

Long distance dispersal, overland migration and extinction in the shaping of tropical African floras

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ABSTRACT

The distribution, ecology, probable modes of dispersal and taxonomic relationships of five species of Chrysobalanaceae and one of Meliaceae and Hernandiaceae are summarized. Most of these show trans-oceanic disjunctions and, in Africa, behave as ecological and chorological transgressors; morphologically they are variable. The potential importance of transgressors in the origin of new species and of evolutionary innovations, and in the interpretation of disjunctions is discussed.

RÉSUMÉ

INFLUENCE DE LA DISPERSION A LONGUE DISTANCE, DE LA MIGRATION DE PROCHE EN PROCHE ET DE L'EXTINCTION DES ESPECES, DANS LA FORMATION DES FLORES TROPICALES AFRICAINES

La répartition, l'écologie, les modes de dispersion probables et les relations taxonomiques de cinq espèces de Chrysobalanacées, d'une Méliacée et d'une Hernandiacée sont résumées. La plupart de ces espèces montrent des disjonctions transocéaniques et, en Afrique, se comportent comme des transgresseurs écologiques et chorologiques; morphologiquement, elles sont très variables. L'importance potentielle des transgresseurs dans l'origine de nouvelles espèces et de changements dus à l'évolution ainsi que dans l'interprétation des disjonctions, est discutée.

'Wide ranging, much diffused and common species vary most' — C. Darwin, Origin of Species (1859).

'It cannot be the same species: the ecology is different' — frequently overheard in herbaria.

INTRODUCTION

From the time of De Candolle (1855) and J. D. Hooker (for refs. see Turrill, 1953) to the present (e.g. Raven, 1972) disjunct distributions of plants have been of perennial interest to botanists, and their possible origins have been the subject of much controversy. The latter has centred largely on the relative importance of long distance dispersal and direct migration over existing and earlier land masses, followed by extinction in parts of the former range. In many cases the problem remains largely unresolved (White, in press, A). In recent years, however, rapid progress in our understanding of earth history, principally in the fields of plate tectonics and Upper Cenozoic world climatic change and deterioration, has led to renewed interest in the subject, and is providing a firmer scientific basis. There has also been an increase in our knowledge of possible modes of dispersal (e.g. Wickens, 1976) and in palaeobotany, though fossil evidence, even in the field of palaeopalynology, remains disappointingly meagre.

Important though these developments are, their value is diminished in the absence of detailed and accurate information on individual species, and on the distribution and salient features of the world's major phytochoria and vegetation types. For Africa, however, there has been significant recent progress in this area. Thanks largely to the efforts of many individual members of AETFAT, who have published monographic studies and revisions, or

have contributed to regional floras or to 'Distributions Plantarum Africanarum', and to the collective enterprise of the AETFAT Vegetation Map Committee (see White, 1976a; in press B (ed.); in press, C), the flora and vegetation of Africa are now probably better known than for most comparable parts of the tropics and subtropics. Much, however, remains to be done. Nevertheless, for several taxonomic groups, it is no longer true to say that 'taxonomic uncertainty and inadequate or uneven collecting' is a serious obstacle to biogeographical reconstruction (Street, 1981), though there may be other limiting factors.

When disjunctions are discussed attention is often focused on wide disjunctions involving taxa which have narrow geographical ranges, and, despite their relatively close relationship, are nevertheless sharply distinct. Such disjunctions are likely to have a long history behind them, and the longer that history is, the more difficult it is to interpret them.

By contrast, the present study is concerned with a small phytogeographical element, composed of species common to the American and African tropics, which appear to be adapted to dispersal by ocean currents, but also have extensive distributions in the interior of the continents, where they occur in several different vegetation types in two or more phytochoria. Hence they can be referred to as ecological and chorological transgressors (White, 1979). They are also very variable in their morphology and are either polytypic or are ochlospecies (White, 1978a). In studying such species, we are seeing evolution in action. Without adopting the doctrine of uniformitarianism in its extreme form, it is clear that situations such as these

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have much to tell us, not only about the nature of disjunctions, but also about the ways in which new taxa and evolutionary innovations arise. A knowledge of such species should also help to guide us in the interpretation of patterns which originated in the more distant past, and for which less evidence remains.

Three species, *Chrysobalanus icaco* (Chrysobalanaceae), *Carapa guianensis* (Meliaceae) and *Gyrocarpus americanus* (Hernandiaceae) are chosen to illustrate this theme. Their families have recently been monographed or are undergoing monographic revision. In order to cover the subject more comprehensively, four additional genera of Chrysobalanaceae, *Hirtella*, *Licania*, *Neocarya* and *Parinari*, are briefly mentioned. Within the single species *Chrysobalanus icaco*, perhaps we can see the beginnings and early stages of the evolution of an obligate strand plant. In the Meliaceae tribe *Xylocarpeae*, we can see both the beginnings and the end product, and for that reason, the mangrove genus *Xylocarpus* is considered alongside its close relative *Carapa*.

CHRYSOBALANACEAE

Of the 454 species in this pantropical woody family, 349 occur in America, 61 in Africa, of which two, *Chrysobalanus icaco* and *Parinari excelsa*, are shared with America (see below), and 46 in Asia and the Pacific. It is probably this striking disparity in floristic richness between the Old and the New Worlds that has led some authors (Raven & Axelrod, 1974, p. 585) to postulate an American origin for the group. This is contradicted, however, by the fact that of the 17 genera all but 3 occur in the Old World and 9 are confined to it.

The fruit of Chrysobalanaceae is remarkably

uniform in basic construction, though dispersal mechanisms are diverse, including transportation by fresh and sea water. The Chrysobalanaceae is one of the few pantropical families that have been comprehensively revised in recent times (Prance, 1972; White, 1976; Prance & White, in prep.).

Chrysobalanus

Two species are currently accepted (Prance & White, in prep.) — the amphiatlantic *C. icaco*, and *C. cuspidatus*, which is confined to the Windward & Leeward Islands (Fig. 1). Two subspecies are recognized in *C. icaco*, which is a transgressor, occurring in a wide range of vegetation types.

C. icaco subsp. *icaco* is widespread in the coastal regions of tropical and subtropical America from Florida to southern Brazil, and along the Atlantic seaboard of Africa from Senegal to Angola. Both in America and Africa it occurs mainly in coastal thicket on sandy shores, often immediately above the strand line. But it is also found on the landward side of mangrove swamps and further inland (up to 200 km in Africa and 600 km in South America) on the banks of rivers and in waterlogged wooded grassland (savanna).

C. icaco subsp. *atacorensis* is confined to Africa, where it is widely distributed in the interior of the continent on the banks of rivers, mostly in the Guineo-Congolian rain forest region, but also in scattered localities in fringing forest far to the north and south of the main blocks of rain forest.

The leaves of subspp. *icaco* and *atacorensis* are very different. Those of the former are coriaceous and orbicular; those of the latter are thinner and acuminate. Intermediates are found, however, wherever the two subspecies come into contact all the way from Liberia to Angola.

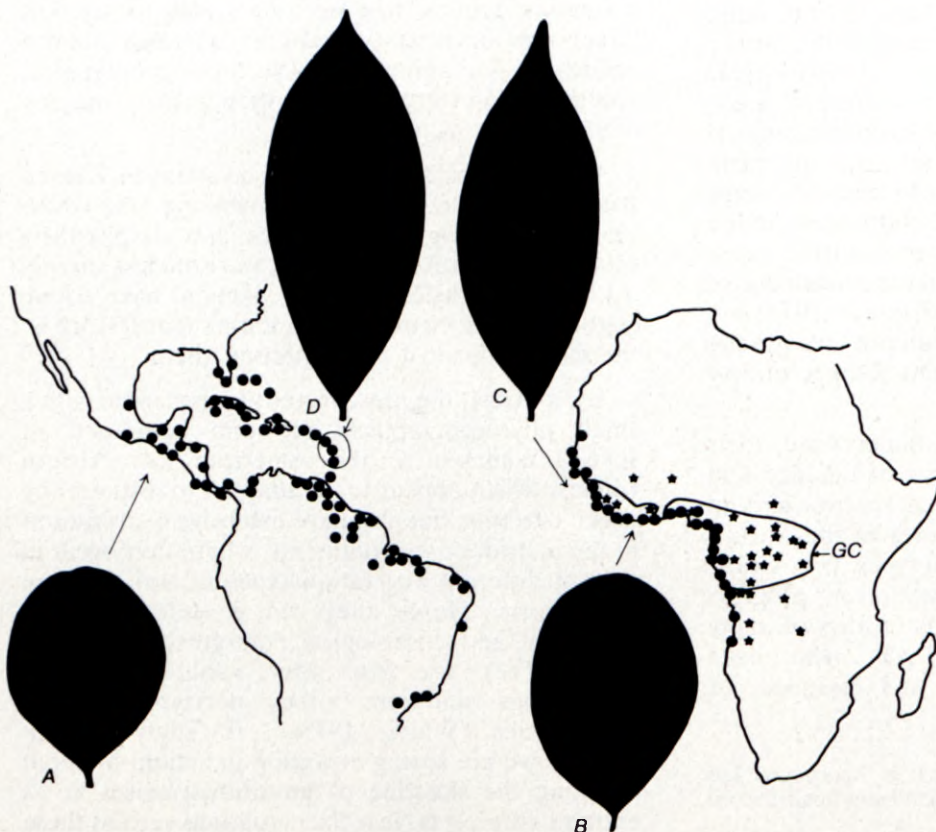


FIG. 1.—Pictorialized distribution map of *Chrysobalanus icaco* subsp. *icaco* (circles) and subsp. *atacorensis* (stars), and *C. cuspidatus* (distribution indicated by line encircling Windward and Leeward Islands) — after Prance (1972) and White (1976b, 1976c). A. *C. icaco* subsp. *icaco* (Standley 22023, El Salvador); B. *C. icaco* subsp. *icaco* (Jacques-Félix 7314, Guinea); C. *C. icaco* subsp. *atacorensis* (Dawe 44, Angola); D. *C. cuspidatus* (after Fl. Neotr. 9, Chrysobal., fig. 2) GC indicates the limits of the Guineo-Congolian region. All leaves $\times 0.5$.

In leaf-shape, *C. cuspidatus* and *C. icaco* subsp. *atacorensis* are similar, though there are differences in the inflorescence. The former is also a forest species, though in this case, it inhabits stunted forest on the crests of wind-swept ridges, where it forms up to 30 per cent of the stand. No intermediates have been found between *C. cuspidatus* and *C. icaco* subsp. *icaco*.

The pattern of relationships described above is complex as must also be its origin. Several alternative explanations can be offered to explain its origin, but the evidence available is indecisive. Leaving aside the less probable hypotheses it can be concluded that, either both the forest and the coastal forms have independently crossed the Atlantic at some time in the past, or that the forest form represents the primitive condition on one side of the Atlantic and has originated independently on the other side by reversion, and de-specialization.

The fruit of *C. icaco* is a fleshy drupe, which is dispersed by bats and ocean currents. It is buoyant because the seed, which can remain viable after the fruit has floated for two months, does not entirely fill the cavity of the endocarp. Large numbers of the latter can be found among the shore-line flotsam.

Hirtella

There are 92 species, of which 91 occur in tropical and subtropical America (Fig. 2). The remaining species, *H. zanzibarica*, occurs in East Africa and Madagascar. On the African mainland it is represented by subsp. *zanzibarica*, whilst four geographically replacing subspecies occur in Madagascar. Subsp. *zanzibarica* is a transgressor. It is widespread in fringing forest and various types of lowland forest, but in Tanzania it also ascends to 1950 m where it occurs in Afromontane rain forest. The closest relative of *H. zanzibarica* seems to be *H. bahiensis*, which is confined to a small area in NE Brazil.

At present it is difficult to account for the disjunct distribution of *Hirtella*, though there are parallels in other genera. This type of distribution has been reviewed by Stearn (1971), who suggested that the disjunct areas had their origin in the far distant past before the breakup of Gondwanaland. Such hypotheses can now be shown, however, to be discordant with recent views on plate tectonics and the early differentiation of the Angiosperms. Hence, it is necessary to seek alternative explanations involving both long distance dispersal and overland migration, accompanied, by extinction over a considerable area.

It is quite likely that taxa which have similar distributions today, were transported by different agents and have had quite different histories. Little is known of the dispersal of *Hirtella*, but the American species that have been studied are dispersed by birds, (G.T. Prance, pers. comn.). This would not, however, rule out the possibility of occasional trans-oceanic dispersal by currents, since the fruit of *Hirtella* is basically similar in construction to that of water-dispersed species of *Chrysobalanus* and *Licania*.

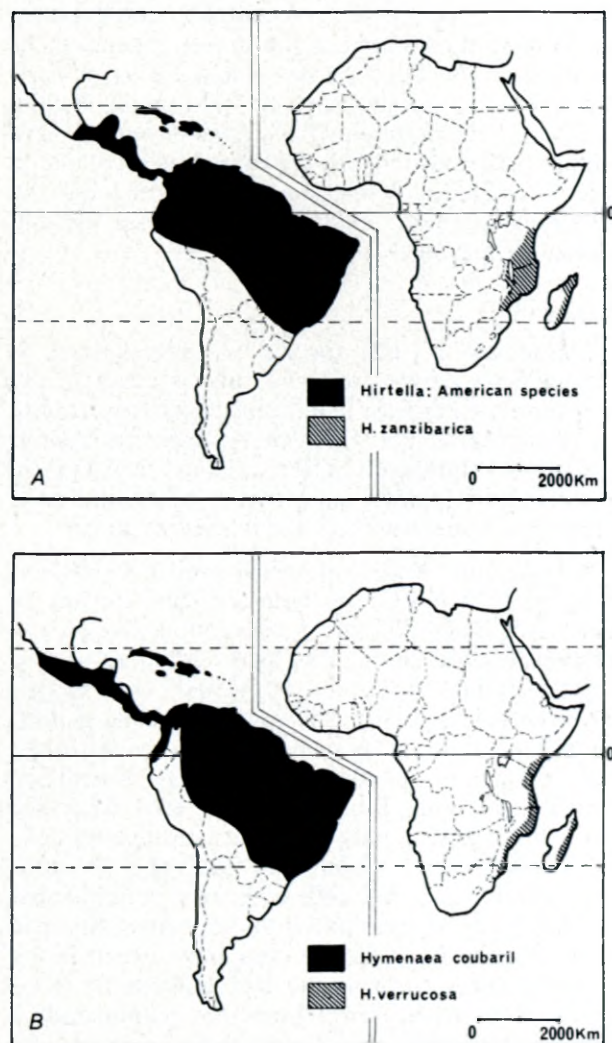


FIG. 2.—A, distribution map of *Hirtella* (after White, 1976b, 1976c, and Prance & White in prep.); B, distribution map of *Hymenaea* (after Langenheim, 1973). Note: the range of *H. coubaril* embraces those of the 16 remaining American species.

The distribution (Fig. 2B) of the genus *Hymenaea* (Leguminosae: Caesalpinioideae) is broadly similar to that of *Hirtella* (Langenheim, 1973; Langenheim & Lee, 1974; Lee & Langenheim, 1975). The only African species of *Hymenaea*, *H. verrucosa*, occurs in East Africa and Madagascar. It is a transgressor and its indehiscent pods are believed to be, at least in part, water-dispersed. Of the 13 American species of *Hymenaea*, *H. coubaril* is widely distributed in Central and South America and the West Indies. It also is a transgressor, and morphologically is very variable. Its pods are frequently encountered in drift and its seeds are said to retain their viability for several years. According to Lee & Langenheim (1975) ocean-dispersed pods of *Hymenaea* (species not stated) are commonly found along the southern shores of Florida. Seeds from this source were found to germinate within 7 – 10 days.

Despite the great disparity in number between the neotropical and African species, Langenheim and Lee believe that *Hymenaea* originated in Africa. They discuss the evidence for this at some length, but the pattern of relationships shown by the African and American taxa, as in *Chrysobalanus* (p. 396

and *Gyrocarpus* (p. 401), is complex, and evidence concerning the history of the group appears to be equivocal. The Leguminosae (including *Detarieae*), however, are good dispersers (Raven & Polhill, 1981), and the possibility that *Hymenaea* might have entered Africa from America cannot be ruled out on present evidence. *Hymenaea* is closely related to the neotropical genus *Peltogyne* which has typical, dehiscent leguminous pods.

Licania

There are c. 170 species. *L. elaeosperma* is confined to Africa, and two species occur in the forests of the Far East. All the others are neotropical in distribution (Fig. 3). The African and Asiatic species are sufficiently different from the American to require separate subgenera, *Afrolicania* and *Angelesia* respectively, to accommodate them.

Most of the American species occur in lowland rain forest, where 30 of them are characteristic of seasonally inundated forest, especially *várzea* forest of the Amazon basin. The fruits of some swamp forest *Licanias* are eaten by fishes (Gottsberger, 1978; Goulding, 1980). The stomachs of a large fish, *Lithodoras dorsalis*, have been found to be stuffed full of the fruits of *Licania longipetala*, which are capable of floating for two or three days. When the fruit skin is perforated or is penetrated by water the fleshy mesocarp, which acts like an air sack, disintegrates and the seeds sink. It is believed that the fish feeds at night and is an important dispersal agent. 'Seeds' (? endocarps) stripped of their fleshy covering, pass through the fish unharmed; those removed from the lower intestines germinated in experimental pots.

L. elaeosperma occupies a narrow coastal strip in West Africa from Guinea to Gabon. It occurs principally at the landward side of mangrove swamps and, further inland, in periodically flooded riparian forest. Its fruits are dispersed by water, but it is not known whether they are eaten by fishes.

L. elaeosperma has no close relatives in America, but it is possible that it is descended from a now extinct American swamp forest species, the fruits of which were transported across the Atlantic. The taxonomically isolated position of *L. elaeosperma* might be due to the extinction in Africa of other

species which formerly provided connecting links between it and the species now occurring on other continents.

It has long been suspected that fishes can effect dispersal, but the extent and importance of this phenomenon have only recently been established (Goulding, 1980). Much remains to be discovered, however. Most fruits eaten by fishes in Amazonia are buoyant and 'buoyancy may be the most important overall mechanism of the flooded forest community for seed dispersal' (Goulding, p. 225). 'The ecological significance of buoyancy', however, 'in relation to predation and dispersal by fishes is not without its mysteries' (*tom. cit.*, p. 226). *Licania* is one of many amphi-atlantic genera with swamp forest species on one or both sides of the Atlantic. Even though the origin of buoyancy and the significance of fishes are imperfectly understood, there can be little doubt that buoyancy of fruits as an adaptation to swamp forest conditions has pre-adapted many genera to transoceanic dispersal.

Neocarya

N. macrophylla, the only member of its genus, is mentioned because, although it is confined to Africa, it is a transgressor with an unusual distribution (Fig. 4). It is common in West Africa in a coastal strip up to 300 km wide extending from Senegal to Liberia. It also has a scattered east-west distribution in the much drier and more continental northern half of the Sudanian Region 700–1 000 km inland. Throughout its range it seems to be confined to sandy soils. Its Sudanian distribution is presumably relictual from a wetter epoch. Other species, which resemble *N. macrophylla* in being abundant in the wetter subcoastal parts of West Africa and also have relictual populations inland, are discussed by Jaeger (1959). Among the latter, the best-known is *Guibourtia copallifera*, which is locally dominant on the sandstone escarpment of Bamako (Mali), where *N. macrophylla* also occurs. Notwithstanding its diverse ecology, in morphology, *N. macrophylla* is not very variable.

Parinari

Forty-four species are currently accepted, 18 in tropical America, 6 in tropical Africa and the remainder in tropical Asia eastwards to Polynesia (Fig. 5).

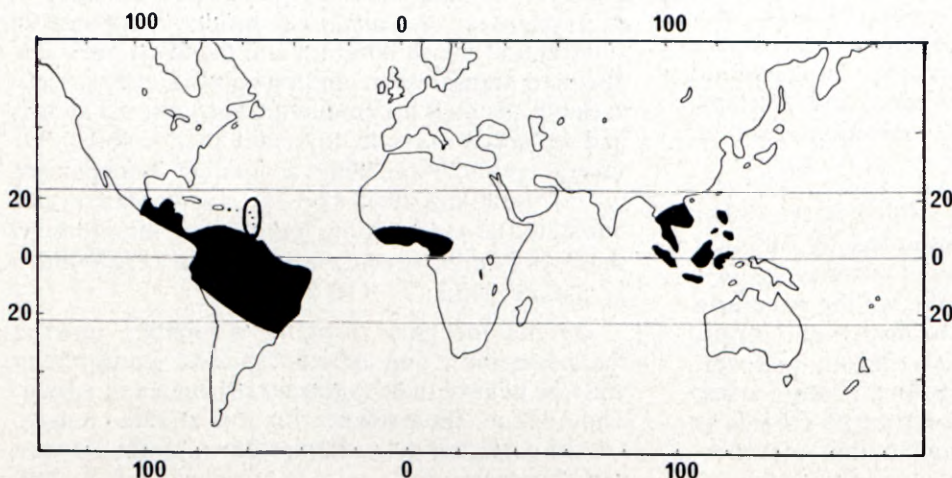


FIG. 3.—Distribution map of *Licania*.

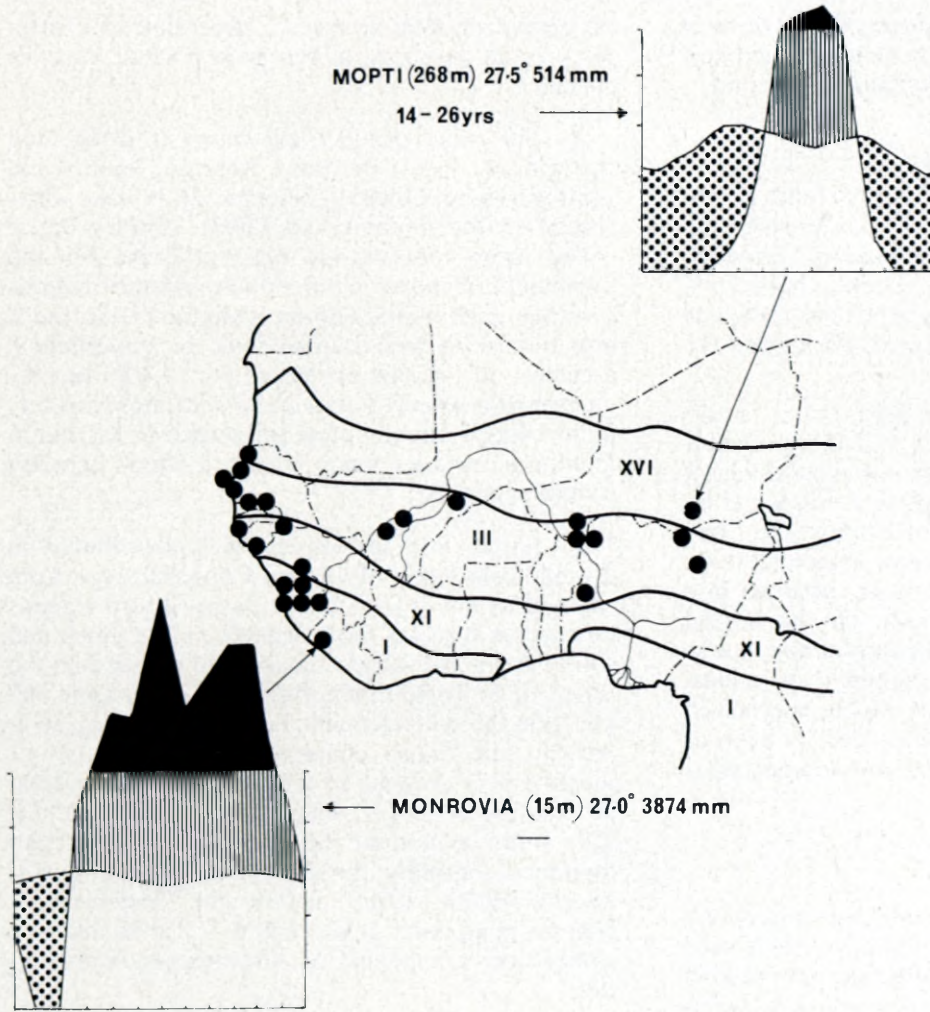


FIG. 4.—Distribution map of *Neocarya macrophylla* (after White, 1976b, 1976c) with climatic diagrams for two stations. I. Guineo-Congolian Region; XI. Guinea-Congo/Sudania transition zone; III. Sudanian Region; XVI. Sahel transition zone.

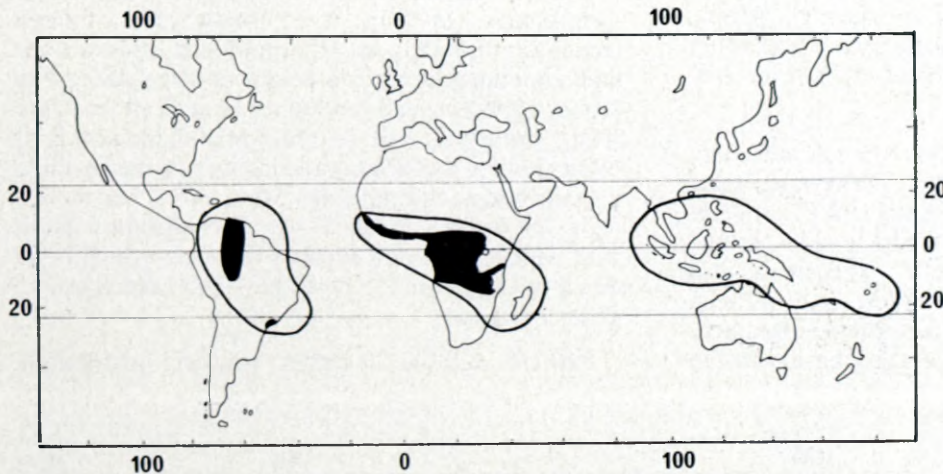


FIG. 5.—Distribution map of *Parinari excelsa* (after Prance, 1972 and White, 1976b, 1976c) is shown in black.

Most species occur in lowland rain forest, though some are found in other forest types, in woodland and in wooded grassland. The most widely distributed American species, which extends from Colombia to south-east Brazil, is thought to be conspecific with the African *P. excelsa*. The African species are closely related to one another, but each one is at least partly sympatric with from one to four others. The evergreen forest species *P. excelsa*, the woodland species *P. curatellifolia* and the geoxylic rhizomatous suffrutex *P. capensis* are extremely similar in the structure of their leaves, flowers and fruits, despite their widely divergent habits and

ecology. Their geographical ranges show substantial overlap and intermediates of putative hybrid origin are virtually non-existent. In Africa, *P. excelsa* is a transgressor. It is widespread in Guineo-Congolian lowland rainforest, in Afromontane rain forest and in Zambezian dry evergreen forest, as well as occurring, often abundantly, in other vegetation types. Morphologically, however, it is rather uniform in Africa, but is much more variable in America. In Africa *P. excelsa* is said to be dispersed by bats, elephants and monkeys. There is no evidence that the fruits of *Parinari* can be successfully transported by ocean currents, but, in view of the

importance of that means of dispersal elsewhere in the family (Prance & White, in prep.), it is likely that such a mechanism has been effective in the past.

MELIACEAE

In this family there are 51 genera and c. 550 species (Pennington & Styles, 1975). Most genera have relatively restricted distributions. *Trichilia*, alone, is pantropical. Only two genera, *Guarea* and *Carapa*, occur in Africa and the neotropics, whereas four, including *Xylocarpus*, occur in Africa and the Far East.

In my opinion, *Carapa* consists of a single ecologically and morphologically variable species. It is an ochlospecies and an ecological and chorological transgressor. Its seeds are adapted to dispersal by fresh water, and in all probability are also successfully transported by ocean currents. It is, however, essentially an inland plant, although in a few places, it occurs sporadically on the littoral itself. *Xylocarpus* is closely related to *Carapa*, but its 2 or 3 species are obligate members of coastal communities and are extremely highly specialized for dispersal by sea water. *Carapa* and *Xylocarpus* are allopatric. An interval of 700 km separates their ranges.

Carapa and Xylocarpus

These genera are closely related and collectively form the tribe *Xylocarpeae*. They have often been united in the past, but no difficulty is experienced in separating them. Ecologically they are very different. *Carapa* is widely distributed in rain forest in tropical America and in West and Central Africa, whereas *Xylocarpus* occurs in mangrove and other coastal habitats from East Africa to Polynesia (Fig. 6).

In *Carapa*, species delimitation is weak and there has been persistent uncertainty concerning their number. Two species, *C. guianensis* and *C. procera*, are currently accepted for America (Fl. Neotr., Meliaceae, p. 406), of which *C. procera* is also widely distributed in Africa. A second African species, *C. grandiflora* is also sometimes recognized. In my opinion, it is doubtful whether these taxa can

be upheld, at least at specific rank. It seems better for present purposes, to recognize a single variable species.

In the neotropics *C. guianensis* is distributed throughout most of the Amazon basin and northwards to Central America. It is also widespread in the Greater and Lesser Antilles but is absent from Jamaica and most of Cuba. On the mainland it is mostly confined to rain forest regions in which its favoured habitat is swamp forest, but it also occurs on well-drained soils. In Venezuela it ascends on mountain slopes to 1400 m. *C. guianensis* is usually found in the understorey, rarely in the canopy, of rain forest and swamp forest, but in Dominica it has been reported from scrubby windswept forest.

In Africa this species is widely distributed in lowland rain forest of Guineo-Congolian type from Senegal to the Lake Victoria Basin. It also extends in riparian forest a short distance to the north and south of the main forest blocks, and is found on the island of S. Tomé in the Gulf of Guinea, some 300 km from the African mainland. As in America, so in Africa, the most characteristic habitat of *C. guianensis* is lowland swamp forest, but it occurs, though less plentifully, where drainage is better. It is also often abundant on some of the African mountains, namely those of the Kivu-Ruwenzori system (White, 1978b) and in the Cameroun-SE Nigeria Highlands. It ascends to 2200 m and is a conspicuous component of Afrotropical communities.

Carapa guianensis is extremely variable in its morphology. In habit it is usually erect, though frequently mis-shapen. In America it often attains and sometimes exceeds a height of 30 m, though in Africa 20 m is usually its upper limit. Tall trees are richly branched, but in the forest understorey it often flowers and fruits precociously in the juvenile unbranched pachycaul stage when only a few metres high. Sometimes it shows an extraordinary habit with widely divergent arcuate branches which bend down to the ground, where they then take root and grow up again.

Other variable features concern leaf-length,

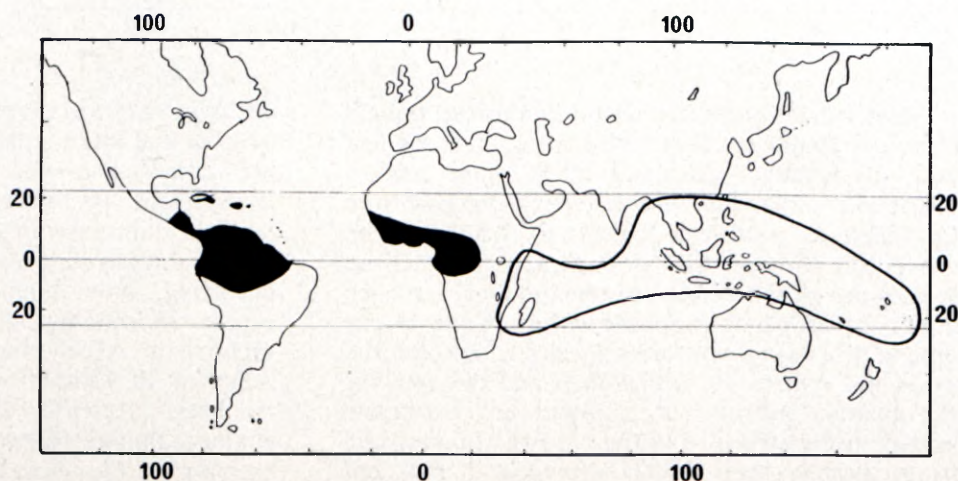


FIG. 6.—Distribution map of *Carapa* (black) and *Xylocarpus* (encircled).

number, size and shape of leaflets, inflorescence-branching, flower-size, and number of floral parts and seeds. Variation in these characters is poorly correlated, both among the characters themselves and with geography and ecology, though some variants are confined to, or occur plentifully in, certain geographical areas of restricted extent and might possibly serve in the recognition of weakly defined infraspecific taxa. The overall pattern, however, is clearly polytopic and indicates that most, possibly all, character states have arisen independently in several different places.

The seeds of *C. guianensis* are eaten by rodents, monkeys and wild pigs, which presumably are mostly destructive. They, or other animals, must, at least occasionally effect dispersal, otherwise the occurrence of *C. guianensis* on high mountains would be difficult to explain. In fresh water swamps and on the banks of rivers the buoyant seeds are transported by water, and have been observed to germinate on the white sand beaches of the Rio Negro (T. D. Pennington, pers. comm.). In Amazonia they are also eaten by fishes (Gottsberger, 1978), but it is not known whether they are ever dispersed by this means. That *Carapa* can be transported by ocean currents is shown by the occurrence of seeds in drift at Pointe Noire on the west coast of Africa (Muir, 1937), and on the shores of Yucatan (B. T. Styles, pers. comm.). It is not known whether such seeds are viable, but it seems likely that oceanic transportation has been responsible for the occurrence of *Carapa* on both sides of the Atlantic.

Although *C. guianensis* probably owes much of its present-day geographical distribution to dispersal by sea water, it seems to occur only exceptionally in coastal habitats. There are a few records, both for America and Africa, from the inner margins of mangrove, but fresh-water swamp forest further away from the coast seems to be a more characteristic habitat. There is, however, one record from the edge of the sea itself. Thus Letouzey (No. 14950) found it growing in Cameroun with *Terminalia catappa* on black volcanic sand just above high-water mark. *T. catappa*, although not indigenous to Africa, is widely naturalized along the West African coast, and is a sea-dispersed species *par excellence*.

The buoyancy of the seed of *Carapa* is due to its light, woody arilloid, which is probably homologous with the fleshy arilloid of *Trichilia* and its relatives, and with the seed wing of *Entandrophragma* and other Swietenioideae. In *Xylocarpus* specialization for water-transport is carried much further. The arilloid is thicker, angular in shape and corky in texture. There is no dormancy and the seeds begin to germinate as soon as they are released into water. According to Troup (1921) it is the germinating seedling, not the dormant seed, that is the unit of dispersal. The thickness of the arilloid is very uneven, but is thinnest at the micropyle. The seed is so constructed that it always floats in a position such that, when the seedlings breaks through, the radicle is submerged and the plumule is emergent from the water (F. White, pers. obs.). Two species of *Xylocarpus* occur in mangrove swamps and have pneumatophores or ribbon-like breathing roots; the third is a plant of sandy and rocky coasts.

HERNANDIACEAE

This family, which has been recently monographed (Kubitzki, 1969), consists of four genera and 58 species. Some species of *Gyrocarpus* and *Hernandia* are widely distributed by ocean currents.

Gyrocarpus

Several species have been described, but Ridley (1930) thought they were all forms of one, the pantropical *G. americanus*, except possibly for *G. hababensis*, which is confined to the Horn of Africa (Fig. 7). Kubitzki keeps a third species, *G. jatrophifolius* separate. It occurs in Mexico and Central America from sea level to 1 800 m, and its range overlaps slightly with that of *G. americanus*. Within the pantropical *G. americanus* Kubitzki recognizes eight, mostly allopatric, but partly overlapping subspecies.

As in *Chrysobalanus icaco* and in *Carapa guianensis*, so in *Gyrocarpus americanus*, we are dealing with a taxon which shows at least one transoceanic disjunction and occurs in diverse habitats in the continental interior. In *Gyrocarpus*, however, the distribution is fragmented, especially in Africa, and the overall pattern of taxonomic relationships is somewhat complex. There can be

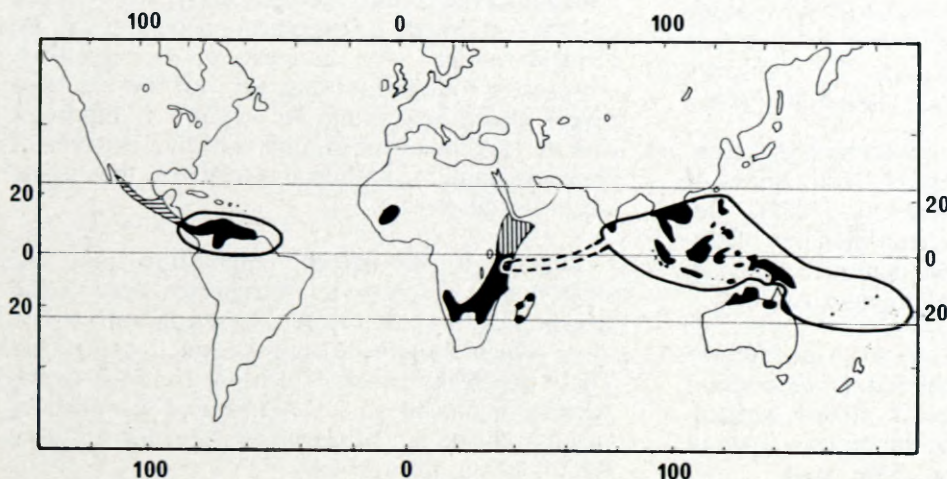


FIG. 7.—Distribution map of *Gyrocarpus*. *G. jatrophifolius* (horizontal lines); *G. hababensis* (vertical lines); *G. americanus* (black, with subsp. *americanus* encircled). After Kubitzki (1969).

little doubt that this complexity is the result of a complex history involving several different successful dispersals between widely separated regions, followed by expansion of range and much subsequent extinction. In a detailed and interesting analysis Kubitzki has attempted to unravel this history, based largely on the geographical distribution of certain 'unidirectional trends'. The differences between taxa in *Gyrocarpus*, however, are so slight that the possibility of a reversal of trends must be borne in mind.

One of the Kubitzki's conclusions is that sea-dispersal in *Gyrocarpus* has been relatively recently acquired, and that some intercontinental disjunctions are of Gondwanic origin. For reasons given elsewhere (White, in press A) it now seems unlikely that many extant genera of Angiosperms were in existence before Africa separated from South America in the Cretaceous. It seems much more likely that there were early transoceanic dispersals of *Gyrocarpus* that were perhaps 'accidental', and that subsequently, in certain parts of its range, but not in all, *Gyrocarpus* became adapted, at least facultatively, to coastal habitats, and hence more dependent on transportation by sea water.

Kubitzki, following a remark of Chevalier (1938) and others, suggests that the present distribution in West Africa of *G. americanus* subsp. *pinnatilobus* might be located near an ancient shore-line, but there seems to be little geological evidence for this. The fact that *G. americanus* subsp. *africanus* south of the equator, has a scattered distribution right across Africa, shows that this species is capable of crossing continents. The isolated position of subsp. *pinnatilobus*, north of the equator, is presumably relictual from a former, wider distribution.

In inland localities the winged fruits of *Gyrocarpus* are dispersed by wind or (down stream) by streams and rivers. Fruits which find their way to the sea can drift to distant coasts and to islands, since they can float and remain viable for at least two months (Ridley, 1930).

Gyrocarpus americanus occurs as a strand plant in only part of its range. In the Far East it is widespread from India, Ceylon and the Cocos Islands to Fiji, Samoa and Tonga, and is often abundant near the shore. Nevertheless, it has an unpredictably patchy distribution in this part of the world and is by no means confined to coastal habitats. On Christmas Island, New Guinea and Tahiti it ascends to 700 m.

In America, *G. americanus* occurs both in coastal habitats, e.g. in coastal thicket with *Spondias mombin* in Venezuela (Aubréville, 1949), and inland, where it is a characteristic member of dry deciduous woodland (A. M. Sugden, pers. comm.). It is absent from the Greater and Lesser Antilles.

In Africa all known stations are from the interior. Even in the East African coastal belt, *G. americanus* subsp. *americanus*, the typical strand variant, occurs, not on the shore, but in various types of forest, some distance from the shore itself.

Ecologically, *G. americanus* is very versatile. It occurs in a wide range of forests, woodlands, bushlands and thickets.

DISCUSSION

Of the seven species described above, one, *Licania elaeosperma*, is taxonomically isolated, ecologically specialized, and has a restricted distribution; it is clearly a relic. All the others are ecological and chrological transgressors, and all but one, *Neocarya macrophylla*, are extremely variable. *Chrysobalanus icaco*, *Hirtella zanzibarica* and *Gyrocarpus americanus* are polytypic, whereas *Parinari excelsa* and *Carapa guianensis* are ochlo-species.

The study of morphologically variable transgressors can contribute much to our understanding of the past, but it should be remembered that at any one time their number is likely to be small. Thus, White (1979) has estimated that only 1.6% of Guineo-Congolian species come into this category, whereas Hall & Swaine (1981), adopting a more elastic concept, regard 12% of the Guineo-Congolian flora in Ghana as transgressors. Also, in the past, transgressors might have shown very different patterns of relationship.

For at least 40 years zoologists have had clear ideas on the predominant mode of speciation — geographical or allopatric speciation — in the animal kingdom, though its universality has recently been questioned (see M. J. D. White, 1978). Nevertheless, 'it is now widely accepted that in most animal groups this is the main, or indeed the only, way in which speciation takes place' (Snow, 1981).

Although botanists have paid lip-service to geographical speciation, for the most part, they have concentrated on such topics as ecotypic differentiation, clinal variation and introgression, which it now seems are relevant to only a small part of the story. My own experience of the African flora leads me to believe (e.g. White, 1955, 1962) that geographic speciation, at least for the larger woody plants, is the predominant mode. I would like to suggest that transgressors, such as those discussed in the present account, when studied with their closest relatives in a monographic context, provide important evidence on ways in which geographical speciation can be brought about. The interest of transgressors, however, is much wider than this, for they can also reveal clues concerning the origin of important evolutionary innovations, and changing patterns of plant distribution, both in the relatively recent and more distant past.

Finally, it should be emphasized that the transgressors described above represent only a small selection of those that exist. I have concentrated on those which show wide trans-oceanic disjunctions. There are many others which are confined to the African mainland or to Africa and its offshore islands, including Madagascar (see for instance White, 1978a; in press, A).

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