

MALAGASY/INDO-AUSTRALO-MALESIAN PHYTOGEOGRAPHIC CONNECTIONS

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ABSTRACT.- Despite the continuous close proximity of Madagascar to Africa since its separation from the continent ca. 165 MYA, the Malagasy flora exhibits a remarkably high affinity with the Indo-austral-malesian floras far to the east. Such phytogeographic connections are especially prevalent among eastern humid forest taxa, and represent both ancient vicariance that has resulted in relictual (Cretaceous) Gondwanan disjunctions, as well as continuous dispersal events across the Indian Ocean. Three major patterns of dispersal/vicariance modality can be identified: 1) Cretaceous dispersal to Madagascar with ensuing distributions from India (and/or South Africa) across Antarctica to South America and Australo-E. Malesia during the time of the initial radiation of the angiosperms; 2) Eocene-Oligocene (and continuing to the present) dispersal to Madagascar (and Africa) from Laurasia and W. Malesia via India (pre- and post-collision with Asia) along « Lemurian Stepping-stones » in the western Indian Ocean; and 3) continuous (and recent) long distance dispersal (LDD) to Madagascar as a function of the prevailing easterly winds and Indian Ocean currents.

KEY-WORDS.- Madagascar, Indo-Australo-Malesian, Phytogeography, Vicariance, Dispersal

RESUME.- Malgré la proximité de Madagascar et de l'Afrique depuis leur séparation, il y a quelques 165 millions d'années, la flore malgache montre une affinité remarquable avec celles de la région Indo-austral-malésienne très éloignée vers l'est. Ces relations phytogéographiques sont particulièrement fréquentes dans les taxons des forêts humides de l'est de Madagascar ; elles représentent d'une part une vicariance ancienne qui a entraîné des disjonctions reliques gondwaniennes (Crétacé) et d'autre part une série continue de dispersion à travers l'Océan Indien. Trois modèles principaux de dispersion/vicariance à Madagascar peuvent être distingués : 1) Au Crétacé une dispersion qui a entraîné des types de répartition qui s'étendent de l'Inde (et/ou l'Afrique du Sud) jusqu'à l'Amérique du Sud et la région australo-est-malésienne à travers l'Antarctique, pendant la période initiale de diversification des angiospermes ; 2) Pendant l'Eocène-Oligocène une dispersion encore actuelle et également africaine, de taxons Laurasiens et ouest Malésiens via l'Inde avant et après son entrée en collision avec l'Asie par l'intermédiaire d'îles (« Lemurian Stepping-stones ») situées dans l'ouest de l'Océan Indien ; 3) Une dispersion à longue distance continue et plus récente due aux vents et aux courants océaniques dominants de l'est.

MOTS-CLES.- Madagascar, Région Indo-austral-malésienne, Phytogéographie, Vicariance, Dispersion

INTRODUCTION

As a former piece of the African continent that has remained in close proximity throughout its evolutionary history, Madagascar would reasonably be expected to

possess a biota whose closest affinities are African. Recognition therefore of phytogeographic connections with floras far to the east has attracted the interest of botanists since the classic work of PERRIER DE LA BATHIE (1936). Subsequent workers have adopted and refined the characterization of floristic affinities by percentage generic overlap within arbitrarily delimited geographic units (« elements »), among which « Asian », « oriental », « paleotropical », and « austral » have been utilized to reflect the eastern affinities (HUMBERT, 1959; KOECHLIN *et al.*, 1972; DEJARDIN *et al.*, 1973). However, as LEROY (1978) correctly pointed out, such analyses of relationship depend upon taxonomic circumscription of genera rather than phylogenetic hypotheses, and fail to address process in historical biogeography. The distinction made by AUBREVILLE (1976) between « Australo-Papoue » as Gondwanan elements and « Asiatico-Malesienne » as Laurasian elements set the stage for a more explicit discussion of the historical patterns leading to modern-day relationships between the floras of Madagascar and Indo-australomalasia. In that context, utilizing data from recent phylogenetic, paleobotanical, and paleogeographic studies, I would like to illuminate further what I believe to be the three major modes of dispersal/vicariance between Madagascar and lands to the east: 1) Cretaceous Gondwanan Relicts; 2) Eocene-Oligocene « Lemurian Stepping-stones »; and 3) Long Distance Dispersal (LDD).

CRETACEOUS GONDWANAN RELICTS

Paleomagnetic data from the western Indian Ocean has firmly established the paleogeographic history of Madagascar (RABINOWITZ *et al.*, 1983). Figure 1 depicts a schematic representation of Gondwanan land masses from the time Madagascar arrived at its current position 121 MYA until the separation of Greater India from Madagascar 88 MYA (STOREY *et al.*, 1995), by which time the break-up of virtually all of the individual Gondwanan land masses had begun. Throughout the period rifting was occurring both between Africa/South America and Greater India/Antarctica, although each pair remained within close proximity through the end of the Cretaceous/early Tertiary. By 80 MYA, direct land routes between New Zealand and New Caledonia and Antarctica/Australia had been severed (MILDENHALL, 1980); very slow rifting between Australia/New Guinea and Antarctica had also begun, but New Guinea did not emerge above sea level until the late Eocene at which time Gondwanan elements first entered (AXELROD & RAVEN, 1982). A dispersal pathway through Antarctica to South America remained possible until the close of the Eocene (RAVEN, 1979).

The time period spanned in Figure 1 is also contemporaneous with the initial radiation of the angiosperms. Insofar as Madagascar began to separate from Africa during the late Jurassic (165 MYA), it is probable that angiosperms were not present on the island during most of its slow rafting to its current position. Paleobotanical data from Madagascar at this critical time period are scant. Palynomorphs from mid-Cretaceous (middle Albian to late Cenomanian) samples near Antsiranana belong to the Gondwana microfloral Province, dominated by bisaccate gymnosperms and ferns, but are lacking angiosperms (HERNGREEN *et al.*, 1982). Another Cenomanian assemblage from Ankanotra is dominated by the conifer *Classopollis*; however, six different angiosperm pollen types are present. Despite the lack of late Cretaceous data, it is reasonable to assume that by the close of the Mesozoic, numerous angiosperm lines had established themselves in Madagascar via either direct land routes through India from the south, or by short distance dispersal across water gaps.

What neobotanical evidence therefore (as well as paleobotanical data from elsewhere in Gondwana) points to the presence of Cretaceous Gondwanan relicts in Madagascar? The break-up of Gondwana by the end of the Cretaceous would have resulted in vicariance in basal angiosperm lineages, and thus, relationships today would be manifest at higher taxonomic levels (VAN STEENIS, 1984). Modern distributions would be essentially austral and/or cool mesic (pre)montane: South America, extending northward along the Andes into Central America; Africa, especially cooler upland East Africa (with survival into the Miocene and then extinction in South Africa (COETZEE & MULLER, 1984)); Madagascar; and Australo-malesia east of Wallace's line, *i.e.*, Australia, New Caledonia, New Guinea, and New Zealand. The possibility of « Noah's Ark » rafting on India, and therefore the presence of relicts on the granitic islands of the Seychelles and India/Sri Lanka, as well as then subsequent dispersal into W. Malesia must also be considered (a scenario rejected by RAVEN & AXELROD, 1974). Mid to late Cretaceous/early Tertiary floras from Antarctica, Australia and New Zealand (BIRKENMAJER & ZASTAWNIAK, 1989; BURGER, 1993; DETTMAN, 1989; DETTMAN & JARZEN, 1990; MILDENHALL, 1980) confirm the notion of a subhumid mesothermal climate across Antarctica, which supported a broad-leaved forest with numerous angiosperm pollen types. Space permits the discussion of only a few examples to illustrate the distribution patterns above:

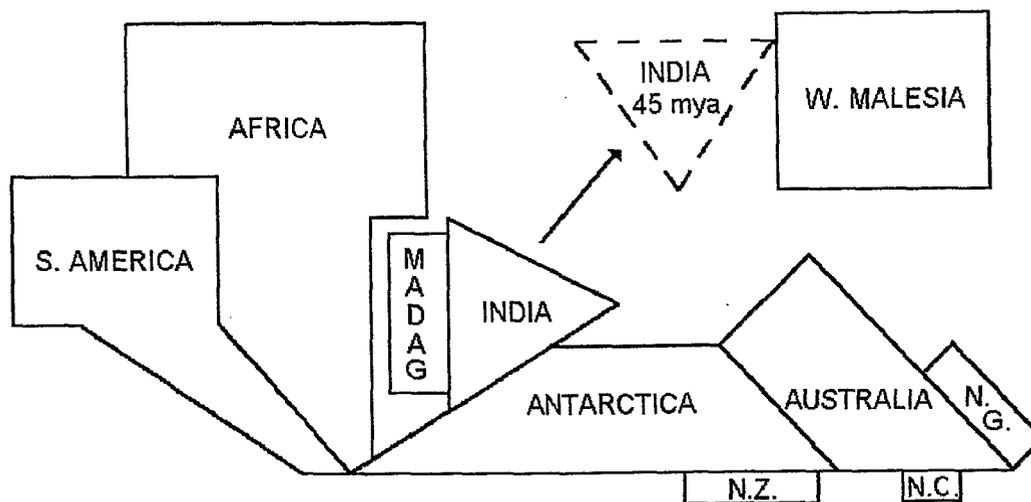


Fig. 1. Schematic representation of Gondwanan land masses during initial Cretaceous radiation of the angiosperms, between the time of arrival of Madagascar at its present position (121 MYA) and the time of separation of Greater India from Madagascar (88 MYA). Throughout the time period, rifting is occurring between both Africa/South America and Greater India/Antarctica, although each pair remains within close proximity at the end of the period. India is also shown (broken border) after collision with Asia (45 MYA), at which point a direct link with W. Malesia is established. Abbreviations: MADAG = Madagascar; N.C. = New Caledonia; N.G. = New Guinea (submerged until late Eocene); N.Z. = New Zealand.

Proteaceae: The studies of JOHNSON and BRIGGS (1981) have revealed two independent relict lines of Proteaceae in Madagascar. Isolated dioecious *Dilobeia* (2

spp.), the sole member of subtribe Dilobeiinae appears to be sister to the subtribe Cenarrheninae consisting of two monotypic genera on Tasmania (*Agastachys* and *Cenarrhenes*), two genera endemic to New Caledonia (*Beaupreopsis* (1 sp.) and *Beauprea* (12 spp.; with fossil distribution in Australia and New Zealand)), and a more xeric taxon *Symphionema* (2 spp.) in N.S. Wales. From a base number of $x = 14$ for subfamily Proteoideae, chromosomal evolution indicates aneuploid reductions from *Cenarrhenes* ($x = 14$) to *Agastachys* ($x = 13$), *Beauprea* and *Beaupreopsis* ($x = 11$), and *Symphionema* ($x = 10$), as well as polyploidy in *Dilobeia* ($x = 24$).

Subtribe Hickbeachiinae of subfamily Grevilleoideae is comprised of *Malagasia* (1 sp.) in Madagascar, *Athertonia* (1 sp.) and *Hicksbeachia* (2 spp.) in N.E. Australia, *Virotia* with 6 spp. probably endemic to New Caledonia (plus 1 sp. doubtfully placed in the genus from Queensland), and *Heliciopsis* with 7 spp. restricted to W. Malesia. Relationships among the genera are not fully resolved, but if *Malagasia* is most closely related to *Heliciopsis* as suggested by JOHNSON and BRIGGS (1981), then one could propose rafting of the ancestors of *Heliciopsis* on India, dispersal into W. Malesia, and subsequent extinction in India.

Basal Apiales: Recent molecular systematic studies by PLUNKETT (1994, pers. comm.) and PLUNKETT *et al.* (1995) suggest a placement for the Malagasy endemic *Melanophylla* (8 spp.) at the base of the Apiales among the genera *Aralidium* (1 sp., W. Malesia), *Toricellia* (3 spp. E. Himalayas to W. China), and *Griselinia* (6 spp., New Zealand and Chile), all of which have been recognized at the family level. Whether they constitute a clade is still unresolved insofar as several shared indels (insertion/deletion events) within the *matK* chloroplast gene are plesiomorphic and also shared with outgroup Cornales. Nevertheless, *Melanophylla* may be closest to *Aralidium*, reflecting possible rafting on India for their common ancestor as well as for *Toricellia*, and, in addition, an austral dispersal for *Griselinia* [(first appearance in New Zealand in Miocene (MILDENHALL, 1980)], a scenario potentially analogous to the Hicksbeachiinae (Proteaceae).

Monimiaceae: The studies of LORENCE (1985) and PHILIPSON (1987) have shed light on the relationships of Malagasy region Monimiaceae. *Hortonia* (2 spp., Sri Lanka), *Peumus* (1 sp., Chile), *Palmeria* (14 spp., New Guinea (mostly), E. Sulawesi and Australia), and *Monimia* (3 spp., Mascarenes) appear to be the most primitive members of the family (although not necessarily forming a clade), suggesting rafting on Greater India for *Hortonia*, and extinction of the ancestors of *Monimia* in Africa/Madagascar given the ages of Mauritius (7.8 MY) and Réunion (2 - 3 MY). *Decarydendron* (3 spp.) and *Ephippiandra* (8 spp.) (both endemic to Madagascar) and *Tambourissa* (ca. 50 spp., Madagascar and Mascarenes) are members of tribe Hedycaryeae, which also includes in E. Malesia: *Hedycarya* (11 spp., New Caledonia (mostly), New Zealand, Australia to Fiji), *Kibaropsis* (1 sp., New Caledonia), and *Levieria* (9 spp., Queensland, New Guinea to Sulawesi), and in Africa: *Xymalos* (1-3 spp., from Sudan to S. Africa and E. Congo, disjunct on Mt. Cameroon and Bioko, occurring from 900 - 2700 m).

Hamamelidaceae: The distribution of subtribe Dicoryphinae mirrors that of the Hedycaryeae (Monimiaceae). Unique tetrasporangiate anthers that dehisce by a single valve per theca constitute a synapomorphy for *Trichocladus* (3-5 spp., mid-altitude E./S. Africa), Malagasy endemic *Dicoryphe* (13 spp.), and monotypic *Noahdendron*, *Neostrearia*, and *Ostrearia* in N.E. Australia (ENDRESS, 1989a,b). Similar univalvate anther dehiscence, albeit with a reduction to only one locule per theca is known in

Archamamelis from the Upper Cretaceous of Sweden (ENDRESS & FRIIS, 1991), as well as modern-day *Hamamelis*, indicating an early Laurasia/Gondwana split in the family.

Didymelaceae/Schizocolpus: Recent molecular data suggest that the affinities of the Malagasy endemic *Didymeles* (Didymelaceae) are with the Buxaceae (M. CHASE, pers. comm.). Distinctive, unique pollen (3-zonocolporate, with 2-orate, operculate colpi and a reticulate, columellate tectum with spinulose muri) has permitted unequivocal identification of the fossil pollen *Schizocolpus marlinensis* as Didymelaceae. *Schizocolpus* is known from the Paleocene to Oligocene along the now-submerged Ninety East Ridge (KEMP & HARRIS, 1977), the Paleocene to lower Eocene of New Zealand (MILDENHALL, 1980) and the middle Eocene Gippsland Basin of Australia (STOVER & PARTRIDGE, 1973), indicating a formerly much larger late Cretaceous/early Tertiary distribution.

Additional probable or possible late Cretaceous/early Tertiary Gondwanan Relicts in Madagascar (or the Mascarenes): *Podocarpus* (Podocarpaceae); *Ascarina* (Chloranthaceae); *Takhtajania* (Winteraceae); some Annonaceae (however not an austral dispersal, but rather an early southern Laurasian/N. Tethys dispersal and/or rafting on India); Myristicaceae; *Cinnamosma* (Canellaceae); *Beilschmiedia*, *Cryptocarya* (Lauraceae); *Ilex* (Aquifoliaceae); *Syzygium/Eugenia* (Myrtaceae); *Pittosporum* (Pittosporaceae); *Weinmannia* (Cunoniaceae); *Elaeocarpus/Sloanea* (Elaeocarpaceae); *Brexia* (basal Celastrales); *Lilaeopsis* (Apiaceae); *Protium* (?) (Bursaceae) and other basal Sapindales, i.e., Rutaceae/Sapindaceae (*Cossinia* ?) (Sapindaceae) - 1 sp. Mauritius, 3 spp. New Caledonia; *Kaliphora* (?) (Kaliphoraceae); some Menispermaceae (?) (*Burasaia*, *Spirospermum*, *Strychnopsis*); some Clusiaceae (?) (*Garcinia*, *Symphonia*, with *Montrouziera* in New Caledonia); *Arthropodium* (Liliaceae); *Cohnia* (?) (Agavaceae) - 1 sp. Mauritius, 2 spp. New Caledonia; Arecaceae: Borasseae (*Borassodendron* rafting on India?); *Beccariophoenix*, *Voanioala* (Butiinae); *Ravenea* (Ceroxyloideae); *Orania* (Oraninae); Iguanurinae (?) (27 genera mainly E. Malesia; absent in Madagascar, *Dictyosperma* (Mauritius), *Bentinckia* (S. India)); Oncospermatinae (*Oncosperma* - Sri Lanka to W. Malesia; absent in Madagascar, 5 genera endemic to Seychelles, 2 to Mascarenes); *Pandanus* (?) (Pandaneaceae); some bamboos (?).

EOCENE-OLIGOCENE « LEMURIAN STEPPING-STONES »

Calling attention to a distributional pattern that included (Africa)/Madagascar, the Seychelles, (India)/Sri Lanka and W. Malesia, VAN STEENIS (1962), in his now infamous paper on the land-bridge theory, asserted that « there must have been an isthmian connection between Madagascar and Ceylon over the Seychelles-Comores bank » operating during the middle to upper Cretaceous, which he named "Lemuria". Modern understanding of the geological history of the Indian Ocean refutes both the timing and existence of such a direct land route (MCKENZIE & SCLATER, 1973), but the distributional pattern nevertheless still stands, and for some taxa also includes China, Japan, and E. Malesia. Such a pattern often involves closely-related species in, and around the periphery of, the Indian Ocean and Africa. As India assumed its current position from the early Eocene onward, global sea levels were dropping, with a marked regression at the Rupellian/Chattian boundary during the Oligocene, i.e., ca. 30 MYA (HAQ *et al.*, 1988). At that time, significant portions of the Chagos/Laccadive Plateau and the contiguous (at that time) Mascarene Plateau (including the Seychelles Bank,

which encompasses over 50,000 km² now at an average depth of 75 m) could have been emergent, and served as stepping-stones for dispersal of essentially Laurasian (mesic) elements between Laurasia/W. Malesia and Africa/Madagascar via India/Sri Lanka as depicted in Figure 2. As such a dispersal track coincides with the «Lemuria» land-bridge of van Steenis, I propose that it be named the «Lemurian Stepping-stones». Xeric affinities between Madagascar and India (e.g., *Commiphora* (Burseraceae), *Delonix* (Fabaceae), *Moringa* (Moringaceae)) are best explained by overland migration through N.E. Africa/Arabian Peninsula, and do not provide additional support for the «Lemuria land-bridge» as WILD (1965) suggested. Although the stepping-stone pathway may only have begun operating during the Eocene, there is no reason to believe that it has not remained active to the present day (Madagascar to Seychelles - 1,000 km; Seychelles to India - 2,600 km), or that migration has not also occurred in an eastward direction [(e.g., *Brexia* (Brexaceae), *Grisollea* (Icacaceae)].

***Alangium* and *Anacolosia*:** Paleochorological analysis of *Alangium* (Alangiaceae) and *Anacolosia* (Olacaceae) (KRUTZSCH, 1989), both originally Laurasian elements that are now restricted to Africa/Madagascar/Asia s.l., supports the stepping-stone hypothesis. Pollen of *Anacolosidites* (= *Anacolosia*) and *Alangium* first appear in India in the upper Eocene, although the former is now absent there. With regard to *Anacolosia* in Madagascar, the two species differ markedly: *A. pervilleana* is a deciduous small-leaved, small-fruited species in the dry west, whereas *A. casearioides* is an evergreen, large-leaved, large-fruited species in humid sublittoral forests along the northeast coast. Insofar as *Anacolosidites* is known from the Miocene of east Africa, it is possible the two Malagasy species arrived by different routes. The pollen study of *Alangium* by REITSMA (1970) suggests a close relationship of dioecious Malagasy *A. grisolleoides* with *A. barbatum* in India, and reveals that African *A. chinense* possesses a distinct and possibly more advanced pollen than the rest of *A. chinense*, suggesting divergence after an early (Eocene-Oligocene) arrival in Africa. The presence of *A. salvifolium* in the Comores on Mayotte (3.65 - 5.4 MY) and Moheli (1.5 MY) must be a more recent dispersal.

***Canarium denticulatum* Group:** The revision of *Canarium* (Burseraceae) by LEENHOUTS (1959) identifies a group of related species («denticulatum Group») that include: endemic species on the Andamans (*C. manii*), Sri Lanka (*C. zeylanicum*), Mauritius (*C. paniculatum*), as well as *C. madagascariense* in Madagascar and E. Africa (further taxonomic work is needed in Madagascar to delimit additional species within highly variable «madagascariense»), and *C. schweinfurthii* in C. and W. Africa. A combination of both primitive and advanced features in *C. schweinfurthii* suggest long isolation from the rest of the group. On 7.8 MY Mauritius, *C. paniculatum* probably represents a recent dispersal from Madagascar.

***Dillenia amplexicaul* Group:** The revision of *Dillenia* (Dilleniaceae) by HOOGLAND (1952) recognizes a basic division within the genus on the basis of the presence/absence of an amplexicaul petiolar wing. Both *D. triquetra*, present in Madagascar and Sri Lanka, and *D. ferruginea*, endemic to the Seychelles, possess the winged petiole. Shared distribution of *D. triquetra* between Madagascar and Sri Lanka implies a more recent dispersal.

The Western Species of *Nepenthes*: Paleochorological analysis reveals that *Nepenthes* was originally a Laurasian element surviving in Europe into the lower Miocene, at the same time as it arrived in Borneo (KRUTZSCH, 1989). The small seeds of *Nepenthes* are undoubtedly easily dispersed, and one could envision long distance dispersal from Malesia to Madagascar. Nevertheless, SCHMID-HOLLINGER (1979) has

suggested that the Western Indian Ocean species of *Nepenthes* (*N. distillatoria* - Sri Lanka; *N. pervillei* - Seychelles; *N. madagascariensis* and *N. masoalensis* - Madagascar) form a closely-related group, implying a single initial dispersal event from Malesia.

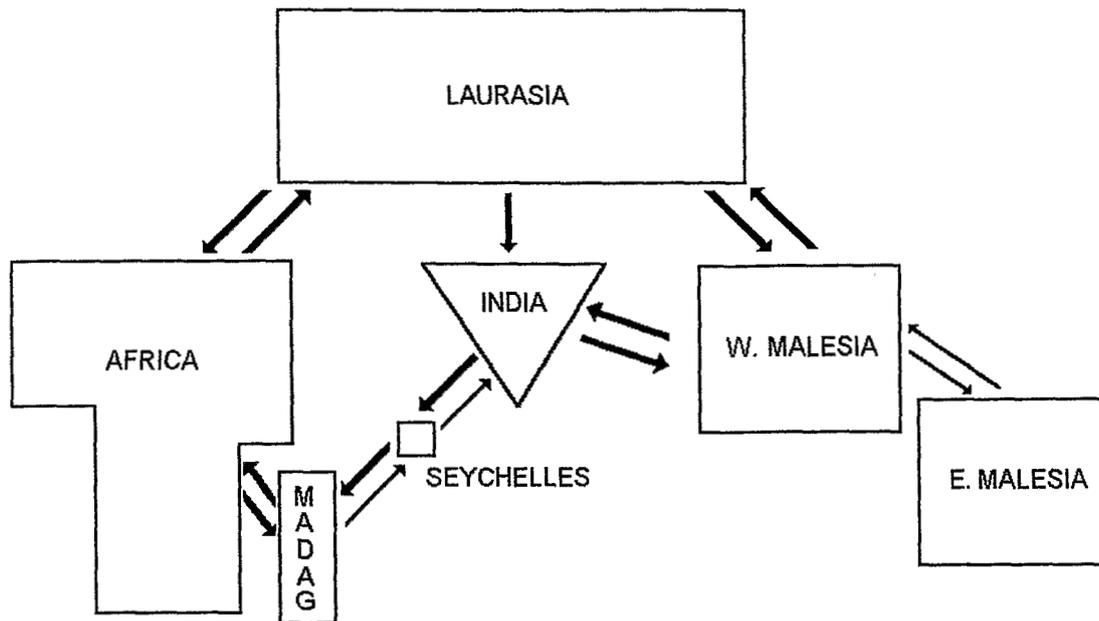


Fig. 2. Schematic representation of migration pathways active during Eocene/Oligocene after India has attained close proximity to Asia, through to post-collision (and continuing to present), a period during which sea-levels were dropping. Mesic Laurasian and W. Malesian elements enter Madagascar/Africa via India and « Lemurian Stepping-stones » in the W. Indian Ocean (emergent portions of the Chagos/Laccadive Plateau and Mascarene Plateau including the Seychelles). Xeric elements are exchanged between N.E. Africa/Arabian Peninsula and Laurasia/India and may disperse to dry western Madagascar. Thickness of arrow represents probability of dispersal.

Additional possible examples of « Lemurian Stepping-stones » dispersal: *Anisophyllea* (Anisophylleaceae); *Fernandoa* (Bignoniaceae); some Clusiaceae (?) - *Calophyllum*; some Euphorbiaceae (?) - *Claoxylon*, *Macaranga*; *Homalium*, *Scolopia* (Flacourtiaceae); *Hugonia* (Hugoniaceae); *Foetidia* (Lecythidaceae); *Leea* (Leeaceae); *Medinilla*, *Memecylon* (Melastomataceae); *Turraea* (Meliaceae); *Streblus* (Moraceae); *Ardisia* (Myrsinaceae); *Paropsia* (Passifloraceae); *Gaertnera*, *Ixora*, *Psychotria*, *Pyrostria* (Rubiaceae).

LONG DISTANCE DISPERSAL (LDD)

The difference between stepping-stone dispersal and long distance dispersal (LDD) is only a matter of distance, which is just one of the factors contributing to probability of dispersal; the former might also be described as short to medium distance dispersal. Any

dispersal across a fragmented space is rendered more probable when a taxon possesses an added degree of vagility (small, resistant, aerodynamic, or buoyant disseminules), and/or time. That dispersal over especially long distances has occurred is undeniably proven by the many Asian taxa that have reached the Hawaiian Islands in recent history, a distance of 8,000 km. As RAVEN (1979) noted, the distance from Australia to Madagascar is only about 2/3 (5,400 km) of that from Asia to Hawaii, and both source and target have existed for an extremely long time. Prevailing easterly winds and ocean currents in the Indian Ocean further increase the probability for LDD from Malesia to the western Indian Ocean (RENVOISE, 1979). Accepting the fact that LDD is potentially continuously occurring, implies that it has undoubtedly occurred recently, as is witnessed by dispersal to the young volcanic Mascarenes [(e.g., a phylloclad *Acacia* of certain Australian affinity (BELL & EVANS, 1978, who nevertheless conclude a former land connection between Australia and Mauritius)].

Despite extrinsic directional forces, LDD is often stochastic in nature, and more often that not results in a highly imbalanced distribution. Two widespread species of *Barringtonia* (Lecythidaceae) are among a long list of mangrove and littoral species (the Indo-Pacific strand flora) to have reached Madagascar by ocean dispersal. Nevertheless, the distributions of *B. asiatica* and *B. racemosa* in the western Indian Ocean contain a random component: *B. asiatica* is present on Mauritius, but not on Réunion, and has failed to reach the E. African coast; *B. racemosa* has reached the E. African coast, but is not present in the Mascarenes; both are present in the Seychelles (PAYENS, 1967). To some extent the distributions reflect differing ecological preferences (*B. asiatica* on sand just above the tide line; *B. racemosa* in estuarine habitat), but there is also a stochastic element. *Strongylodon* (Fabaceae) includes a widespread species, *S. lucidus*, that has reached Hawaii and Tahiti (HUANG, 1991). In the western Indian Ocean, *S. lucidus* is present only on Réunion, although Madagascar also harbors a distinct section *Cravenia* with two species, indicative of an earlier dispersal event. Additional examples of imbalanced distributions include: *Gluta* (Anacardiaceae) - 1 sp. Madagascar, 28 spp. Malesia; *Hibbertia* (Dilleniaceae) - 1 (variable) sp. Madagascar, > 100 spp. Malesia, centered in Australia; *Keraudrenia* (Sterculiaceae) - 1 sp. Madagascar, 8 spp. Australia.

CONCLUSIONS

As disjunct outliers of the current Indo-australo-malesian flora, those Malagasy humid forest species whose affinities lie far to the east possess especially high information content, and therefore increased conservation value (VANE-WRIGHT *et al.*, 1991). Barring the discovery of fossil evidence of former distribution (COETZEE & MULLER, 1984), extant taxa provide our only means of constructing historical biogeographic hypotheses. From a phylogenetic standpoint, relict taxa constitute long basal branches critical for understanding both ingroup, and broader, higher level outgroup relationships. Extinctions of outlying taxa have greater biogeographic (and possibly evolutionary) consequences than extinctions of core-area taxa, although, of course, neither is desirable. Just as the Malagasy language and customs continue to reveal the S.E Asian origin of the Malagasy people, let us hope that the Malagasy flora will also retain its far eastern character.

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