocene Yatuo Group of Japan (Oyama, 1950). The fossil record of the Ellobiidae, along with hypothesized current patterns during the Tertiary, suggest that this family of molluscs probably inhabited the tropical intertidal prior to the evolution of mangroves. No phylogenetic information is available for the Potamididae, but we note that the predominantly ACEP genus *Cerithidea* is known from the Miocene of Japan (Oyama, 1950) and the Oligocene of North America (Dall, 1912, 1915). *Telescopium* has probably always been restricted to the IWP (Oyama, 1950; Houbrick, 1991), but *Terebralia* had a much broader geographical distribution during the Tertiary, extending from southern Europe eastward to the central Pacific Islands (Houbrick, 1991; Plaziat, 1995).

In sum, the fossil records of mangroves and their associated gastropods support two of the predictions of the vicariance hypothesis (Table 1): both groups are initially restricted to the shores of the Tethys Sea, and the generic ages of most mangroves and associated gastropods, 40–50 Mya, are concordant. Available phylogenetic information does not accord with hypothesized dispersal tracks radiating out from the IWP. That is, there is no clear association between ancestral taxa and the IWP, or between derived taxa and the ACEP.

Are the statistics informative?

The statistical analyses of the biogeographic patterns of mangroves and associated gastropods support further the conclusions drawn from analyses of the fossil record. Modern distributions of mangrove species and all genera of gastropods are strongly unimodal, whereas the distribution of all gastropods pooled is strongly bimodal (Fig. 3). For mangroves, the unimodality simply reflects the comparatively high species richness in the IWP. Whereas this distribution could result from a single centre of origin, the lack of support for this hypothesis provided by the mangrove fossil record implies that the single mode of mangrove species richness results from other factors, such as the observed strong species-area relationship. The unimodality of each distribution of species richness of each gastropod genus similarly reflects their local areas of endemism or recent evolution. The ‘all gastropod genera pooled distribution’ is expected to be multimodal, because it is a mixture of distributions with different, known modes (Efron & Tibshirani, 1993). It is striking that a distribution derived from eight genera, each with its own mode, is only bimodal, as opposed to having more than two modes. This observation suggests that isolation of the IWP and the ACEP since the Late Miocene has encouraged *in situ* speciation of these groups.

The species-area relationship in and of itself could explain the diversity ‘anomalies’ of both mangroves and associated gastropods. While estimates of available mangrove area in corresponding locations throughout the Tertiary could be used to test the prediction that mangrove species richness and available area have been similarly well-correlated throughout the development of this ecosystem, such estimates are unavailable. Overall, however, the high species richness of mangroves and of associated gastropods in different biogeographic regions supports McCoy & Heck’s (1976) prediction relating geographical isolation to local species richness.

The analysis of nested distribution patterns, and more importantly, identification of those species that are not nested with respect to geography, further supports a Tethyan origin for mangrove ecosystems. Darlington (1957) and Cook & Quin (1995) interpreted community-wide nestedness as an indicator of colonization from a centre of origin, whilst other authors (reviewed by Patterson, 1990) infer localized extinctions from nested distributions. The former interpretation (colonization from a centre of origin) is difficult to support in this case for two reasons. First, geographical (longitudinal) ordering of sites is not preserved following packing of the mangrove, all gastropods, and *Littoraria* matrices. Second, species identified as 'outliers' using the Wilcoxon-Mann–Whitney rank sum test are found throughout the world, and include both cosmopolitan species and geographical endemics. The latter interpretation (localized extinctions) is more plausible given the community-wide nested distribution of both mangroves and *Littoraria* (Tables 4, 5). This interpretation would require an initial large species pool in all sites (perhaps around the Tethys Sea as implied by the mangrove fossil record) followed by selective extinction events as local habitats degraded over geological time (e.g. Wolfe, 1972; Graham, 1977). The fossil record of mangroves (Table 2, Fig. 2) supports this scenario, but the poor fossil record (Table 3) of *Littoraria* is uninformative. Among modern communities, the absence of nested distributions of other gastropod genera most probably results from low number of species; the nestedness of the overall gastropod community in mangroves (all genera pooled) reflects the numerical dominance of *Littoraria* species in these communities.

Interestingly, when analysed at a species level, all ACEP species of mangroves and *Littoraria* are not nested with respect to the IWP peak of species richness of these groups. In general, all these species have geographical ranges much larger than their dispersal ranges (Reid, 1986), suggesting that assembly of mangrove ecosystems in the ACEP has proceeded independently of those in the IWP, at least since the end of the Miocene. Patterns of non-nestedness of other gastropod species further identifies independent assemblages in the Pacific Islands, southern Japan (the northern limit of mangroves in the IWP), and Madagascar/southern Africa. The latter group includes three endemic species of mangrove as well (*Aegialitis rotundifolia*, *Heritiera fomes*, and *Sonneratia griffithi*). These three species were the only other mangroves to have positive (albeit nonsignificant using a cut-off of $\alpha = 0.05$) Z-scores for nestedness (Table 4). Endemics are likely to have positive Z-scores, because their occurrences will be clumped in a particular area, but not necessarily in the area of highest species richness. In other words, the presence-absence vectors of endemics would look like [0, 0, 0, . . ., 0, 1, 1, 1, . . ., 0, 0, 0, . . ., 0]. *Aegialitis* was thought by van Steenis (1949) to have a vicariant distribution (the other species in the genus, *A. annulata*, is restricted to northern Australia and eastern Malaysia).

In sum, the statistical analyses support the remaining three predictions of the vicariance hypothesis (Table 1). Mangrove flora and fauna have similar diversity anomalies and there are significant species-area relationships of both mangroves and associated gastropods. Whereas mangrove *Littoraria* communities are significantly nested on a global basis, the lack of nestedness of individual species in the ACEP and Indian Ocean suggests independent evolution of mangroves and gastropods in these regions.

CONCLUSIONS

We draw five principal conclusions from this study. First, the fossil record supports the hypothesis that mangrove ecosystems originated in the Palaeocene/Eocene around the Tethys Sea. Second, the fossil record also supports the hypothesis that all mangrove genera (except *Excoecaria*) had evolved before the Tethyan connection between the Atlantic and the Indo-West Pacific closed in the Late Miocene. Third, reconstructions of palaeocirculation patterns suggest that dispersal of mangrove taxa prior to the closure of the Tethys proceeded from east to west. Fourth, patterns of community-wide nestedness support the hypothesis of a Tethyan origin for mangroves followed by differential extinction (at the generic level) as environmental conditions changed regionally and locally. Fifth, distributions of gastropods associated with mangrove taxa show similar patterns of species richness, and these patterns are well correlated with available area for mangrove ecosystems. Based on available data and detailed statistical analysis, we conclude that mangrove taxa, associated gastropods, and the entire mangrove ecosystem originated around the Tethys Sea, and modern distributions result almost entirely from vicariance events. The data are not consistent with an IWP centre of origin for these species or ecosystems.

ACKNOWLEDGMENTS

This research was supported by NSF grants DEB 92–53743 and DEB 97–41904 to AME. We thank Nick

Gotelli, Earl McCoy, and Bruce Tiffney for helpful discussions of these ideas, and Dan Simberloff for explaining nestedness statistics to us. Bruce Patterson contributed to this research by making his nestedness temperature calculator software publicly available on the world-wide-web (http://www.aics-research.com/nestedness/tempcalc.html). We thank the referees for helpful critiques of the submitted manuscript. Portions of this paper were presented at the ICSEB V meetings in Budapest (1996) and the ESA meetings in Albuquerque (1997).

REFERENCES

Atmar, W. & Patterson, B.D. (1993) The measure of order and disorder in the distribution of species in fragmented habitat. *Oecologia,* **96,** 373–382.

Atmar, W. & Patterson, B.D. (1995) The nestedness temperature calculator. *A Visual Basic Program, Including 294 Presence- Absence Matrices.* AICS Research, Inc., University Park, New Mexico, and The Field Museum, Chicago, Illinois.

Aubréville, A. (1964) Problémes de la mangrove d'hier det d'aujourd'hui. *Adansonia, N.S.* **4,** 19–23.

Ball, M.C. (1988) Ecophysiology of mangroves. *Trees* **2,** 129–142.

Berggren, W.A. & Hollister, C.D. (1977) Plate tectonics and paleocirculation – commotion in the ocean. *Tectonophysics,* **38,** 11–48.

Berry, A.J. (1963) Faunal zonation in mangrove swamps. *Bull. Nat. Mus., Singapore,* **32,** 90–98.

Bouchet, P. (1977) Distribution des mollusques dans les mangroves du Senegal. *Malacologia,* **16,** 67–74.

Brande, M.B. & Prakash, U. (1986) The tertiary flora of southeast Asia with remarks on its palaeoenvironment and phytogeography of the Indo-Malayan region. *Rev. Palaeobot. Palynol.* **49,** 203–233.

Brown, D.S. (1971) Ecology of Gastropoda in a South African mangrove swamp. *Proc. Malac. Soc. Lond.* **39,** 263–279.

Cantera, J., Arnaud, P.M. & Thomassin, B.A. (1983) Biogeographic and ecological remarks on molluscan distribution in mangrove biotopes. 1. Gastropods. *J. Moll. Stud.* Suppl. **12A,** 10–26.

Cavagnetto, G., Laurain, M. & Meyer, R. (1980) Un sol de mangrove fossilise dans les lignites du soissonais (Ypresien) a Verzenay (Marne). *Geobios,* **13,** 795–801.

Chandler, M.E.J. (1951) Note on the occurrence of mangroves in the London Clay. *Proc. Geol. Ass.* **62,** 269–272.

Chandler, M.E.J. (1954) Some Upper Cretaceous and Eocene frutis from Egypt. *Bull. Br. Mus. (Nat. Hist.), Geol.* **2,** 149–187.

Chandler, M.E.J. (1964) *The lower Tertiary floras of southern England. IV. A summary and survey of findings in the light of recent botanical observations*. British Museum (Natural History), London.

Chapman, V.J. (1976) *Mangrove vegetation.* J. Cramer, Vaduz.

Churchill, D.M. (1973) The ecological significance of tropical mangroves in the early Tertiary floras of southern Australia. *Geol. Soc. Aust. Spec. Pub.* **4,** 79–86.

Cody, M.L. (1975) Toward a theory of continental species diversities: bird distributions over Mediterranean habitat gradients. *Ecology and evolution of communities* (ed. by M.L.Cody and J.M.Diamond), pp. 214–257. Harvard University Press, Cambridge, Massachusetts.

Collinson, M.E. (1983) *Fossil plants of the London Clay.* The Palaeontological Association, London.

Collinson, M.E. & Hooker, J.J. (1987) Early Tertiary of southern England. *The Origins of angiosperms and their biological consequences* (ed. by E.M.Friis, W.G.Chaloner and P.R.Crane), pp. 259–304. Cambridge University Press, Cambridge.

Cook, R.R. & Quinn, J.F. (1995) The influence of colonization in nested species subsets. *Oecologia,* **102,** 413–424.

Cookson, I.C. & Eisenack, A. (1967) Some early Tertiary microplankton and pollen grains from a deposit near Strahan, Western Tasmania. *Proc. R. Soc. Victoria,* **80,** 131–140.

Coomans, H.E. (1969) Biological aspects of mangrove mollusks in the West Indies. *Malacologia,* **9,** 79–84.

Cruz, R.A. & Jiménez, J.A. (1994) *Moluscos asociados a las áreas de manglar de la Costa Pacífica de América Central.* Editorial Fundacíon UNA, Heredia, Costa Rica.

Cytel Software Corp (1995) *Statxact for Windows*, *Version 3.* Cambridge, Massachusetts.

Dall, W.H. (1912) New species of fossil shells from Panama and Costa Rica. *Smithsonian Misc. Coll.* **59**, no. 2.

Dall, W.H. (1915) A monograph of the molluscan fauna of the Orthaulax Pugnax zone of the Oligocene of Tampa, Florida. *U. S. Nat. Mus., Bull.* **90**.

Darlington, P.J. (1957) *Zoogeography: the geographical distribution of animals.* John Wiley and Sons, New York.

Deekae, S.N. & Henrion, R. (1993) Multivariate analysis of species distribution: a survey on occurrence of mangrove molluscs in the Bonny and New Calabar rivers of the Niger delta. *Acta Hydrochim. Hydrobiol.* **21,** 273–279.

Dodd, R.S., Rafii, Z.A., Fromard, F. & Blasco, F. (1998) Evolutionary diversity among Atlantic coast mangroves. *Acta Oecol.* **9,** 323–330.

Dolianiti, E. (1955) Frutos de *Nipa* no Paleoceno de Pernambuco. *Bol. Div. Geol. E Mineral, Brasil*, **158,** 1–36.

Duke, N.C. (1991) A systematic revision of the mangrove genus *Avicennia* (Avicenniaceae) in Australasia. *Aust. Syst. Bot.* **4,** 299–324.

Duke, N.C. (1992) Mangrove floristics and biogeography. *Tropical mangrove ecosystems* (ed. by A.I. Robertson and D.M. Alongi), pp. 63–100. American Geophysical Union, Washington, D.C.

Duke, N.C. (1995) Genetic diversity, distributional patterns and rafting continents–more thoughts on the evolution of mangroves. *Hydrobiologia*, **295,** 161–181.

Duke, N.C., Ball, M.C. & Ellison, J.C. (1998) Factors influencing biodiversity and distributional gradients in mangroves. *Global Ecol. Biogeogr. Letts.* **7,** 27–48.

Efron, B. & Tibshirani, R.J. (1993) *An introduction to the bootstrap.* Chapman & Hall, New York.

Elsik, W.C. (1974) Characteristic Eocene palynomorphs in the Gulf Coast, USA. *Palaeontogrphica Abt. B,* **149,** 90–111.

Farnsworth, E.J. & Farrant, J.M. (1998) Reductions in abscisic acid are linked with viviparous reproduction in mangroves. *Am. J. Bot.* **85,** 760–769.

Farrant, J.M., Pammenter, N.W., Berjak, P., Farnsworth, E.J. & Vertucci, C.W. (1996) Presence of dehydrin-like proteins and levels of abscisic acid in recalcitrant (desiccation sensitive) seeds may be related to habitat. *Seed Sci. Res.* **6,** 175–182.

Frederiksen, N.O. (1985) Review of early Tertiary sporomorph paleoecology. *Am. Assoc. Stratigraph. Palynol. Contr. Ser.* **15,** 1–92.

Germeraad, J.H., Hopping, C.A. & Muller, J. (1968) Palynology of Tertiary sediments from tropical areas. *Rev. Palaeobot. Palynol.* **6,** 189–348.

Gibson-Smith, J. & Gibson-Smith, W. (1979) The genus Arcinella (Mollusca: Bivalvia) in Venezuela and some associated faunas. *Geos*, **24,** 11–32.

Gibson-Smith, J. & Gibson-Smith, W. (1985) A second melampid (Plumonata: Basommatophora) from the early Miocene of Venezuela. *Nautilus* **99,** 87–89.

Glibert, M. (1949) Gastropodes du Miocene Moyen du bassin de la Loire. *Inst. R. Sci. Nat. Belg., Mems., 2°Ser.* **30,** 1–235.

González-Guzmán, A.E. (1967) *A palynological study on the upper Los Curevos and Mirador formations (lower and middle Ecoecne; Tibú area, Columbia).* E. J. Brill, Leiden.

Graham, A. (1976) Studies in neotropical paleobotany. II. The Miocene communities of Veracruz, Mexico. *Ann. Mo. Bot. Gdns,* **63,** 787–842.

Graham, A. (1977) New records of Pelliceria (Theaceae/ Pelliceriaceae) in the Tertiary of the Caribbean. *Biotropica,* **9,** 48–52.

Graham, A. (1985) Studies in neotropical paleobotany. IV. The Eocene communities of Panama. *Ann. Mo. Bot. Gdns,* **72,** 504–534.

Graham, A. (1987) Miocene communities and paleoenvironments of southern Costa Rica. *Am. J. Bot.* **74,** 1501–1518.

Graham, A. (1988a) Studies in neotropical paleobotany. V. The lower Miocene communities of Panama – the Culebra formation. *Ann. Mo. Bot. Gdns,* **75,** 1440–1466.

Graham, A. (1988b) Studies in neotropical paleobotany. VI. The lower Miocene communities of Panama – the Cucaracha formation. *Ann. Mo. Bot. Gdns,* **75,** 1467–1479.

Graham, A. (1989) Studies in netropical paleobotany. VII. The lower Miocene communities of Panama – the La Boca Formation. *Ann. Mo. Bot. Gdns,* **76,** 50–66.

Graham, A. (1991a) Studies in neotropical paleobotany. VIII. The Pliocene communities of Panama: introduction and ferns, gymnosperms, and angiosperms (monocots). *Ann. Mo. Bot. Gdns,* **78,** 190–200.

Graham, A. (1991b) Studies in neotropical paleobotany. IX. The Pliocene communities of Panama – angiosperms (dicots). *Ann. Mo. Bot. Gdns,* **78,** 201–223.

Graham, A. (1991c) Studies in neotropical paleobotany. X. The Pliocene communities of Panama – composition, numerical reprentations, and paleocommunity paleoenvironmental reconstructions. *Ann. Mo. Bot. Gdns,* **78,** 465–475.

Graham, A. (1993) Contribution toward a Tertiary palynostratigraphy for Jamaica: the status of Tertiary paleobotanical studies in northern Latin America and preliminary analysis of the Guys Hill Member (Chapelton Formation, middle Eocene) of Jamaica. *Mem. Geol. Soc. Am.* **182,** 443–461.

Graham, A. (1994) Neotropical Eocene coastal floras and ^{18}O/^{16}O-estimated warmer vs. cooler equatorial waters. *Am. J. Bot.* **81,** 301–306.

Graham, A. (1995) Diversification of Gulf/Caribbean mangrove communities through Cenozoic time. *Biotropica,* **27,** 20–27.

Graham, A. (1998) Studies in Neotropical paleobotany. XI. Late Tertiary vegetation and environments of southeastern Guatemala: palynofloras from the Mio-Pliocene Padre Miguel Group and the Pliocene Herrería Formation. *Am. J. Bot.* **85,** 1409–1425.

Graham, A. & Dilcher, D.L. (1998) Studies in Neotropical paleobotany. XII. A palynoflora from the Pliocene Rio Banano Formation of Costa Rica and the Neogene vegetation of Mesoamerica. *Am. J. Bot.* **85,** 1426–1438.

Graham, A. & Jarzen, D.M. (1969) Studies in neotropical paleobotany. I. The Oligocene communities of Puerto Rico. *Ann. Mo. Bot. Gdns,* **56,** 308–357.

Gruas-Cavagnetto, C., Tambareau, Y. & Villatte, J. (1988) Donnees paleoecologiques nouvelles sur le Thanetien et l'Ilerdien de l'avant-pays pyreneen et de la Montagne Noire. *Inst. Francais Pondichery, Sect. Sci. Tech.* **25,** 219–235.

van der Hammen, T. & Wymstra, T.A. (1964) A palynological study on the Tertiary and Upper Cretaceous of British Guiana. *Leid. Geol. Meded.* **30,** 183–241.

Haseldonckx, P. (1973) The palynology of some Palaeogene deposits between the Río Esera and the Río Segre, southern Pyrenees, Spain. *Leid. Geol. Meded.* **49,** 145–165.

Houbrick, R.S. (1991) Systematic review and functional morphology of the mangrove snails *Terebralia* and *Telescopium* (Potamididae; Prosobranchia). *Malacologia,* **33,** 289–338.

Kedves, M. (1969) *Palynological studies on Hungarian Early Tertiary deposits*. Akadémia Kiadó, Budapest.

Kemp, E.M. (1978) Tertiary climatic evolution and vegetation history in the southeast Indian Ocean region. *Palaeogeogr., Palaeoclim., Palaeoecol.* **24,** 169–208.

Kuyl, O.S., Muller, J. & Waterbolk, H.T. (1955) The application of palynology to oil geology with reference to Western Venezuela. *Geologie Mijnbouw N.S.* **17,** 49–75.

Ladd, H. (1972) Cenozoic fossil mollusks from western Pacific islands, gastropods (Turritellidae through Strombidae). *U. S. Geol. Surv. Prof. Paper* **532**.

Lakhanpal, T.N. (1952) *Nipa sahnii*, a palm fruit in the Tertiary of Assam. *Palaeobotanis,t* **1,** 289–294.

Langenhem, J.H., Hackner, B.L. & Bartlett, A. (1967) Mangrove pollen at the depositional site of Oligo-Miocene amber from Chiapas, Mexico. *Bot. Mus. Leaflets, Harvard Univ.* **21,** 289–323.

Leopold, E.B. (1969) Miocene pollen and spore flora of Eniwetok Atoll, Marshall Islands. *U. S. Geol. Surv. Prof. Pap.* **260-II**.

Machin, J. (1971) Plant microfossils from Tertiary deposits of the Isle of Wight. *New Phytol.* **70,** 851–872.

Macnae, W. (1968) A general account of the fauna and flora of mangrove swamps and forests in the Indo-West Pacific region. *Adv. Mar. Biol.* **6,** 73–270.

Mahabalé, T.S. & Deshpande, J.V. (1955) The genus *Sonneratia* and its fossil allies. *Palaeobotanist,* **6,** 51–64.

Marshall, A.B. & Lord Medway (1976) A mangrove community in the New Hebrides, south-west Pacific. *Biol. J. Linn. Soc.* **8,** 319–336.

Martin, K. (1899) Die Fossilien von Java. 1, Gastropoda. *Sammlungen Des Geologisches Reichsmuseums Leideni, Ser.* **1,** 232–237.

Martins, A.M. de F. (1996) Anatomy and systematics of the Western Atlantic Ellobiidae (Gastropoda: Pulmonata). *Malacologia,* **37,** 163–332.

Mazer, S.J. & Tiffney, B.H. (1982) Fruits of *Wetherellia* and *Palaeowetherellia* (?Euphorbiaceae) from Eocene sediments in Virginia and Maryland. *Brittonia,* **34,** 300–333.

McCoy, E.D. & Heck, K.L. Jr (1976) Biogeography of corals, seagrasses, and mangroves: an alternative to the center of origin concept. *Syst. Zool.* **25,** 201–210.

Medus, J. (1975) Palynologie de sédiments tertiaires du Sénégal méridional. *Pollen Spores,* **17,** 545–608.

Mepham, R.H. (1983) Mangrove floras of the southern continents. Part I. The geographical origin of Indo-Pacific mangrove genera and the development and present status of the Australian mangroves. *S. Afr. J. Bot.* **2,** 1–8.

Morton, J.E. (1955) The evolution of the Ellobiidae with a discussion on the origin of the Pulmonata. *Proc. Zool. Soc. Lon.* **125,** 127–168.

Muller, J. (1964) A palynological contribution to the history of the mangrove vegetation of Borneo. *Ancient Pacific floras: the pollen story* (ed. by L.M. Cranwell), pp. 33–42. University of Hawaii Press, Honolulu.

Muller, J. (1978) New observations on pollen morphology and fossil distribution of the genus *Sonneratia* (Sonneratiaceae). *Rev. Palaeobot. Palynol.* **26,** 277–300.

Muller, J. & Caratini, C. (1977) Pollen of *Rhizophora* (Rhizophoraceae) as a guide fossil. *Pollen Spores,* **19,** 361–389.

Murty, A.S. & Rao, M.B. (1977) Studies on the ecology of mollusca in a south Indian mangrove swamp. *J. Moll. Stud.* **43,** 223–229.

Orians, G.H. & Paine, R.T. (1983) Convergent evolution at the community level. *Coevolution* (ed. by D.J.Futuyma and M.Slatkin), pp. 431–358. Sinauer Associates, Sunderland.

Oyama, K. (1950) Studies of fossil molluscan biocoenosis, no. 1. Biocoenological studies on the mangrove swamps, with descriptions of new species from Yatuo Group. *Rep. Geol. Surv. Japan* **132,** 1–16.

Patterson, B.D. (1990) On the temporal development of nested subset patterns of species composition. *Oikos,* **59,** 330–342.

Plaziat, J.-C. (1975) Mollusc distribution and its value for recognition of ancient mangroves. *Proceedings of the International Symposium on Biology and Management of Mangroves, Volume 2.* (ed. by G.E. Walsh, S.C. Snedaker and H.J. Teas), pp. 456–465. University of Florida, Gainesville.

Plaziat, J.-C. (1984) Mollusk distribution in the mangal. *Hydrobiology of the Mangal* (ed. by F.D. Por and I. Dor), pp. 111–143. Dr W. Junk, The Hague.

Plaziat, J.-C. (1995) Modern and fossil mangroves and mangals: their climatic and biogeographic variability. *Marine palaeoenvironmental analysis from fossils* (ed. by D.W.J. Bosence and P.A. Allison), pp. 73–96. Geological Society Special Publication no. 83, London.

Plaziat, J.-C., Koeniguer, J.-C. & Baltzer, F. (1983) Des mangroves actuelles aux mangroves anciennes. *Bull. Soc. Géol. France,* **25,** 499–504.

Prakash, U. (1960) A survey of the Deccan Intertrappean flora of India. *J. Paleontol.* **34,** 1027–1040.

Ramanujam, C.G.K. (1956). On the occurrence of fossil wood of *Sonneratia*: *Sonneratioxylon dakshinenes* sp. nov. from the Tertiary of South Arcot District, Madras. *Palaeobotanist,* **5,** 78–81.

Recher, H.F. (1969) Bird species diversity and habitat diversity in Australia and North America. *Am. Nat.* **103,** 75–80.

Reid, D.G. (1985) Habitat and zonation patterns of *Littoraria* species (Gastropoda: Littorinidae) in Indo-Pacific mangrove forests. *Biol. J. Linn. Soc.* **26,** 39–68.

Reid, D.G. (1986) *The littorinid molluscs of mangrove forests in the Indo-Pacific Region*. British Museum (Natural History), London.

Reid, D.G. (1989) The comparative morphology, phylogeny and evolution of the gastropod family Littorinidae. *Phil. Trans. R. Soc. Lond.* B, **324,** 1–110.

Reid, D.G. (1990) Trans-Arctic migration and speciation induced by climatic change: the biogeography of Littorina (Mollusca: Gastropoda). *Bull. Mar. Sci.* **47,** 35–49.

Reid, D.G. (1996) *Systematics and evolution of Littorina*. The Ray Society, London.

Reid, D.G. (1999) The genus *Littoraria* Griffith & Pidgeon, 1834 (Gastropoda: Littorinidae) in the tropical Eastern Pacific. *Veliger* **42**, 21–53.

Ricklefs, R.E. (1987) Community diversity: relative roles of local and regional processes. *Science,* **235,** 167–171.

Ricklefs, R.E. & Latham, R.E. (1993) Global patterns of diversity in mangrove floras. *Species diversity in ecological communities* (ed. by R.E. Ricklefs and D. Schluter), pp. 215–229. University of Chicago Press, Chicago.

Sacco, F. (1895) Cerithiidae, Triforidae, Cerithiopsidae, e Diastomidae. *I Molluschi Dei Terreni Terziarii Del Piemonte E Della Liguria,* **17,** 1–83.

Saenger, P., Hegerl, E. & Davie, J. (1983) Global status of mangrove ecosystems. *The Environmentalist,* **3,** 1–88.

Salard-Cheboldaeff, M. (1981) Palynologie masestrichtienne et tertiare du Cameroun. Resultats botanique. *Rev. Palaeobot. Palynol.* **32,** 401–439.

Schimper, A.F.W. (1903) *Plant geography* (translated by W. R. Fisher). Clarendon Press, Oxford.

Simberloff, D. & Martin, J.-L. (1991) Nestedness of insular avifaunas: simple summary statistics masking complex species patterns. *Ornis Fenn.* **68,** 178–192.

Smith, M. (1940) *World-wide sea shells*. Tropical Photographic Laboratory, Lantana, Florida.

Smith, A.G. & Briden, J.C. (1977) *Mesozoic and Cenozoic paleocontinental maps.* Cambridge University Press, Cambridge.

Spalding, M., Blasco, F. & Field, C. (eds) (1997) *World mangrove atlas.* The International Society for Mangrove Ecosystems, Japan.

Statistical Sciences, Inc (1995) *S-Plus for Windows, Version 3.3.* Seattle.

Stewart, G. & Popp, M.C. (1987) The ecophysiology of mangroves. *Plant life in aquatic and amphibious habitats* (ed. by R. Crawford), pp. 333–345. Blackwell Scientific Publications, Oxford.

van Steenis, C.G.G.J. (1949) Vicarism in the Malaysian flora. *Flora Malesiana*, **1,** 59.

van Steenis, C.G.G.J. (1962) The distribution of mangrove plant genera and its significance for palaeogeography. *Proc. Kon. Net. Amsterdam, Ser. C,* **65,** 164–169.

Stover, L.E. & Partridge, A.D. (1973) Tertiary and late Cretaceous spores and pollen from the Gipplsand Basin, southeast Australia. *Proc. R. Soc. Victoria* **85,** 237–286.

Suárez, B.E. & Castaing, R.A. (1984) Distribución arborea de los gastrópodos *Cerithidea montagnei* (Mollusca: Potamidae) y *Littorina* spp. (Mollusca: Littorinidae) en el manglar de Mata de Limón, Costa Rica. *Uniciencia,* **1,** 47–54.

Tesch, P. (1920) Jungtertiäre und Quartäre Mollusken von Timor. *Paläontologie Von Timor,* **8,** 41–121.

Thanikaimoni, G. (1987) Mangrove palynology. *Inst. Francais Pondichery, Sect. Sci. Tech.* **24,** 1–100.

Tomlinson, P.B. (1986) *The botany of mangroves.* Cambridge University Press, Cambridge.

Tracey, S., Todd, J.A. & Erwin, D.H. (1993) Mollusca: Gastropoda. *The fossil record 2* (ed. by M.J. Benton), pp. 131–167. Chapman & Hall, London.

Tralau, H. (1964) The genus *Nypa* van Wurmb. *Kungl. Svenska Vetenskap. Handling.* **10,** 5–29.

Vermeij, G.J. (1974) Molluscs in mangrove swamps: physiognomy, diversity, and regional differences. *Syst. Zool.* **22,** 609–624.

Warmoes, T., Jocqué, R. & Janssens, L. (1990) The littorinid fauna of the Comoros (Gastropoda, Prosobranchia, Littorinidae). *J. Afr. Zool.* **104,** 157–163.

Way, K. & Purchon, R.D. (1981) The marine shelled mollusca of West Malaysia and Singapore, Part 2. Polyplacophora and Gastropoda. *J. Moll. Stud.* **47,** 313–321.

Westage, J.W. & Gee, C.T. (1990) Paleoecology of a middle Eocene mangrove biota (vertebrates, plants, and invertebrates) from southwest Texas. *Palaeogeogr., Palaeoclim., Palaeoecol.* **78,** 163–177.

Wijmstra, T.A. (1968) The identity of *Psilatricolporites* and *Pelliciera*. *Acta Bot. Neerland.* **17,** 114–116.

Wissema, G.G. (1947) *Young Tertiary and Quaternary Gastropoda from the Island of Nias (Malay Archipelago).* Louis H. Becherer, Leiden.

Wolfe, J.A. (1972) An interpretation of Alaskan Tertiary floras. *Floristics and paleofloristics of Asia and Eastern North America* (ed. by A. Graham), pp. 201–233. Elsevier Publishing Company, Amsterdam.

Wolfe, J.A. (1977) Paleogene floras from the Gulf of Alaska region. *U. S. Geol. Surv. Prof. Pap.* **997.**

Woodring, W.P. (1928) Miocene mollusks from Bowden, Jamaica. Part II. Gastropods and discussion of results. *Carnegie Inst. Wash.*, Publ. no. 385, Washington, D.C.

Worthen, W.B. (1996) Community composition and nested-subset analyses: basic descriptors for community ecology. *Oikos,* **76,** 417–426.

Worthen, W.B., Carswell, M.L. & Kelly, K.A. (1996) Nested subset structure of larval mycophagous fly assemblages: nestedness in a non-island system. *Oecologia,* **107,** 257–264.

Wright, D.H., Patterson, B.D., Mikkelson, G.M., Cutler, A. & Atmar, W. (1998) A comparative analysis of nested subset patterns of species composition. *Oecologia,* **113,** 1–20.

Zilch, A. (1959) Gastropoda. *Handbuch der Palaozoologie 6* (ed. by O.H.Schindewolf), pp. 1–200. Gebruder Borntraeger, Berlin.