COMPOSITION, ORIGIN, AND AFFINITIES OF THE MADAGASCAN VASCULAR FLORA

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ABSTRACT

The Madagascan vascular flora which is composed of over 160 families is exceptionally interesting not only because it is prodigiously rich and diversified, but because it has preserved a number of relicts. In this review, presented roughly according to the phylogenetic system of Cronquist, every family has been tentatively, although shortly, analyzed wih regard to its composition, origin, and affinity. The hypothesis that the Madagascan flora was a part of the large Cretaceous Gondwanian flora at the time when Angiosperms originated and that the flora became greatly impoverished on the African continent due to far-reaching climatic changes accounts for many present characteristics of the Madagascan flora. In this context the existence of a Madagascan region sensu lato (Madagascar, Mascarene Islands, eastern and southern Africa), where many austral genera or taxa of higher taxonomic rank exist—some of which belong to Magnoliidae and to the most primitive parts of Dilleniidae and Rosidae—becomes understandable. Equally understandable become many discontinuities of range and the existence of many endemic uni- or paucispecific genera. Briefly, the present Madagascan vascular flora probably resulted from a progressive differentiation of the autochthonous Gondwanian stock and natural introduction of taxa in time through long-distance dispersal.

In this paper, I do not intend, of course, to present an exhaustive enquiry concerning the origins and affinities of the Madagascan flora. I think an enormous amount of basic research remains to be done in order to get an accurate general view on the matter. And how could we do so, since we mostly cannot establish a satisfactory connection between taxonomic classification and distributional patterns, in order to express the true taxogenesis?

Since Perrier de la Bâthie and Humbert's geographical works on the Madagascan flora many papers and books have been published, but no new concept significant enough to have important implications has been proposed. Some recent publications of great interest pertaining to this matter have appeared, but they are not especially devoted to Madagascar. A very limited number of valuable papers have to be mentioned, insofar as they contribute to Madagascan phytogeography, such as those by Stearn (1971), Dejardin et al. (1973), Koechlin et al. (1974), Wild (1975).

In fact, any attempt at a comprehensive synthesis of this kind at this time would be premature because we need to know much more with respect to palaeobotany and phylogeny.

Although no important general conclusion has been reached concerning the biogeography of the Madagascan plants for some decades, the same does not hold true for strictly taxonomic knowledge, which has much progressed, thanks in particular to outstanding research by the late forester and botanist R. Capuron. We are indebted to him for an exceptional improvement in the analysis of the woody plants of Madagascar. But even in taxonomy we are far from having

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sufficient information, and, in spite of the efforts by Capuron and many others, among them the botanists of the Muséum National d'Histoire Naturelle and O.R.S.T.O.M., many families, certain of which are the largest such as the Poaceae, Orchidaceae, Euphorbiaceae, and Leguminosae, have not yet been revised in their entirety.

In 1959 Humbert posed a problem, which was in his opinion a very perplexing challenge to botanists and zoologists, namely, where and what have Madagascan taxa originated from? Have they as a whole been derived from a Cretaceous stock in place for a long time or are they for the most part newcomers that arrived there during the Tertiary and later. If the latter is the case, which seems supported by some evidence, how did seed plants manage to reach Madagascar from Australia or America or, in particular, from Africa with which so many links are evident? As viewed by Humbert, who principally limited his considerations to relations with Africa, plants might have reached Madagascar either by direct land migration (land bridges) or long-distance dispersal (by means of sea and wind currents, birds, bats, drift wood, rafts, etc.). In his paper, Humbert, far from discarding long-distance dispersal, discussed at length two aspects of the question; but in his opinion it was a secondary process that was not very effective. One can explain the immigration by sea water of a few plants in this manner, but these are well-known species which always remain confined to, or next to, sandy and rocky beaches. In particular, Humbert believed that long-distance dispersal could not explain the presence in Madagascar of certain genera such as *Cycas*, *Nepenthes*, and *Ceriops*. In the same way, although attaching more importance to wind currents, he did not trust in their efficiency. In order to support his thesis, he invoked evidence drawn from the Compositae. Let us take, he wrote, the three genera *Helichrysum* (100 species in Madagascar), *Vernonia* (100 species) and *Senecio* (60 species) which have a percentage of endemism close to 100%. In comparison with what we know about the evolution of Tertiary floras in the Mediterranean basin and East Africa, we must admit a similar differentiation in Madagascar. Any addition to the flora by long-distance dispersal would have diminished the percentage of endemism, which is in contradiction with known data. It is clear that in Humbert's opinion, we have to view the increasing number of species as the result of a differentiation from the ancestral flora, even though the relevant plants are readily dispersed.

I think Humbert's concept does not fully account for many fundamental problems with which we have to deal. Perrier de la Bâthie (1948), in contrast, suggested that differentiation might, at least for a small part, have proceeded from chance immigration, and he referred, in particular, to the case of *Calophyllum*, several species of which have differentiated in the Mascarenes and the Madagascan interior, from possibly only a single widespread species, namely *Calophyllum inophyllum*.

One could allege that many of the widespread species that we know, such as many littoral ones, are generally isolated and rather stable, although polymorphic, in every country where they occur. But this objection is hardly defensible for at least three reasons. First, every pioneer species is not necessarily

the potential source of a new "taxogenesis." Second, the pioneer species we know have not possibly had time enough to differentiate. Third, opportunities in relation with changes of environment may have not occurred.

However that may be with respect to present conditions, it is now generally admitted that past events dealing with biogeography have to be explained by the theory of plate tectonics. According to this, the history of the earth is a continuous process, and continents may be rafted as much as 2,000–3,000 km apart after having been joined, or, on the contrary, to become joined after a long separation. So, there is no longer any essential difference between long-distance dispersal and direct migration by land bridges. One can consider both of these mechanisms as the two extreme limits of a single process. The different biota of the Globe are presently massive wholes which have been built up slowly during geological times as plates approached to, or moved away from each other. Let us not forget that the opening of the South Atlantic began only 125–130 m.y. BP in the Lower Cretaceous. By the Paleocene, the gap between South America and Africa was only 800 km and "populated with volcanic islands" (Raven & Axelrod, 1974). Madagascar separated from Africa about the mid-Cretaceous and from India at the same time or possibly later, but opportunities for exchanges with Africa across the Mozambique sea barrier lasted a long time and are still presently possible. By mid-Cretaceous time, direct migrations between India-Madagascar-Africa and Australia became more and more difficult as these lands moved away.

If no essential distinction is made between the notion of long-distance dispersal and that of direct migration, then we have much more flexible bases at our disposal for attempting to understand biogeographical facts.

In Humbert's paper (1959), "Origines présumées et affinités de la flore de Madagascar" all the Madagascan flowering plants are briefly reviewed in turn. My present contribution is only a complement aimed to bring the Humbert compilation up to date, not only, of course, in taking new taxonomic and floristic data into account, but also in considering them in the light of the plate tectonic theory, which is now reliable enough to be taken as a foundation of biogeography. Further, certain families are emphasized either for distributional patterns that are especially significant in relation to Madagascan biogeography or for having been recently revised. Thus, such families or orders as Winteraceae, Canellaceae, Saxifragales, Theales, Tiliales, Malvales, Guttiferae, Celastraceae, Malpighiaceae, Meliaceae, Combretaceae, Araliaceae, Verbenaceae, Asteraceae, and others are worth detailed analysis.

With regard to relationships between neotropical and African-Madagascan floras, authors often concur in the belief that the species of the same genus or the members of the same species occurring on both sides of the Atlantic Ocean have not crossed the present ocean, but have always inhabited the site where they grow today. So, for 90 m.y. BP some genera or species would not have evolved at all. In my opinion, one should not forget that by the Lower Eocene (about 50–55 m.y. BP) the Atlantic probably did not yet form an absolute barrier for living beings. Dejardin et al. (1973) admitted judiciously, among other possibilities, that such a species as *Rhipsalis baccifera* could have reached Africa

a long time after the original separation of the continents. I agree with Raven & Axelrod (1974) that one must suppose that "numerous islands afforded ready migration across the opening Atlantic into the Early Tertiary." Later, difficulties for crossing became stronger and stronger but transmigration continued to occur. Although this process appears unlikely, just as evolution itself, yet so must it have happened.

In terms of the above explanation, *Christiana africana* is possibly a newcomer in either Africa-Madagascar or America, and the distributional patterns of families mentioned by Dejardin et al. (1973) such as Bromeliaceae, Rapateaceae, Humiriaceae, and Vochysiaceae, insofar as they can be comparable must also belong to the same explanation—and this even though several species of *Rhipsalis*, manifestly directly derived from the same ancestor, are in existence in Madagascar.

I think that the obstacle in the way of understanding biogeographical facts is presently not so much what has happened with oceans and sea barriers or geological considerations, but our own ignorance about plant taxonomy and phylogenetics. Statistical figures about composition and endemism percentages classically used since Perrier de la Bâthie (1936) and Humbert's (1959) works are interesting data, as also are the data provided recently by Dejardin et al. (1973), among others, but we now need multidisciplinary and biological monographs—why not by international teams?—of only a few especially chosen families.

Taking into consideration a number of recent important biogeographical works on the one hand, and, on the other, certain data from my own research, I am led to some general hypothetical principles which can be outlined as follows:

1. Primitive angiosperms originated in Gondwanaland (possibly in West Gondwanaland, according to Raven & Axelrod, 1974, with whom I agree), then extended their range northward long before Gondwanaland broke up, possibly during the last part of the Lower Cretaceous.

2. As soon as the Upper Cretaceous, two large floras must have been established: a Laurasian one (Magnoliaceae, Ranuculaceae, Amentifereae, . . .) and a Gondwanian one (Annonaceae, Winteraceae, Myristicaceae). The concept that the angiosperms empire is divided into two great floras, was recently, and rightfully I think, emphasized by Aubréville (1974a).

3. At the close of the Cretaceous and by the Early Palaeocene almost all modern families were in existence.

Every modern family has evolved sufficiently for adapting to new geologic or climatic conditions. Some have diversified in many directions, and they have succeeded in colonizing the most diverse regions on the Globe (Orchidaceae, Compositae, Poaceae, . . .). Others, even though narrowly specialized, have kept a combination of both advanced or very advanced characters and primitive or very primitive characters: they represent the so-called "primitive angiosperms."

4. The biogeographical definition of Madagascar should rest on two concepts:

a. The "Grande Ile" is fundamentally a fragment of Africa; its biota, taken

as a whole, is obviously an African one. Dejardin et al. (1973) said that this idea is now a classic one, and I agree. According to the estimates of Perrier de la Bâthie (1936), accepted by Humbert, the African element in the Madagascan flora would be around 27%, the pantropical and Asian elements being respectively 42% and 7%. The austral element contributes 3% and the recent element whose transport is due to long-distance dispersal, 15%. The remaining 6% represents the true Madagascan element. The studies of Dejardin et al. (1973) have complemented earlier ones. In particular, they recognize the existence of a neotropical element. Besides, they unite the pantropical and the "recent exotic" elements which Perrier had separated. Further, they add a seventh element, namely the palaeotropical one, which they subdivide. Thus, as one sees, their analysis goes much farther than the previous ones.

However, such a recognition of groups of elements and of percentages does not account for several essential factors.

What precise significance is to be given to these elements which we think are arbitrarily delimited? Their interrelationships should be analyzed more thoroughly. Insofar as Madagascar is a part of Africa, a Madagascan element is *ipso facto* an African one. Let us for example take the genera *Garcinia* and *Rheedia*, which Dejardin et al. (1973) have classified, respectively, in the palaeotropical element and neotropical element. These genera are in fact, not at all clear-cut and could be merged into one genus, which would then be a pantropical one. This case shows that any judgement concerning floristic affinities if founded on percentages of composition depends greatly upon taxonomic concepts. Moreover, the mere report of a common occurrence of a taxon in several areas may not reveal the true situation. In their paper, Dejardin et al. place *Symphonia* with neotropical elements, although it is in fact a genuine Madagascan one. Further, they reduced the Madagascan element to the endemic one. So, for Dejardin et al. terms such as "Madagascan element" and "endemic element" are synonymous. In fact, many so-called pantropical or palaeotropical or neotropical genera really belong to Madagascan stock. Although they are strictly Madagascan elements, they occur also in other areas.

b. Madagascar is a fragment of Africa, but it represents with its neighboring islands and eastern and southern Africa, a natural entity to which could be given the name "Madagascan region sensu lato." A number of reasons can be given to support this concept:

—A number of genera are common to eastern and southern Africa and Madagascar.

—Madagascar and the eastern coasts of Africa are the western border of the Indian Ocean.

—Madagascar, eastern and southern Africa were linked together, even though possibly separated by the sea, at the time when Gondwanaland was in existence.

—The uplift of the central mountain range in Africa during Tertiary times and the climatic changes in relation to this event increased the barrier between western and eastern Africa so as to reinforce the isolated position of all the eastern territories of which Madagascar is one part.

It is well known (Lebrun, 1961; Perrier de la Bâthie, 1936; Aubréville, 1955; Dejardin et al., 1973) that the African tropical flora must be divided into two parts, the Guineo-Congolese one having almost no affinity with the Madagascan one, and the Sudano-Zambezian flora whose relationships with the Madagascan one are very important. The strong disjunction is rather between the two African parts, than between Africa and Madagascar.

I shall now give a summary of the more significant taxa which support the concept of a close relationship between the floras of Madagascar and eastern and southern Africa. After that, I shall briefly survey the whole of the Madagascan flora by considering each family, except some unrevised ones, in its turn.

Close Relationships Between the Floras of Madagascar and Eastern and Southern Africa

1. Families, subfamilies or tribes confined to the Madagascan region sensu lato and having at least one representative on either side of the Mozambique channel:

Myrothamnaceae (a monotypic family extending somewhat up to Zaïre) allied to the Hamamelidaceae and, possibly, to Didymelaceae, Hydrostachyaceae (we need detailed research on these two austral families, which were considered as primitive and linked within Pittosporales (suborder Brunineae) by Thorne, 1975; but the Hydrostachyaceae are placed in the Scrophulariaceae by Cronquist, 1968), Ptaeroxylaceae, Androstachyaceae.

2. Families or groups of plants with wide distributions represented in the Madagascan regions sensu lato but not elsewhere in Africa:

Winteraceae (a subfamily in Madagascar), Canellaceae, Hamamelidaceae, Moringaceae, Cunoniaceae, Brexiaceae, Proteaceae, Myoporaceae, Velloziaceae.

3. Some families or tribes of wide distribution, including West Africa, but characteristically of the Madagascan region sensu lato:

Monimiaceae, Montiniaceae, Meliaceae—Turraeeae, Portulacaceae, Palmae—Borassoideae, Pandanaceae, Poaceae—Bambuseae.

4. Some genera confined to the Madagascan region sensu lato (having at least one species on either side of Mozambique channel):

Otoptera (Leguminosae, 1 sp. in S. Africa, 1 sp. in Madagascar); *Xanthoceris* (Leguminosae, 1 sp. in S. Africa, 1 sp. in Madagascar); *Thilachium* (Capparaceae, 20 spp., 9 of which are in Madagascar and the Mascarene Islands, 1 sp. nonendemic); *Calantica* (Flacourtiaceae, 5–7 spp. in Madagascar and possibly in E. Africa, Airy Shaw, 1966); *Apholia* (Flacourtiaceae, 4–5 spp. or only 1 polymorphic species which reaches E. Africa, Airy Shaw, 1966); *Ludia* (Flacourtiaceae, 7 spp. in Madagascar and possibly in E. Africa, Airy Shaw, 1966); *Cassinopsis* (Cellastraceae, 2 spp. in S. Africa, 4 spp. in Madagascar, all endemic); *Hyalocalyx* (Turneraceae, 1 sp. in Madagascar and Mozambique); *Sparmannia* (Tiliaceae, 1 sp. in S. Africa, 1 sp. common in Madagascar and E. Africa, 1 sp. in Madagascar; this genus belongs to an entirely African tribe); *Gossypioides* (Malvaceae, 1 sp. in

E. Africa and Madagascar); *Dais* (Thymelaeaceae, 1 sp. in E. and S. Africa, 1 sp. in Madagascar); *Sphedamnocarpus* (Malphighiaceae, 1 sp. endemic to S.W. Africa, 15 spp. in Madagascar); *Lepidotrichilia* (Meliaceae, 1 sp. in E. Africa, 3 spp. in Madagascar); *Erythrophysa* (Sapindaceae—Koelreuterieae, 3 spp. in E. Africa, 6 spp. in Madagascar); *Macphersonia* (Sapindaceae—Schleichereae, several species in E. Africa-Madagascar); *Camptolepis* (Sapindaceae—Schleichereae, 1 sp. common to E. Africa and Madagascar, 2 spp. in Madagascar); *Stadmannia* (Sapindaceae-Nephelieae, 1 sp. common to the Mascarene Islands, Madagascar and E. Africa: *S. oppositifolia*; Capuron has described 5 Madagascan species representing a very distinct group, flowers of which are dioecious and with petals); *Protorhus* (Anacardiaceae, 1 sp. in S.W. Africa, 20 spp. in Madagascar); *Rhoicissus* (Vitaceae, 10 spp. in E. Africa, one of which reaches the Comores Islands); *Rhigozum* (Bignoniaceae—Tecomeae, 3 spp. in S. Africa, 1 sp. in Madagascar); *Hydnora* (Hydnoraceae, 10 spp. in S. and E. Africa, only 1 sp. in Madagascar, which represents a section of its own, *Neohydnora*; the other genus *Prosopanche* of this bitypic family is endemic to S. America—Paraguay, Argentina); *Kniphofia* (Liliaceae, many spp. in E. and S. Africa, 1 sp. in Madagascar); *Geissorrhiza* (Iridaceae, many spp. in S. Africa, 2 spp. in Madagascar); *Gonioma* (Apocynaceae—Alstonieae, 1 sp. in S. Africa, 1 sp. in S.W. Madagascar, Markgraf, 1976); *Mascarenhasia* (Apocynaceae—Mascarenhasiinae, a monotypic tribe; 12 spp. in Madagascar, 1 of which reaches E. Africa); *Pachypodium* (Apocynaceae—Pachypodiinae, a monotypic tribe; a genus with 17 spp., 12 of which are in Madagascar, the other species are in S.E. and S.W. Africa); *Hazunta* (Apocynaceae—Tabernaemontanoideae, 7 spp. in Madagascar, 1 of which extends to E. Africa, *H. coffeoides*); *Uncarina* (Pedaliaceae; it is the single genus of the Pedaliaceae endemic to Madagascar; this genus is closely allied to *Harpagophyton* of S. and E. Africa); *Medemia* (Palmae, 3 spp. in N.E. Africa and Madagascar).

5. Some genera characteristically of the Madagascan region sensu lato but nonendemic to this region and absent from western Africa:

Ocotea (Lauraceae, 270 spp. in America, several spp. in S.E. Africa, 16 spp. in Madagascar; *Ocotea* could have some distant affinity with *Hypodaphnis* a monotypic genus of W. Africa); *Hirtella* (Chrysobalanaceae, 100 spp. in tropical America, 1 in E. Africa, 4 spp. in Madagascar—3 endemic—1 sp. common to E. Africa and Madagascar; this genus is related to the Madagascan endemic genus *Grangeria*); *Carpodiptera* (Tiliaceae, 3 spp. in Cuba and West Indies, 1 sp. in E. Africa and Madagascar); *Piriqueta* sect. *Erblichia* (Turneraceae, 1 sp. in Central America, 1 sp. in southern Africa, 3 spp. in Madagascar; the genus *Piriqueta* is greatly diversified in America; a Madagascan species, *Piriqueta integrifolia*, is an isolated taxon whose status needs restudy); *Vepris* (Rutaceae, 20 spp. in S. and E. Africa, 24 spp. in Madagascar); *Tristellateia* (Malpighiaceae, a palaeotropical genus with 20 spp. in Madagascar, 1 sp. in E. Africa); *Nesogenes* (Verbenaceae, 6 spp.; this genus, closely allied to the Madagascan endemic genus *Acharitea* (1 sp.), has one endemic sp. in Madagascar, the other species being in E. Africa and Polynesia; these two genera belong to a group, a family of its

own according to some authors [Dicrastylidaceae], which is essentially Australian; they are closely related to the Verbenaceae—Stilboideae, a small subfamily of 5 monotypic genera, endemic to S. Africa); *Dicoma* (Compositae—Mutisieae, 35 spp. in E. and S. Africa, 1 sp. in tropical Asia, 4 spp. in Madagascar, all endemic); there are many genera in the Compositae—Inulae with a comparable distribution: *Polycline*, *Athrixia*, *Iphiona*, *Humea*, *Brachylaena*, *Stenocline*, etc.).

6. Some genera characteristically of the Madagascan region sensu lato, nonendemic to this region and weakly represented in tropical West Africa:

Buxus (Buxaceae, 6 spp. in S. and E. Africa and Madagascar, 1 sp. belonging to another group in W. tropical Africa); *Delonix* (Leguminosae, a genus of several spp. in Madagascar and E. Africa); *Commiphora* (Burseraceae, a genus with many spp. of warm Africa and India; some spp. in W. tropical Africa, more than 20 spp. in E. Africa, even more in Madagascar); *Philippia* (Ericaceae, 40–50 spp. in Madagascar, 10 spp. in E. and S. Africa, 1 sp. on Mt. Cameroon); *Vaccinium* (Ericaceae, some spp. in Madagascar, many in S. Africa but none on mountains in tropical Africa); *Dombeya* (Sterculiaceae, 200 spp., 20 of which are in E. and S. Africa and a few elsewhere in tropical Africa); *Gravesia* (Melastomataceae, 100 spp. in Madagascar, 7 of which are common to E. Africa, 2–3 spp. in W. Africa); *Mimusops* (Sapotaceae, a genus of 18–19 spp. in Madagascar, the Comores, Mascarene and Seychelles Islands, 12 in E. and S. Africa, only 2 in W. Africa); *Sphaerothylax* (Podostemaceae, 1 sp. in Cameroon, 1 in S. Africa, reaching Angola and Zambia, 1 in E. Africa, Ethiopia, and Madagascar); *Kalanchoe* (Crassulaceae, 1 section in S. Africa, 3 sections in Madagascar—Dejardin et al., 1973); *Streptocarpus* (Gesneriaceae—Cyrtandroideae, a genus of many species in S. and E. Africa, some 40 spp. in Madagascar—where a genus closely allied, *Colpogyne*, is confined—some spp. in W. tropical Africa); *Helichrysum* (Compositae—Inulae, a palaeotropical genus of 500 spp.—extending to Australia—of which over 100 occur in Madagascar and 200 in S. Africa); *Stoebe* (Compositae—Inulae, 30 spp. in S. Africa, 1 sp. in Angola, 1 in Rhodesia, 2 spp. endemic to Madagascar, 1 sp. endemic to Réunion); *Aloe* (Liliaceae, a genus well developed in Madagascar, where it has 30 endemic spp. also in E. and S. Africa); *Coleotrype* (Commelinaceae, 5 spp. in Africa and Madagascar).

7. The littoral formations, mangroves included, along east African coasts also offer characteristic features of the Madagascan region. These formations are composed of plants unknown on the Atlantic coast such as *Barringtonia racemosa*, *Sonneratia alba*, *Lumnitzera racemosa*, *Bruguiera gymnorhiza*, *Rhizophora mucronata*, *Ceriops tagal*, *Heritiera littoralis*, *Xylocarpus* (the two species) and *Cycas thouarsii*. A few mangrove species of Madagascar do not reach the African coast, but many other species of the oriental mangroves reach neither the Madagascan coast, nor the eastern African one. The Madagascan mangrove flora is a typical oriental flora, but a strongly impoverished one.

Biogeographical Survey of the Madagascan Flora
(Families are arranged roughly according to Cronquist's system)

I

Winteraceae (8 gen., 57 spp.), which are clearly among the most primitive families of the angiosperms, are represented in Madagascar by a unique species, the so-called "*Bubbia*" *perrieri*, which is the single representative of the family in Africa-Madagascar. The other genera but one are concentrated in some Pacific islands and Australia: *Pseudowintera* (3 spp. in New Zealand); *Exospermum* (1 sp. in New Caledonia); *Bubbia* (30 spp. in New Caledonia, New Guinea, and Australia); *Belliolum* (4 spp. in New Caledonia, 4 spp. in the Solomon Islands); *Zygogynum* (6 spp. in New Caledonia); *Tasmannia* (5 spp. from Malesia to Australia, a genus often treated as a subgenus of *Drimys*); and *Drimys* (4 spp. in S. America–Mexico).

The Madagascan species wrongly described as *Bubbia* is indeed a quite different genus, and I proposed (Leroy, 1977a) considering it as a subfamily of its own. Thus, the distributional pattern of the Winteraceae is not only typically austral, but the Madagascan species bears witness that the Madagascan region is a part of what was the cradle of the *Winteraceae*; therefore, a part of the cradle of primitive angiosperms.

But more is to be said. "*Bubbia*" *perrieri* has an advanced gynoecium that is a pseudo-monomerous ovary composed of 2 carpels united and opened, a type only known in two families in the order Magnoliales, the Annonaceae—Monodoroideae and the Canellaceae. Let us not forget that all of these plants occur in one and the same area, except for the Canellaceae which occur also in tropical America. The Winteraceae, which have no representative in Africa, and the Canellaceae form an integral whole because of their close relationships, and they should not be too separated.

Annonaceae 125 gen., only 9 of which are represented in Madagascar: 1 endemic, *Ambavia* (2 spp.); 3 African-Madagascan, *Isolona* (19 spp., 5 in Madagascar), *Monanthotaxis* (some spp. in Africa and Madagascar), *Hexalobus* (6 spp., 1 in Madagascar); 4 palaeotropical, *Uvaria* (120 spp., 15 in Madagascar), *Artabotrys* (100 spp., 6 in Madagascar), *Polyalthia* (100 spp., 15 in Madagascar), *Popowia* (50 spp., 16 in Madagascar); 1 pantropical, *Xylopia* (100 spp., 25 in Madagascar). All but some of the species (the total number of which is 100) are endemic.

Annonaceae are rather poorly represented in Madagascar. As a whole, their affinities are palaeotropical and especially African. A remarkable fact is that the subfamily Monodoroideae, principally characterized by a compound ovary, and composed of 2 genera (*Isolona* in Africa and Madagascar, and *Monodora* in Africa), palynologically akin (Walker, 1971), is endemic to Africa-Madagascar.

Myristicaceae (16 gen., 5 of which in America—Uphof, 1959—300 spp.). This family is represented in Madagascar by 3 endemic genera (Capuron, 1972a, 1973b): *Haematodendron* (1 sp.), *Brochoneura* (3 spp.), and *Mauloutchia* (6 spp.); in tropical Africa by 4 endemic genera; in tropical Asia by 4 endemic genera. Taking the family as a whole, almost 50% of the genera are African-

Madagascan. None of them is pantropical. The Madagascan genera, like the African ones, have few species, always less than 7.

Furthermore, the genus *Haematodendron* is, as compared to the others, strongly differentiated with some very primitive characters (stigma sessile, subapical-lateral, slightly oblique, with two well-marked papillose lips, separated by a sutural groove which nearly extends down to the bottom of the carpel; therefore, certainly a monomerous ovary!) and some very advanced characters (plants dioecious, flowers with united sepals, ovary stipitate, seeds exarillate, albumen ruminate).

So it is easy to assign a Gondwanian origin to this very archaic family, whose specific differentiation has been active in America (Smith & Wodhouse, 1938) and, above all, in Asia. The African-Madagascan genera appear to be isolated survivors with few species.

The *Canellaceae* is a small tropical and subtropical family of 5 genera (11 spp.) whose distribution is restricted to America and Africa. Genera are endemic to any parts of the region: 3 of them in America; 1 in S. Africa; 1 in Madagascar: *Cinnamosma* (3 spp.). The most striking fact is that the family is a very natural one and closely allied to the Winteraceae: they have partly the same distributional pattern and the same ovarian type (Leroy, 1977a). It is probable that they have had a common ancestor (with a monosulcate pollen, which is the one of present Canellaceae, and free carpels), which inhabited Gondwanaland.

The *Monimiaceae* (25 gen.) is one more example of a panaustral family almost absent from the Guineo-Congolese flora, but richly represented in the Madagascan region sensu lato. There is a strong concentration of endemic genera in Madagascar and the Mascarene Islands, possibly 6: *Ephippiandra* (1 sp.); *Phanerogonocarpus* (2 spp.); *Decarydendron* (1 sp.); *Hedycaryopsis* (1 sp.); *Monimia* (4 spp.); *Tambourissa* (26 spp.). Two genera are recognized in Africa: *Xymalos* (2–3 spp.) almost restricted to E. and S. Africa but reaching Mt. Cameroon; *Glossocalyx* (3–4 spp.) confined to the Guineo-Congolese flora. The latter genus is strongly differentiated and often considered as the single African member of the separate family Atherospermataceae. According to Hutchinson (1964), no representative of the Monimiaceae occurs in Africa, since he places *Xymalos* in the Trimeniaceae. Two other genera of Monimiaceae have been seen as types of separate families. It has been proposed that *Hortonia* of Ceylon be raised to the family level, a status which is generally granted to *Amborella* of New Caledonia. In spite of the unsatisfactory taxonomic treatment applied to the Monimiaceae, it is clear that this group of related plants, which is widely dispersed in the Southern Hemisphere, is characterized by its discontinuous area, the morphological isolation of certain genera, and its near absence from Africa.

Lauraceae (35–40 gen., 2,000 spp. tropical & subtropical). This primitive family is very poorly represented in Africa-Madagascar, but its distribution offers a great interest. Aside from the parasitic vine *Cassytha filiformis*, present in both Africa and Madagascar, there are 4 genera in continental Africa, of which one is an endemic monotypic genus (*Hypodaphnis*) and belongs to a tribe of its own.

Beilschmiedia, a pantropical genus of 200 species, with 80 species in Africa, is absent from Madagascar. Two genera, *Ocotea* and *Cryptocarya*, are common to Africa and Madagascar; the latter is a large American genus with 8 species in Madagascar and some species restricted to E. and S. Africa. The American genus, *Ocotea*, has 18 species in Madagascar, and only a few in tropical and E. and S. Africa. There are 3 other genera in Madagascar: *Ravensara*, an endemic genus (18 sp.) related to *Cryptocarya* (Cryptocaryeae); *Potameia*, a genus with many Madagascan species (19) and a few (3) in tropical Africa; *Apollonias*, a widely spread genus with 6 endemic species in Madagascar, absent from continental Africa but present in the Canaries (with *Persea* and *Laurus*).

It is to be noted that the tropical African center is very poorly provided with genera of Lauraceae, the chief centers of distribution being S.E. Asia and S. America. The family is better represented in the adjoining islands (Canaries, Madagascar) than on the continent.

Hernandiaceae. This small pantropical family of 4–5 genera and 60 species has a typically austral distribution. It is of the utmost theoretical importance in that it offers not only an austral distribution, but also a wide range of isolated genera with many very primitive characters. There is undoubtedly evidence for a Gondwanian origin of the whole family (Kubitzki, 1969). Hernandiaceae are represented in Madagascar by 4 genera: *Hernandia* subgen. *Hernandia* (2 spp., 1 of which is endemic; 1 sp. endemic to the Mascarenes); *Hazomalania* (*Hernandia* subgen. *Hazomalania* (Capuron, 1966b; Kubitzki, 1969) (1 sp.); *Illigera* (1 endemic sp.); *Gyrocarpus* (1 sp., *G. americanus*). According to Kubitzki, most primitive components occur in Australia (*Hernandia* subgen. *Valvanthera*) and Madagascar (*Hazomalania*). The fifth genus, *Sparattanthelium*, is endemic to tropical America. Kubitzki has divided *Gyrocarpus*, a pantropical genus dispersed by sea currents, into 8 species, 3 of which are endemic to Madagascar; it, almost certainly, belongs to the mechanism of diffenentiation to which such species as *Calophyllum inophyllum* are also answerable.

Chloranthaceae. This small family is of exceptional interest for both its morphological characters, some of them being very primitive, and its distributional pattern. If the Madagascan genus *Ascarinopsis* (Humbert & Capuron, 1955) (1 sp.) is reduced to *Ascarina*, of which, at the best, it could be a special section, the Chloranthaceae is composed of 4 genera, which are, of course, related with one another, but only distantly, and their distributional area is extremely discontinuous. And what is more, the only genus *Hedyosmum*, which has 40 species in tropical America and the West Indies, and 1 species in S.E. Asia, represents a strongly differentiated, isolated line with at least special subfamily status. In particular, it offers evolutionary characters some of which are most advanced and some others most primitive. It seems its distribution might have resulted, more or less recently, from a post-Gondwanian extension. The other 2 genera are: *Chloranthus* (15 spp., in E. Asia and Indomalaysia) and *Sarcandra* (3 spp. in the same area). Obviously, I agree with Smith (1972) that the present genera of Chloranthaceae are only a few remnants of an old, large Angiosperm flora which has almost entirely disappeared from the earth. With this interpretation the presence of one *Ascarina* species in Madagascar has no clear significance,

as the species may have come by long-distance dispersal at any time during the Tertiary.

Piperaceae, *Aristolochiaceae*, *Nymphaeaceae*, *Ceratophyllaceae*, *Ranunculaceae*, *Papaveraceae* (cf. Humbert, 1959).

Menispermaceae (65 gen., 350 spp., chiefly in the tropical Old World). They are particularly well represented in Africa with 21 genera, 12 of which are endemic, and 65 species. There are perhaps 12 genera in Madagascar, 5 of which are endemic (*Orthogynium*, *Burasaia*, *Rhaptonema*, *Spirospermum*, *Strychnopsis*). Two genera are common to Madagascar and Africa (*Anisocycla*, *Triclisia*). To summarize, 19 genera are endemic to Africa-Madagascar and the remainder, except for 2, are palaeotropical. There is no direct link with America. This pattern of distribution, typically Gondwanian, poses a major problem because the other families in the order Berberidales are without doubt Laurasian.

II

Hamamelidaceae. This family, composed of 22–25 genera and about 100 species, ranges from S. and N. America to Australia, but occurs principally in S.E. Asia; it has 2 elements in Africa and Madagascar: *Dicoryphe* in Madagascar with 15 species and *Trichocladus* in tropical E. Africa and S. Africa with 5 species. According to Hutchinson this pattern of distribution resembles that of Magnoliaceae. There are however some interesting differences in that the latter family is absent from Australia and Africa and present in S. America. In spite of their very strong diversification in the Northern Hemisphere, principally in S.E. Asia, Hamamelidaceae are characterized by a widespread and discontinuous distribution that includes Africa and Australia. This pattern of distribution provides evidence of primitiveness and possibly that Hamamelidaceae might have originated in Gondwanaland according to one of two hypotheses envisaged by Raven & Axelrod (1974).

Myrothamnaceae is a monotypic family with 2 closely related species: one endemic to Madagascar, the other in E. and S. Africa (but also in Angola, Zambia and S. Zaïre).

Hydrostachyaceae. A monotypic family with the same pattern of distribution as the previous one, but with many species (18 endemic spp. in Madagascar, some 30 in S. Africa).

We need detailed researches on these small austral families considered as primitive and bunched together within Pittosporales (suborder Brunineae) by Thorne (1968, 1975), but the Hydrostachyaceae are placed in the Scrophulariales by Cronquist (1968).

Didymelaceae. A monotypic family of 2 species endemic to Madagascar whose taxonomic position is still uncertain. It is a rather primitive taxon (with solitary carpel and scalariform perforations) considered sometimes as close to Euphorbiaceae or Hamamelidales, or sometimes as an order of its own (Takhtajan, 1969).

Myricaceae. (4 gen., 40 spp.). This family, which is widely dispersed in temperate regions and tropical mountains of both hemispheres, is divided into two

subfamilies, one of which, monotypic and very archaic, the Canacomyricoideae, is endemic to New Caledonia (Leroy, 1949, 1957). The genera *Comptonia* (endemic to N. America, with 1 sp.), *Gale* (1 sp. in the Northern Hemisphere), and *Myrica* (temperate and tropical zones) are closely allied. The family is present in S. America, in Africa (many spp. in S. Africa), and in Madagascar with the genus *Myrica* (6 spp.).

Myricaceae is generally considered as a Laurasian family, but two facts argue against this view. First, the tropical distribution of *Myrica*, and, in particular, its abundance in S. Africa. Second, the existence of *Canacomyrica* in New Caledonia, where it certainly is a completely isolated survivor. *Comptonia* and *Gale* are possibly Laurasian segregants, but *Myrica* and, above all *Canacomyrica*, might indicate greater antiquity.

Moraceae. This family divided into 3 subfamilies (Moroideae, Artocarpoideae, Conocephaloideae), 75 genera, and 2,000 species is widespread in warm regions and the tropics and is represented in Madagascar by 11 genera and 42 species. If, following Hutchinson's division, we accept 9 tribes, all of them are represented in Madagascar, each of them by one or two genera (the small subfamily Conocephaloideae being excluded). Fatoueae: *Fatoua*, a genus with only 2 species, of which 1 occurs in Madagascar, the other in Asia, New Caledonia. Dorstenieae: *Dorstenia*, a pantropical genus with 100 species of which 2 occur in Madagascar. Strebleae: *Streblus*, a palaeotropical genus with 4–5 species, of which 1 occurs in Madagascar; *Maillardia*, an endemic genus with 4 species. Moreae: *Ampalis* and *Pachytrophe*, 2 endemic and monotypic genera. Broussonetieae: *Allaeanthus*, an endemic and monotypic genus. There are 4 genera in the Artocarpoideae: Euartocarpeae: *Treculia*, an African-Madagascan genus with 12 species of which 4 occur in Madagascar. Brosimeae: *Bosqueia*, another African-Madagascan genus with 12 species, of which 7 occur in Madagascar. Olmedieae: *Antiaris*, a palaeotropical genus with 10 species, of which 2 occur in Madagascar. Ficeae with 16 species in Madagascar.

The Madagascan Moraceae offer a basis for some interesting comments. First, we have to emphasize that the whole family is represented in Madagascar by all the tribes. Even the endemic genera are distributed into 3 tribes. Judging from these facts, one has good justification to uphold the hypothesis of Madagascar as a center of survival. Second, since there are 4 endemic genera, 2 African-Madagascan ones and 3 palaeotropical ones, links with America are weak. Third, it is noteworthy that the tribe Moreae, represented by 2 endemic genera, has no representative of *Morus*, a widespread genus, one subgenus of which occurs in tropical Africa, another in Asia, and yet another in America.

Urticaceae. A family of 50 genera (800 spp.) mostly in warm regions and tropics, is particularly well represented in America. There are 14 indigenous genera in Madagascar, one of which, *Neopilea* (2 spp.) is endemic, and 51 species (41 endemic) occur on the island.

As with the Moraceae, all tribes (5) of Urticaceae are represented in Madagascar, but endemism is weak, and pantropical or widespread genera are as many (6 in number) as palaeotropical ones. There is also an American-Madagascan genus, *Phenax*, with 20 species in America and 3 in Madagascar and the

Mascarenes. Further, one palaeotropical genus, *Pipturus*, reaches the Comores (1 nonendemic sp.) but neither Madagascar nor Africa.

Ulmaceae (15 gen., 150 spp.). This family has 4 genera in Madagascar: *Celtis* (3 Madagascan spp.; 1 of which is palaeotropical, the other 2 are related to African species); *Trema* (2 Madagascan spp., 1 of which is endemic with eastern affinities); *Aphananthe* (1 sp., endemic; the genus is closely related to *Celtis*); *Chaetacme* (1 African-Madagascan sp.).

Casuarinaceae (cf. Humbert, 1959).

III

Nyctaginaceae (cf. Humbert, 1959).

Phytolaccaceae (12 gen., 100 spp.). A family particularly well represented in America and S. Africa. Four genera are present in Madagascar, 1 of which, *Barbeuia*, is endemic, monotypic, and morphologically isolate (ovary 2-carpellate, syncarpous, 2-loculary). There is an endemic species of *Phytolacca*.

Didiereaceae. This remarkable family, endemic to South and Southwest Madagascar, consists of 4 genera: *Decaryia* (1 sp.); *Alluaudiopsis* (2 spp.); *Alluaudia* (6 spp.); *Didierea* (2 spp.).

Didiereaceae, certain of which have a habit resembling American Fouquieriaceae, are, with arborescent aphyllous euphorbias, the most striking feature of the southern Madagascan vegetation; it recalls somewhat the Brazilian "Caatinga" (Koechlin, 1972). According to Rauh's work (Rauh & Reznik, 1971), the family has definite affinities with the American family Cactaceae and must be placed in Centrospermae.

Cactaceae. It is a family of many genera, perhaps over 100, and 1,500 species almost wholly American. *Rhipsalis*, the single genus with representatives outside America, has one species, *R. baccifera* (J. S. Mill.) Stearn in tropical Africa, Ceylon, and Madagascar. And what is more, the Madagascan plant is so variable that several species have been described. According to Guillaumet (1972) there are at least two well characterized forms, each of them inhabiting a special ecological region: *R. horrida* (eastern littoral forest) and *R. suarezensis* (western Domain). This pattern of distribution has given rise to discussions, but it is probable that this differentiation has originated secondarily. A study of the whole genus *Rhipsalis* is needed before any opinion can be attempted.

Aizoaceae (*Molluginaceae* included) (130 gen., 1,200 spp., chiefly S. African). This unrevised family has some nonendemic genera in Madagascar (*Mollugo*, *Sesuvium*, *Trianthema*, . . .) with about a dozen species (Baron, quoted by Humbert, 1959).

Caryophyllaceae. This family is represented by 7–8 nonendemic genera (subfamily Alsinoideae) and 11 species, 8 of which are endemics. There are 2 endemic species of the palaeotropical genus *Corrigiola* and 5 species of the tropical and subtropical genus *Polycarpaea* (Perrier de la Bâthie, 1936).

Portulacaceae. This is a very interesting family of about 20 genera, most of them American. But 7 genera occur in Africa sensu lato, 4 of them endemic to Madagascar: *Talinella* (2 spp.), or South Africa: (*Ceraria*, 4 spp.; *Portulacaria*,

2 spp.; *Calyptrotheca*, 2 spp.) (Brenan, 1949; McNeill, 1974). The genus *Anacampseros* (50 spp.) is common to S. Africa and Australia. The genera *Portulaca* and *Talinum* are represented; the former in Madagascar (3 spp.), the latter in the Mascarenes (1 sp.). Although the family has two main centers of distribution, S. America and western N. America, it is as a whole a rather austral one. Moreover, it is closely related with the large family Aizoaceae, absent from Madagascar, but primarily represented in S. Africa. With respect to Portulacaceae, Madagascar and Australia look as if they were parts of a borderland.

Basellaceae, *Chenopodiaceae*, *Amaranthaceae*, *Polygonaceae*, *Plumbaginaceae* (cf. Humbert, 1959).

IV

Dilleniaceae (10 gen., 400 spp.). This family is represented in Madagascar by 3 nonendemic genera: *Hibbertia*, a genus of 155 species, 130 of which are in Australia, 24 in New Caledonia and Fiji, 1 (*H. coriacea*) in Madagascar (this one is closely related to Australian species); *Tetracera*, a pantropical genus of 50 species with 3 species in Madagascar, all of them endemic, and about 10 species in Africa. *Dillenia*, an Asian-Australian genus of 60 species, 1 of which, nonendemic is in Madagascar, and another endemic to the Seychelles. Apart from *Tetracera*, none of the genera of Dilleniaceae occur in Africa. According to Hutchinson there is one more genus, endemic to the Seychelles (*Neowormia*), related to *Dillenia*. Let us also not forget that the genus *Schumacheria* (3 spp.) is endemic to Ceylon. One must, it seems, put apart *Hibbertia*, which may have arrived by long-distance dispersal. But with *Neowormia* and *Schumacheria* we have possibly an indication of a much more ancient settlement for the family. Besides, the pantropical genus *Tetracera* belongs to the tribe Delimeae, largely American. One feels as if the Dilleniaceae, almost absent from Africa today, must have been much more numerous in the past and would have become extinct during the Tertiary. We are also badly in need of a detailed monograph of this especially interesting family.

Ochnaceae. (30 gen., 250 spp.) is an almost entirely tropical family, especially well represented in S. America. Its Madagascan representatives, which belong to subfamily Ochnoideae, tribe Ochneae (Kanis, 1968), are: *Ochna*, a palaeotropical genus of about 100 species in Africa south of the Sahara, Arabia, Madagascar, the Mascarenes, and 4 species in tropical Asia with perhaps 20 endemic species in Madagascar. *Gomphia* (= *Campylospermum*), a palaeotropical genus of 12 species, of which 5 are endemic to Madagascar, and 3 in Africa. *Brackenridgea* (= *Pleuroridgea*), another palaeotropical genus, containing 10 species, of which 2 endemic to Madagascar.

It is striking that there is no endemic genus. With the Madagascan Ochnaceae we deal with a part of a palaeotropical group, even though the family is chiefly South American.

Diegodendraceae (1 gen., 1 sp.). An endemic family (Capuron, 1963b).

Sphaerosepalaceae. This is an endemic family of Madagascar which consists of 2 genera of woody plants: *Rhopalocarpus* (15 spp.) and *Dialyceras* (3 spp.).

The best place for this family seems next to Diegodendraceae within Ochnales, but there are also links with Malvales.

Sarcolaenaceae (10 gen., 35 spp.). An endemic family.

Elatinaceae (2 gen., 45 spp.) (cf. Humbert, 1959).

Guttifereae and *Hypericaceae* represent a chiefly tropical group of 1,000 species in 40 genera, of which 8 are endemic to Africa-Madagascar. If we put aside *Hypericum*, an herbaceous genus of wide distribution throughout temperate regions and tropical mountains, 2 genera offer a widespread distribution: *Garcinia* and *Calophyllum*. However, both are far more highly differentiated in Asia-Australasia than in America or Africa; *Calophyllum*, which has 16 Madagascan species, is completely absent from Africa. *Symphonia* is abundantly diversified in Madagascar with many species or "morphological entities" merging into one another, but there are also 1–2 species in Africa and America. Its affinities are with *Montrouziera* of New Caledonia. Twenty species or so of *Mammea* inhabit Madagascar, all of them endemic, over 20 other ones occur in Asia-Indonesia, extending to New Guinea, except for Australia, but only 1 is met in Africa and another in S. America.

There are 3 endemic genera: *Eliaea*, related to the Asian genus *Cratoxylum*, *Ochrocarpos*, and *Paramammea* (Leroy, 1975, 1977b), each of them belonging to a different tribe. Finally, the other 2 genera, *Harungana* and *Psorospermum*, are common to Africa and Madagascar.

From these data, which are difficult to understand, one can however draw some conclusions:

Guttifereae are comparatively better represented in Madagascar than in Africa. The affinities between certain genera such as *Mammea-Paramammea* on the one hand, and *Garcinia-Ochrocarpos* on the other hand, show that these genera are probably not newcomers and that they probably differentiated there.

Such genera as *Symphonia* and *Mammea* look as if they had originated and evolved in Madagascar, although their affinities are with Asian-Pacific genera.

There is some evidence that as a whole, the Guttifereae-Hypericaceae of Madagascar and Africa may have differentiated there, when S. America, Africa, and Australia were no longer in contact.

The fact that 14 endemic species of *Calophyllum* (Stevens, 1976) occur in Madagascar, the genus being unknown in Africa, poses a problem. According to Perrier de la Bâthie (1936) all of the Madagascan species are derived from the beach species *Calophyllum inophyllum*. There is a great need for thorough research in evolutionary biology of this very interesting problem. Whatever the answer will be, it is quite certain that *Calophyllum* has occurred there for a very long time.

Dipterocarpaceae. This family of 18 genera, which has until now been considered as a typically palaeotropical one, has at least one representative (a monotypic subfamily) in Guyana (Maguire et al., 1977). It is basically divided into 2 very distinct subfamilies: Dipterocarpoideae and Monotoideae. The former is Asian with 13 genera and 247 species in only Borneo, a number that quickly decreases going toward India where only 6 genera and 14 species occur. However, it is surprising enough to meet as many as 10 genera and 44

species in Sri Lanka (Ceylon). Moreover, one genus, *Vateriopsis*, is endemic to the Seychelles and several Tertiary fossils have been found in E. Africa (Aubréville, 1976a). The Monotoideae comprises 2 genera: *Monotes* with 1 endemic species in Madagascar, 1 species in western tropical Africa, and 40 species or so in dry tropical S. Africa; *Marquesia*, with 4 species in tropical Africa. Some Tertiary fossils of this subfamily have been described from the temperate Northern Hemisphere, but their identity is not always convincingly established.

One can perhaps presume that Dipterocarpaceae has been a pantropical family which has become particularly impoverished in Africa during the Tertiary era owing to geological and climate alterations. It would have found a center of survival in Southeast Asia which has also become a new center for development (Meijer, 1974). It is however noteworthy that the family is very poorly represented in Madagascar, and absent from Australia.

Theaceae: cf. *Asteropeiaceae*.

Asteropeiaceae. This unigeneric family, endemic to Madagascar, contains 5–6 species which occur both in the western and eastern parts of the country. It is of great interest due to its close affinities with Theaceae (Melchior, 1925), from which it is distinguished by minor characters; *Asteropeia* is clearly a relict. We have to emphasize that Theaceae are represented in Africa-Madagascar by only 2 species of the large genus *Ternstroemia* (Hepper, 1968; Letouzey, 1977b) and 2 genera endemic to Africa: *Melchiora* (3 spp.) and *Ficalhoa* (1 sp. ?).

Medusagynaceae. (An unispecific family endemic to the Seychelles.)

Elaeocarpaceae. This family (8 gen., 400 spp.) is closely allied to Tiliaceae, of which it is considered often as a subfamily or a tribe, and is typically of southern distribution (S. America, Australia, New Zealand, New Caledonia, New Guinea), the only genus *Elaeocarpus* reaching northward India, China, and Japan. Curiously enough, there are 2 endemic species of *Elaeocarpus* in Madagascar (though none in Africa) and 1 endemic species of *Sloanea*, a widespread genus (likewise absent from Africa). They "probably reached Madagascar by long-distance dispersal around the Indian Ocean" (Raven & Axelrod, 1974). One must not exclude, however, that this mechanism may have operated early in the Tertiary when Australia was closer to Africa.

Tiliaceae is a predominantly woody family (60 gen., 1,200 spp.) mostly of tropical and subtropical distribution. Following Capuron (1963a, 1964), 7 genera occur in Madagascar: *Christiana* (1 African-Madagascan sp.); *Carpodiptera* (1 sp. in E. Africa and Madagascar, 3 spp. in Cuba and the West Indies); *Sparrmannia* (1 Madagascan sp., 1 Madagascan-E. African, 2 S. African); *Grewia* (more than 400 spp. of the tropics and subtropics); *Pseudocorchorus* (a monotypic tribe Pseudocorchoreae, 6 spp.); *Corchorus* (6 spp., nonendemic); *Triumfetta* (5 spp., nonendemic).

We also have to note the singular bipolar distribution of the genus *Carpodiptera*, the distribution of *Sparrmannia*, a genus of an entirely African tribe, and the fact that *Christiana* is a morphologically very isolated genus. The family is curiously anchored on Madagascar with an endemic tribe. Madagascan Tiliaceae are, however, strongly linked to Africa of which they are only a part.

Sterculiaceae is a woody family (38 gen., 1,000 spp.; Hutchinson, 1967) widely distributed in the tropics and subtropics. Out of 11 tribes recognized by Hutchinson, 6 are present in the Madagascan region, containing 22 genera (250 spp.). The tribe Dombeyeae, which is wholly palaeotropical, is composed of 11 genera, of which 8 occur in the Madagascan region, 6 being endemic; the nonendemic genera are: *Dombeya*, common to Madagascar and Africa but far more diversified in Madagascar, and *Melhania*, a widespread genus extending to Africa, Asia, and Australia.

Another fact must be pointed out: it is that 3 genera offer a very restricted endemism: *Astiria* (1 sp.) and *Trochetia* (5 spp.) to Mauritius, and *Ruizia* to Réunion. A third remark is the very important development of the African-Madagascan genus *Dombeya* in Madagascar and the Mascarenes, where about 200 species have been described, that is four-fifths of the whole.

The tribe Helmiopsideae consists of 3 genera, 2 of which are endemic to Madagascar, the third, *Nesogordonia*, having 10–12 species, half of which are Madagascan, the other half African.

The tribe Hermannieae has 3 Madagascan representatives but is deprived, it seems, of any biogeographical significance. The genus *Keraudrenia* (Lasiopetaleae, 12 genera) has one species in Madagascar (a single and ancient herbarium number is known of this plant).

More interesting is the tribe Byttnerieae with 2 genera indigenous in Madagascar: the pantropical *Byttneria* and the Asian-Australian *Rulingia* (25 spp.), one species of which is endemic to Madagascar.

Sterculieae is present with 1 pantropical genus, *Sterculia*, and 2 palaeotropical genera: *Firmiana* and *Pterygota*.

There are 2 genera of the palaeotropical tribe Tarrietieae: *Hildegardia* (2 spp. out of 7) and *Heritiera* (1 sp. out of 7).

In summary, such isolated representatives as *Keraudrenia* and *Rulingia* have possibly no particular meaning from a biogeographical point of view; as Raven & Axelrod have noted, these species probably reached Madagascar "by long-distance dispersal around the Indian Ocean."

But I want to emphasize some important facts: a very strong endemism of a part of the family in Africa-Madagascar (Dombeyeae, Helmiopsideae); a high degree of endemism in the Mascarene; the affinities of the Madagascan Sterculiaceae are with the palaeotropical flora. Many genera both monotypic or paucispecific and endemic, particularly in the Mascarenes, appear to be survivors.

Bombacaceae is a family of 31 genera and 225 species (Hutchinson, 1967), wholly woody and confined to the tropics, mainly the American ones. The Durioneae, generally considered as one of the primitive tribes, is Asian-Australasian, but the other tribes are either strictly American or represented in America. Bombacaceae are represented in Africa and Madagascar only by the tribe Adansonieae, with 15 species distributed in 4 genera: the palaeotropical *Bombax* (2 spp. in Africa), the endemic genus *Rhodognaphalon*, closely related, if not similar to the American *Bombacopsis*, with 6 species in Africa, and *Adansonia* which extends from Africa (1 sp.) and Madagascar (8 spp.) to Australia (1 sp.). A third genus (*Ceiba*, tribe Ceibeae, also exists in Africa, but

it is unanimously considered as an American newcomer. Judging from the present evidence, one may suggest a Gondwanian (South American-African) origin for the Adansonieae. A noteworthy fact recalled by Aubréville (1975a) is the African disjunction in the pattern of distribution concerning the whole family.

Malvaceae. This family (88 gen., 2,300 spp.) is world wide both in temperate and tropical regions. It is represented in Madagascar by 3 tribes: Malveae (5 gen., 17 spp.), Ureneae (3 gen., 5 spp.), Hibisceae (13 gen., 7 of which endemic, and 80 spp., 60 of which endemic). There are only 3 endemic species within Malveae (*Abutilon*—Bates, 1968) and 2–3 endemic species within Ureneae (*Pavonia*) in Madagascar-Africa. The tribe Hibisceae, which is composed of 29 genera (Hutchinson, 1967), is well represented in Madagascar and Africa, even better in Madagascar with 13 genera, of which 7 are endemic, than in Africa with 12 genera, of which only 3 are endemic. The only genus, *Hibiscus*, occurs abundantly in Madagascar with 45 species, 30 of which are endemic. The endemic genera are paucispecific and not always neatly separated: *Megistostegium* (3 spp.), *Perrierophytum* (9 spp.), *Humbertiella* (3 spp.), *Macrostelia* (3 spp.), *Humbertianthus* (1 sp.), *Helicteropsis* (2 spp.), *Jumelleanthus* (1 sp.). The genus *Gossypioides* (2 spp.) is endemic to E. Africa-Madagascar.

Such genera as *Cienfuegosia* (Fryxell, 1974) (America, Africa, Australia), *Kosteletzkya*, and *Thespesia* are represented respectively by 1, 7, and 1 endemic species. Two genera of Madagascan Hibisceae have no endemic species: *Abelmoschus* and *Gossypium*.

Nepenthaceae (1 gen., 80 spp.). The genus *Nepenthes* is confined to the Indian Ocean with 2 endemic species in Madagascar and 1 endemic in the Seychelles.

Droseraceae (1 gen., 90 spp.). Five species inhabit Madagascar, one of which endemic.

Lecythidaceae. Hutchinson (1964) has divided this family into two in accepting the Barringtoniaceae of Lindley, this one forming "a very natural group" of 4 genera, *Barringtonia* (Africa and Madagascar), *Combretodendron* (Africa), *Careya* (Indomalaysia), *Planchonia* (S.E. Asia, Australia); the genus *Foetidia*, confined to the Madagascan region, is retained in Lecythidaceae with *Napoleona* and *Crateranthus* of tropical Africa. For his part, Airy Shaw (1966) considers *Foetidia* as the type and the single member of the new family Foetidiaceae. *Foetidia* has 5 species (and several to be described), one of which is endemic to the Mascarenes and another reaching the African coast (Zanzibar). About the latter "there is no reason why it should not be native, but whether a recent arrival or a relicts of a one wider distribution is unknown," Sangai (1971) noted. *Barringtonia*, with 39 species, ranges from Africa and India to Australia; two species confined to sandy and rocky beaches, reach E. Africa and the Madagascan region.

Thus, there are two parts in this whole: a palaeotropical one with *Barringtonia* (and *Combretodendron* in Africa) and a neotropical one with *Foetidia* (distantly allied to some African genera), this one having evolved separately for a long time. Nevertheless, *Barringtonia* is to be considered in a special category as a readily dispersed mangrove genus.

Flacourtiaceae. This pantropical family of 84 genera (1,300 spp.) has 28 endemic genera in Africa sensu lato (including Madagascar and the Mascarenes) and thereby offers a special interest. It is well represented in Madagascar with 110 species and 14 genera, 8 of which are endemic (but 2 of them, *Calantica* and *Aphloia* reach E. Africa); the most evolved tribe (according to Hutchinson, 1967), Bembicieae, is endemic to Madagascar. There are 2 large pantropical genera: *Casearia* (160 sp.; 1 endemic to Madagascar and 1 to the Mascarene Islands; 11 endemic to Africa—Sleumer, 1971); *Homalium* (180 spp.; 59 spp. in Africa sensu lato, 38 of which in Madagascar, all of them endemic). Three genera are palaeotropical: *Erythrospermum* (5 spp., 2 of which endemic to Madagascar sensu lato, none in Africa); *Scolopia* (37 spp., 14 of which in Madagascar, all endemic); *Flacourtia* (60 sp.; 1, nonendemic, in Madagascar). The endemic genera are frequently pausispecific: *Prockiopsis* (1 sp.—Capuron, 1968d); *Bivinia* (2 spp.); *Bembicia* (1 sp.); *Bembiciopsis* (1 sp.); *Aphloia* (4–5 spp. or 1 polymorphic species); *Calantica* (7 spp.); except for *Tisonia* (15 spp.) and *Ludia* (23 spp.). The genus *Xylotheca* of tropical and E. Africa has 1 species in Madagascar. In the same way, *Aphloia* reaches E. Africa (Airy Shaw, 1966).

Such great a number of highly differentiated genera, that is one-third of the total number, are endemic to Africa-Madagascar that we may suppose the family to have originated there.

Violaceae (20 gen.) is represented by 3 nonendemic genera: *Viola* (1 sp., nonendemic); *Hybanthus* (75 spp., most part tropical, 4 spp. in Madagascar, 3 of which endemic); *Rinorea* (250 spp. tropical and subtropical, many African, but also well represented in South America; 27 spp. in the Madagascan region, all but one endemic).

Onagraceae (= *Oenotheraceae*) is a family of 21 genera and 640 species widespread through temperate and tropical regions, mostly as perennial herbs. There are 2 indigenous genera in Madagascar: *Epilobium* with 6 species, some of which are endemic, and *Ludwigia* with 9 species.

Turneraceae is a family of 8 genera, 6 of which are endemic to Africa-Madagascar. Two other genera also occur in this area, but are principally American: *Piriqueta* and *Turnera.* There are 3 genera in Madagascar: *Piriqueta* (3–4 endemic spp.); *Hyalocalyx*, a monotypic genus with herbaceous habit, also present in Mozambique; *Turnera* (1 nonendemic sp.). *Mathurina* (1 sp.) is a monotypic genus endemic to Rodrigues. A species attributed to *Piriqueta*, *P. integrifolia*, is an isolated taxon whose status needs to be restudied.

Passifloraceae is a family of 12 genera (600 spp.) of shrubs, vines and herbs of tropical and warm temperate regions. Two indigenous genera occur in Madagascar, *Adenia* and *Deïdamia.* The former, a palaeotropical genus of 100 species, is represented in Madagascar by 13 endemic species. The latter is an African-Madagascan genus with 6 species endemic to Madagascar and the Comores and 1 species confined to tropical Africa.

Physena. This is an isolated genus of 2 species endemic to Madagascar classified in turn in Passifloraceae, Capparidaceae, and Flacourtiaceae.

Begoniaceae. This is a small family of 5 genera particularly well represented in northern South America, but also in Pacific islands (Barkley & Golding, 1974). The genus *Begonia* with over 800 species, mostly American (Baranov & Barkley, 1974), is important in Madagascar where at least 50 species occur (Humbert, 1959).

Cucurbitaceae (116 gen., 1,200 spp.) (data according to Keraudren, 1966). This family of mainly tropical and subtropical distribution is well represented in Madagascar with 21 indigenous genera, of which 8 are endemic. Two endemic genera, *Xerosicyos* (4 spp.) and *Zygosicyos* (1–2 spp.), related to the African genus *Gerrardanthus*, are considered as primitive. The other endemic genera are: *Seyrigia* (5 spp.), related to some American genera; *Trochomeriopsis* allied to the *Seyrigia*; *Ampelosicyos* (3 spp.); *Lemurosicyos* (1 sp.); *Zombitsia* (1 sp.); and *Tricyclandra* (1 sp.). One genus, *Peponium*, is restricted chiefly to Madagascar (12 spp.) but reaches E. and S. Africa. There are 4 other African-Madagascan genera: *Oreosyce* (5 spp. in Africa, 1 sp. common to Africa and Madagascar); *Raphidiocystis* (5 spp., 1 of which special to Madagascar); *Cyclantheropsis* (3 spp., 1 of which special to Madagascar); and *Cucumella* (1 sp. in E. and S. Africa, and Madagascar). Five genera are palaeotropical: *Zehneria* with 9 Madagascan species (5 endemic); *Kedrostis* with 6 endemic Madagascan species; *Muellerargia* with 1 of its 2 species endemic to Madagascar, the other endemic to Malaysia. The American genus *Cayaponia* has some species in Africa, one of which is also in Madagascar. The pantropical (chiefly African) genus *Corallocarpus* has 3 Madagascan species, 2 of which endemic.

All of these facts support the thesis of an ancient distribution of the family in Madagascar.

Salicaceae are represented in Madagascar by 2 endemic species of *Salix*.

Capparaceae. This family of 50 genera and 800 species, primarily pantropical, has 8 genera in Madagascar, but none are endemic. Two of them, closely akin, are common to Madagascar and E. and S. Africa: *Boscia* (30 spp., 3 endemic in Madagascar) and *Thilachium* (20 spp., 9 spp. in Madagascar sensu lato, 8 endemic). The other genera are pantropical; *Crataeva* (3–4 spp. endemic to Madagascar); *Capparis* (4 spp. in Madagascar, 1–2 endemic); *Cleome* (7 spp. in Madagascar, 3 endemic); or palaeotropical: *Cadaba* (40 spp., 1 endemic in Madagascar); *Maerua* (100 spp., 5 endemic in Madagascar); *Gynandropsis* (1 adventitious sp.).

It is very surprising that this family, particularly well represented in Africa with 15 endemic genera, has no genus endemic to Madagascar. This lack of generic endemism may mean that Capparaceae reached Madagascar from Africa at a late date (about the genus *Physena*, cf. Passifloraceae).

Cruciferae (cf. Humbert, 1959).

Moringaceae (1 gen., 10 spp.). This monotypic family consists of about 10 species, 2 in India, the others in Africa-Madagascar. Aside from *Moringa oleifera*, known to be introduced, there are 2 endemic species in Madagascar, *M. hildebrandtii* and *M. drouardii*. They occur in the south and southwest of Madagascar with plants such as *Adansonia* or euphorbias and all of the genera of

Didiereaceae. In this region grow many xerophilous plants such as *Xerophyta dasylirioides*, *Selaginella nivea*, *Pachypodium* sp., *Aloe divaricata*, *Aloe suzannae*, *Rhigozum madagascariensis*, *Uncarina* sp., etc. The African species of *Moringa* are distributed in a discontinuous area in the Southwest (*M. ovalifolia*) and in the Northeast (*M. longituba*, *M. stenopetala*, *M. peregrina*). Two species are known in N. India (*M. concanensis*, *M. oleifera*) (Keraudren, 1965).

Ericaceae (*Vacciniaceae* included) (50 gen., 1,350 spp.). This is a family of cosmopolitan plants or one inhabiting mountains in the tropics. It is divided into 3 subfamilies, 1 of which, Ericoideae, is well represented in Europe and Africa, whereas the other 2 subfamilies (Vaccinioideae, Rhododendroideae) are absent or nearly so from Africa. Three genera occur in the Madagascan region: *Agauria* (7 spp.) and especially *Philippia*, with nearly 40 species, that is half of the whole genus. The widespread and very distinct genus *Vaccinium* (a special family for some authors) has only 4 Madagascan species. This genus, which occurs in S. Africa, appears absent from tropical African mountains.

According to Stevens (1970, 1971) and others, *Agauria* is closely related to the American genus *Agarista*.

Sapotaceae. Following Aubréville (1972, 1974b), the Madagascan Sapotaceae have 11 genera (85 spp., all endemics) divided into 2 subfamilies. Mimusopoideae: *Manilkara* is a pantropical genus having more than 60 species, with 7 endemic in Madagascar. Three genera are endemic: *Labramia* (8 spp.); *Fauchera* (11 spp.); and *Labourdonnaisia* (3 spp. in Madagascar, 2 spp. in the Mascarenes). *Mimusops* is a genus common to E. and S. Africa (12 spp.), the Comores (1 sp.), Madagascar (13–14 spp.), the Mascarenes (3 spp.), and the Seychelles (1 sp.) but with 1 species is widely spread over palaeotropics to the Pacific islands.

Sideroxyloideae: 3 African-Madagascan genera: *Sideroxylon*, a genus with about 15 species, well known for its disjunct distribution (Madeira, Cape Verde Islands, Teneriffe, E. Africa, Madagascar, Mascarenes); 6 species are in Madagascar and 6 species in the Mascarenes; *Donella*, 4 species in the Guineo-Congolese forest, 1 species in E. Africa, 8 species in Madagascar; *Austrogambeya*, a genus from S. Africa and Zambia, close to *Donella* and *Gambeya*, with 1 species in Madagascar. *Gambeya*, a genus principally African, with 1 species in Madagascar, but with also 1 species in S. America. Two endemic genera: *Tsebona* (1 sp.) and *Capurodendron* (22 spp.).

Judging from these data based on Aubréville's work, we must conclude that Sapotaceae appears to represent a very important and strongly differentiated Madagascan nucleus. A high degree of generic endemism, a strange disjunct distribution in Madagascar-Africa (*Sideroxylon*), an intensive differentiation of *Mimusops* species in Madagascar, many strong links with Africa where the family reaches a very high development, such are the most noteworthy aspects concerning the distributional pattern of the Madagascan Sapotaceae, from which we could infer with Raven & Axelrod (1974) that an origin in West Gondwanaland "appears most probable, almost certainly before the close of the Cretaceous."

Madagascar and its surrounding islands must have taken a considerable part

in saving from extinction many Gondwanian genera which are today morphologically and geographically isolated, such as *Sideroxylon*, *Labourdonnaisia*, and other palaeoendemics. One genus, *Northea* (5 spp.), is endemic to the Seychelles.

Ebenaceae (2 gen., 450 spp.). The pantropical *Diospyros* is represented in Madagascar by ca. 100 species, 6–7 of which occur on the African mainland or have close relatives there. The remainder are endemic to Madagascar and do not seem to be closely related to the mainland species. *Euclea* (12 spp. in Africa) has 1 species on the Comores. There are the same number of species of *Diospyros* in Madagascar as in tropical Africa, and ca. 80 species in tropical America. About 250 species are currently accepted from tropical Asia, but this figure must be much too high (F. White, personal communication). Although he has not yet given any serious thought to the place of origin of the family, White inclines to the belief that it might have been the African part of Gondwanaland (White, pers. comm.).

Myrsinaceae (35 gen., 1,000 spp.). This family is a very natural one whose 7 genera occur in Madagascar: 2 pantropical: *Rapanea* (190 spp., 1 in the Seychelles, 1 in Madagascar, 2 in the Comores) and *Ardisia* (2 spp. in Madagascar, 2 spp. in the Macarene); 2 palaeotropical: *Embelia* (100 spp. in 8 subgen., 2 of which in Madagascar containing 8 spp.) and *Myrsine* (7 spp. in China, India, Africa, Azores; 1 endemic sp. in Madagascar); 3 endemics: *Monoporus* (8 spp. from sea coast to mountains), *Oncostemon* (97 spp. in Madagascar, 3 in the Comores, 3 in Mauritius), *Badula* (14 spp. in the Madagascan region: 3 in Madagascar, 3 in the Réunion, 7 in Mauritius, 1 in Rodriguez).

It is interesting to note that the pantropical genus *Ardisia* is represented in Madagascar by a subgenus endemic (*Madardisia*) and in Africa by another subgenus (*Afrardisia*). These facts seem to at least prove some antiquity of the genus in Africa-Madagascar.

Madagascar must have been a part of the ancient continent where Myrsinaceae originated. Let us note in passing an unusual intense speciation in the genus *Oncostemon*.

Primulaceae (cf. Humbert, 1959).

V

Cunoniaceae. This typically austral family (27 gen., 260 spp.) is represented in Madagascar by only the genus *Weinmannia* and over 20 species. This genus with 150 species ranges from the Philippines and New Caledonia to tropical America, where it is particularly abundant, but it is absent from Africa, India, and Australia. There are 2 genera of Cunoniaceae in S. Africa: *Cunonia* (about 15 spp. in the Malay Archipelago and New Caledonia, 1 endemic species in S. Africa); and *Platylophus*, the latter being monotypic and endemic. All of the Madagascan species, which Bernardi (1965) has divided into 4 sections, are endemics.

In spite of its scanty representation in the Madagascan region (Madagascar and S. Africa), the family Cunoniaceae provides some most valuable facts. First, there is one and only one endemic genus, and this one is monotypic: a fact

whose significance is obvious: the genus *Platylophus* testifies in favor of S. Africa as a center of survival for Gondwanaland inhabitants. Second, the link between S. Africa and Madagascar is not less obvious. Third, the genus *Weinmannia* has been subjected to very active speciation since Madagascar separated from Africa. The lack of fossils prevents a definite statement about its possible presence in Africa in the past.

Pittosporaceae. This typically palaeotropical family of 9 genera, 8 of which are endemic to Australasia, is represented in tropical Africa sensu lato by the genus *Pittosporum* which contains over 150 species, spread from Hawaii to the Canary Islands. There are perhaps 25 species in tropical Africa, 10 of which are in Madagascar; all of them, but 1, endemics.

This family offers a remarkable case of biogeographical meaning. The distribution pattern of the genus *Pittosporum* (Cufodontis, 1960), if regarded as an isolated genus, is almost meaningless, but in relation with the whole of its family, it becomes probable that its distribution center must have been Australasia, perhaps in the Upper Cretaceous or later when Australia and Africa were still in close proximity. However, the relationships of the family being somewhat problematic, it is difficult to know for certain where it originated.

Crassulaceae. This is a family of wide, cosmopolitan distribution consisting of 35 genera and 1,500 species, often growing in dry regions, chiefly in S. Africa and the Mediterranean region, but also in Asia and Central America. It is represented in Madagascar by 3 genera: *Crassula* (5 ssp. all of them endemic), *Sedum* (1 sp., endemic) and *Kalanchoë* (57 spp. of which 55 endemic). There is no endemic genus. Affinities are strongly African (P. Boiteau, pers. comm.).

Saxifragaceae. For want of being revised this family proved difficult to interpret. Many genera formerly included in it (*Brexia*, *Roussea*, *Forgesia*, *Grevea*, *Montinia*) are now either incorporated with Escalloniaceae (Hutchinson) or distributed among small new families. Given our present knowledge, the latter alternative seems the best one.

Brexiaceae is a small family of 2–3 genera with only a few species: *Brexia* in Madagascar and the Seychelles (1–2 spp., 1 of which is also in E. Africa); *Roussea* (1 sp. in the Mascarene); *Ixerba*, the affinities of which are uncertain, in New Zealand.

Montiniaceae is a family of tropical Africa and South Africa consisting of two very distinct genera (each of them should be raised to the subfamily level): *Montinia* (1 sp. in South Africa) and *Grevea* (3 spp., one of which reaches the western parts of Madagascar). The recently discovered *Grevea bosseri* Letouzey by P. Sita in Zaïre (Letouzey, 1977a) confirms Africa as probable center of origin for Montiniaceae and extends the area of the remarkable genus *Grevea*. It is noteworthy that *Grevea madagascariensis* is present on Madagascar, as, conversely, *Brexia madagascariens*is is on the African coast: the Mozambique canal has been a poor gap between Africa and Madagascar.

Escalloniaceae. Following Airy Shaw (1966), I maintain, at least provisionally, the genus *Forgesia* in this ill-defined family. This genus is monotypic and endemic to the Mascarene Islands.

Rosaceae is a family of wide distribution which contains 124 genera and over

3,300 species. It is represented in Madagascar by only 6 indigenous genera, one of which, *Grangeria*, is endemic. Besides the genus *Rubus*, they belong in two tribes: first, *Pygeum* (3 spp., 1 endemic), second, *Parinari* (a pantropical genus with 2 spp. endemic to Madagascar), *Licania* (a large austral genus with 1 Madagascan nonendemic sp.), *Hirtella* (another large austral genus, with 4 sp. endemic to Madagascar, 2 of which described by Capuron, 1972b), *Grangeria* (a monotypic and endemic genus).

Although very poorly represented, the family Rosaceae is interesting in that its links with Africa, are well marked by the genera *Hirtella* and *Grangeria*, which belong in one and the same tribe.

Leguminosae (*Caesalpiniaceae*, *Mimosaceae*, *Papilionaceae*). The revision of the Madagascar Leguminosae by M. Peltier is in progress but still far from complete. So, it is impossible to form an accurate opinion about Madagascan elements. In referring to work by Capuron (1967a, 1968b, 1970b), Viguier (1944), and Peltier (pers. comm.), there would be approximately 98 genera and 600 species. Since the Humbert's (1959) essay, Capuron (1967a) has described 2 new genera of Caesalpinioideae: *Elignocarpus* and *Mendoravia*, bringing the number of endemic genera to 11 out of 25. This is a very strong generic endemism. And this fact concerning the most primitive subfamily seems all the more important as the number of endemic genera is proportionally inferior in Papilionoideae and reduced to one in Mimosoideae. At the specific level, endemism is about 50% in Papilionioideae, 70–75% in both of the other subfamilies. One genus, *Bremontiera* (1 sp.), is endemic to the Mascarenes.

Podostemaceae (40 gen., 200 spp.) (according to C. Cusset, 1974, oral comm.). This family taken sensu stricto is represented in Madagascar by 4 genera, only 1 of which nonendemic: *Sphaerothylax* (3 spp.: 1 confined to Cameroon; 1 to S. Africa, reaching Angola and Zambia; 1 in E. Africa, Ethiopia and Madagascar). The 3 endemic genera are: *Thelethylax* (2 spp. endemic), closely allied to *Ledermanniella*, an African genus of 47 species, particularly abundant in Cameroon-Gabon; *Endocaulos*; and *Palaeodicraeia*. These last 2 genera are morphologically noteworthy with their deciduous leaves, the blade falling off and the persistant sheath becoming thick. This character unknown in African Podostemaceae exists in Asia (*Hydrobryum*, *Zeylanidium*). With respect to other characters, affinities are likewise with Asia. There is no link with the American element (C. Cusset, pers. comm.).

Tristichaceae, a family often merged into Podostemaceae, consists of 4–5 genera: 1 in Amazonia, 2 in Asia, 1 pantropical (with several spp., of which 1, *Tristicha trifaria*, in Madagascar and S. Africa; another, *T. alternifolia* in Madagascar and Africa [and America?]; 1, *T. hypnoides* in South and Central America; 1 in Australia—possibly a new genus) (C. Cusset, pers. comm.).

This distributional pattern, with 3 endemic genera in Madagascar, seems to indicate that the Podostemaceae could have had a Gondwanian origin by the close of the Cretaceous times.

Haloragaceae (6 gen., 120 spp.) (cf. Humbert, 1959).

Lythraceae. A family of herbs (often hygrophilous) and shrubs widespread throughout the World containing 25 genera and 550 species. It has 6 indigenous

genera in Madagascar, one of which is endemic, and 20 species, half of which are endemic. One genus, *Tetrataxis* (1 sp.), is endemic to the Mascarenes.

No clear meaning is to be drawn from the presence in Madagascar of widespread genera such as *Nesaea*, *Rotala*, *Ammania*, whose 10 or so species are nevertheless endemic to Madagascar. In contrast, we have to focus interest on *Woodfordia* and *Pemphis* which are small palaeotropical genera, each of them consisting of 2 species: *Woodfordia* with 1 African species and a widespread one ranging from Africa and Madagascar to Indonesia; *Pemphis* with 1 species, littoral, reaching the Pacific Islands, and the other endemic to Madagascar. Moreover, a monotypic genus, endemic to Madagascar, *Capuronia*, was described by Lourteig (1960); it is the single dioecious Lythraceae.

Sonneratiaceae. This small family of 2 genera and 7 species is of special interest in that it is centered in South Asia, although the mangrove genus *Sonneratia* reaches the African coast with one species. But this very distribution provides evidence in favor of links between the Madagascan region (including E. Africa) and E. Asia, to the exclusion of the West African coast. It is one of the characteristic elements of the floristic oriental belt.

Thymelaeaceae (*Aquilarioideae* included) (50 gen., 600 spp.). Mainly in temperate regions (Mediterranean region, S. Africa, Australia . . .), this family is very akin to the families Penaeaceae (5 gen.) and Geissolomataceae both of of them endemic to S. Africa. There are 7 genera in Madagascar, 2 of which palaeotropical (*Lasiosiphon*, *Gnidia*). Four genera are common to Madagascar and Africa: *Peddiea*, 1 endemic species in Madagascar; *Synaptolepis*, 1 endemic species in Madagascar; *Dais*, 1 endemic species in Madagascar, 1 species in S. Africa; *Octolepis*, 3 species, morphologically isolated and primitive (with a perianth deprived of tube), represented in Madagascar by 1 species (which will have to be raised at the subgeneric level), which is dioecious and endemic. One genus, *Stephanodaphne*, is composed of 9 species, 1 of which is endemic in the Comores.

The family, therefore, is strongly attached to Africa. According to Léandri (1947) the genus *Synaptolepis* is related to the American genus *Lophostoma*. The family is an heterogenous assemblage divided into several phyla, in particular the *Synaptolepis* one, the *Stephanodaphne* one, the *Peddiea* one.

Myrtaceae (100 gen., 3,000 spp.). This is a family mainly developed in Australia and tropical America, but with a monotypic, endemic subfamily (Heteropixioideae) in S. and S.E. Africa. There are 3 indigenous genera in Madagascar: *Myrtus* with 2 endemic species, *Eugenia* (35 spp.), and *Syzygium* (20 spp.). Many species also occur in the Mascarenes and Seychelles, and one monotypic family, possibly related to the Myrtaceae, the Psiloxylaceae, is endemic to the Mascarenes.

Melastomataceae (250 gen., 4,000 spp.). The Madagascan Melastomataceae being in badly need of revision, it is not possible to have any clear view about their composition and affinities. According to Perrier de la Bâthie (1951), there are 10 indigenous genera, 5 of which endemic. Since then, the genus *Rousseauxia* has been restated (Jacques-Félix, 1973) and the geographical distribution of two genera given as Madagascan has been altered.

In any case, there are 4 genera endemic to Madagascar-Mascarenes: *Rhodosepala* (1 sp.), *Dionycha* (3 spp.), *Amphorocalyx* (5 spp.), and *Rousseauxia* (13 spp.), and 5 common to Africa: *Gravesia* (100 spp. in Madagascar, 7 sp. reaching E. Africa and some spp. in tropical Africa), *Dichaetanthera* (20 spp. in Madagascar, 1 endemic to Africa), *Tristemma* (15 spp.), *Anthostemma* (1 sp. in Africa, 1 in Madagascar), *Dissotis* (2 African spp.). The other two genera are palaeotropical: *Medinilla* (70 spp. in Madagascar) and *Memecylon* (56 spp. in Madagascar).

Combretaceae. As stated by Exell (1972) and Exell & Stace (1966), this family is composed of 19 genera (475 spp.): 13 in Africa-Madagascar, with 7 endemic, 3 palaeotropical, 2 widespread, 8 in Asia with 2 endemic, 8 in America with 4 endemic, 3 in Australia with 1 endemic. There are overall 14 genera endemic to any region, 2 widespread genera, and 3 mangrove genera, and the family is centered in Africa (Liben, 1971). There are 62 species in 5 genera in Madagascar (Capuron, 1973a), 2 of which have a pantropical distribution: *Terminalia* (50 spp. in Malaysia, 35 in Madagascar, 30 in Africa, 30 in America, only some in Australia) and *Combretum* (100 spp. in Africa, 35 in America, 35 in Asia, and only 4 in Madagascar). *Meiostemon* is an African-Madagascan genus of 2 species: 1 species is endemic to Madagascar, and 1 species is endemic to the Sudano-Zambezian area. The endemic genus *Calopyxis*, which is characterized by lacking petals and by the corollalike structure of its receptacle, has as many species as 22, which is a very high number proportionally to the area. Madagascar, like Amazonia, and the Malaysian Islands, is a center of strong speciation (Exell & Stace, 1966).

Some facts must be noted. First, the active speciation of 2 genera (*Terminalia*, *Calopyxis*) might have started after Madagascar separated from Africa. One can add that *Lumnitzera*, the fifth genus in Madagascar (1 mangrove sp.), is a strictly palaeotropical genus. All of tribes and subtribes are represented in, one of which (*Pteleopsidineae*) is endemic to, the African-Madagascan area. A subfamily, Strephonematoideae (raised by some authors—Venkateswarlu & Rao, 1971—to familial level) containing 7 species, is endemic to Africa.

Proteaceae (75 gen., 1,000 spp. according to Johnson & Briggs, 1975). This family is mainly of southern tropical distribution with two major centers: Australia (45 gen. with 35 endemic) and South Africa (14 gen.). However, some genera reach Central America, Ethiopia and China. Johnson and Briggs have divided the family into 5 subfamilies, 2 of which are present in Madagascar: Proteoideae (1 tribe, Conospermeae, out of 3) and Grevilleoideae (1 tribe, Macadamieae, out of 7). All of the 14 South African genera, 2 of which (*Faurea*, *Protea*) extend far northward, belong to the Proteoideae.

There are 3 genera in Madagascar with 2 endemic. The monotypic genus *Dilobeia* stands apart and represents a subtribe of its own (Conospermeae—Dilobeiinae). *Faurea* (18 spp.), a tropical African genus classified in the Conospermeae—Proteinae, has one species in Madagascar. The third genus, *Malagasia*, with only one species, is the only representative of the subtribe Hicksbeachiinae (Macadamieae) in the African region; its closer ally in the same tribe could be *Heliciopsis* the sole genus endemic to Asia to the west of

Wallace's Line. It is noteworthy that another monotypic and isolated genus in the Macadamieae, *Brabeium*, inhabits S. Africa.

The Madagascan Proteaceae (besides *Faurea*) are obviously some rare relicts of a continuous ancient southern area. Johnson and Briggs think that the family could have originated in Gondwanaland in the Albian at the latest.

Rhizophoraceae. This family (160 spp.), which includes 18 genera, is basically palaeotropical. In the Madagascan-African area one finds 9 genera, 4 of which are endemic: *Anopyxis* (3 spp.), *Macarisia*, *Comiphyton* (1 sp.) (Macarisiae—Floret, 1974), and *Poga* (1 sp.) (Anisophylleae). All of the tribes are represented in this area, and the Macarisieae, which reaches America (*Sterigmapetalum*, an endemic genus of 3 spp.) and India (*Blepharistemma*, a monotypic and endemic genus) has its principal center of differentiation here (Floret, 1976).

There are 7 genera in Madagascar (22 spp. with 17 endemic): 3 mangrove genera (Rhizophoreae): *Ceriops*, a genus with 2 species, palaeotropical, 1 of which, *C. tagal*, reaches E. Africa, Madagascar, and the Seychelles; *Bruguiera*, with 6 species, palaeotropical, 1 of which, *B. gymnorrhiza* also reaches E. Africa, the Seychelles, and Madagascar; *Rhizophora*, a genus of 7 tropical species, 1 of which, palaeotropical, *R. mucronata*, occurs in E. Africa, Madagascar, the Seychelles, and the Mascarenes. The palaeotropical genus *Carallia* (Gynotrocheae) has 10 species of which *C. brachiata*, reaches the Madagascan rain forests. The other 3 genera are *Macarisia* and *Cassipourea* (Macarisieae) and *Anisophyllea* (1 endemic sp.) (Anisophylleae). The tribe Macarisieae is strongly rooted on Madagascar with the endemic genus *Macarisia* (2 spp.) and *Cassipourea*, a large genus reaching S. India and S. America, with 10 species endemic to Madagascar.

The family has only 2 genera endemic to America: *Polygonanthus* (Anisophylleae) and *Sterigmapetalum.*

From this distribution, one may suppose that the differentiation of the family might have begun by the time when America and Africa started separating so that a small part of the first members of it were trapped in America. Africa-Madagascar-India might have been the principal primary center of taxogenesis later in the Cretaceous. In any way, the family is obviously centered around the India Ocean.

Concerning the position of the Rhizophoraceae in the Myrtales, the recent work on wood anatomy by van Vliet (1976) suggests the family does not belong to this order, but rather to Cornales (following the Thorne's [1968] classification).

Alangiaceae. This monotypic family which has for a long time been included in Cornaceae covers a typically oriental area: Vietnam (7 spp.), China (6 spp.), Sumatra (8 spp.), Borneo (8 spp.), Java (7 spp.), Japan (2 spp.), E. Australia (1 sp.), New Caledonia (1 sp.). However, the genus *Alangium* is also represented in the African-Madagascan area by 3 very distinct species, one of which, *A. griselleoides* Capuron, is endemic in Madagascar. Judging from the incomplete material at his disposal, Capuron (1962) suggested wrongly that it could belong to section *Conostigma.* In all certainty, the Madagascan species is to be placed with *A. chinense* and *A. barbatum* in section *Marlea* Baill. close to

section *Angolum* Baill. to which belongs *A. salviifolium*. The present Indo-Malesiano-Australian area displays one African-Madagascan branch with 3 species. Besides, it is notable that the Madagascan species is dioecious and is the single one within the genus to be so. In all probability, this advanced character must have been acquired after Madagascar separated from Africa, possibly recently. Moreover, the Madagascan species, unlike the species of *Conostigma*, does not have a primitive secondary xylem with scalariform perforation plates (Eyde, 1972).

The fossil material of Alangiaceae, *Alangioxylon*, *Alangiopollis* (Reitsma, 1970), at our disposal shows that the distribution of the family reached Europe and N. America during Eocene-Miocene times. For Reitsma, *Alangiopollis eocaenicus* Krutzch (Germany, London Clay Flora) could be considered to be one of the ancestors of the family and, though referring only to pollen, he thinks *A. griselleoides* might represent the end product of a line coming from this fossil taxon through *A. barbatum*. The placement of *A. griselleoides* in *Marlea* supports this hypothesis.

I agree with Aubréville (1976b) that this member of the Madagascan flora belongs to a Laurasian line. It might have reached Madagascar in the late Eocene when the Thethys became interrupted, permitting connections between Africa and the northern continents.

Cornaceae. It is not certain that this family occurs in Madagascar, the two Madagascan genera formerly attributed to it being now considered to constitute a special endemic family Melanophyllaceae (Airy Shaw, 1972). It is even possible that this one will have once again to be divided as the morphological gap between the two genera appears substantial. *Melanophylla* has 9 species, *Kaliphora* only one.

Olacaceae is a tropical family (24 gen., 230 spp.) that has 4 genera in Madagascar, of which 1 is endemic with 3 species: *Phanerodiscus*. There is 1 pantropical genus, *Ximenia*, with 3 species out of 12 over the World, with 2 endemic, and 1 common to Madagascar and Africa. There are 2 palaeotropical genera: *Olax* (50 spp.) with 7 species in Madagascar and the Mascarene Islands of which 6 are endemic and 1 is common to Madagascar and Africa; *Anacolosa* (16 spp.) with 2 species in Madagascar (Capuron, 1968a).

Opiliaceae is a palaeotropical family of 8 genera of which 1, *Rhopalopilia*, is endemic to Madagascar-tropical Africa: 5 species are endemic to Africa, 2 are endemic to Madagascar, and 1 is common to Madagascar and Africa (Capuron, 1968a).

Santalaceae, *Loranthaceae* (cf. Humbert, 1959).

Balanophoraceae (18 gen., 45 spp.). This family of parasitic plants has 3 genera in Madagascar, 5 in Africa, 1 of which, *Balanophora*, is a palaeotropical genus that occurs in Madagascar and W. Africa. One Madagascan genus, *Ditepalanthus*, is endemic and monotypic, the third is *Langsdorffia*, a genus classically known as confined to America, but present also in New Guinea (Hansen, unpublished paper 1976). *Langsdorffia malagasica* (= *Thonningia malagasica*) is a dioecious parasite on roots of *Elaeocarpus quadrilobus*, an austral genus absent from Africa.

What is of particular interest is that 5 genera are endemic to Madagascar-Africa, distributed in 4 subfamilies of which 2 endemic. *Mystropetalon* (1–2 spp.) is endemic to S. Africa (according to Airy Shaw, 1966, this genus should be given family rank). The Sarcophytoideae is composed of 2 genera: *Sarcophyte* (2 spp. in E. Africa and Transvaal) and *Chlamydophyton* (equatorial West Africa). The subfamily Balanophoroideae has 2 genera in Africa: *Balanophora* and *Thonningia*, an endemic genus. The Helosioideae, in which the Madagascan *Ditepalanthus* is placed, is absent from Africa but has 3 endemic genera in America (*Scybalium*, *Helosis*, *Corynaea*) and 3 others in Asia. *Ditepalanthus* is related to *Rhopalocnemis* (Himalaya, Vietnam, Indonesia) (Hansen, unpublished paper, 1976).

It is to be noted that *Langsdorffia malagasica* and *Ditepalanthus* are landmarks between America and Palaeotropics.

The distributional pattern of the Balanophoraceae is typically austral and supports the idea that the family must have had a Gondwanian origin.

Hydnoraceae (2 gen., 20 spp.). This is a very interesting bitypic family of parasites of the Southern Hemisphere restricted to the Madagascan region sensu lato and America. *Hydnora* is composed of about 10 species, one of which is endemic to Madagascar and represents a section of its own, *Neohydnora*; the other species inhabit in S. and E. Africa. The other genus *Prosopanche* is endemic to S. America (Paraguay, Argentina).

The placing Hydnoraceae (Rafflesiales) near Santalales is of special interest because the Balanophoraceae-Hydnoraceae is a biogeographically homogenous unit.

Rafflesiaceae (8 gen., 50 spp.). There are 3 endemic species of *Cytinus* in Madagascar, a genus confined to Africa and W. Europe.

Celastraceae (*Hippocrateoideae* excluded). This is a family of tropical and temperate plants dispersed all over the world, although more abundantly in S. America, and contains 60–90 genera (800–1,000 spp.). According to Lobreau-Callen's (1975) work, it is, with the Icacinaceae and several small families, a member of an austral complex. It is of special interest with respect to Madagascar where at least 14 genera occur (4 of them being still undescribed), 10 of which are endemic: *Polycardia*, 9 species; *Ptelidium*, 2 species; *Hartogiopsis*, 1 species; *Salvadoropsis*, some species; *Brexiella*, 2 species; *Evonymopsis*, 4 species. The other genera are widespread (*Celastrus*) or pantropical (*Elaeodendron*, *Maytenus*), or African-Madagascan (*Mystroxylon*).

So generic endemism is extraordinarily high, a proportion of 2:3. But this interpretation is only a provisional account as the family is in badly need of revision. One monotypic genus (*Herrya*) is endemic to Réunion.

Hippocrateoideae (N. Hallé, unpublished paper) (24 gen., 320 spp.). This subfamily is mainly developed in Africa-Madagascar with 17 genera, 9 of them endemic, and 150 species. There are only 6 genera (11 sp.) with none endemic in Madagascar: *Apodostigma* (1–2 spp. common to Madagascar and Africa); *Reissantia* (1 sp. in Madagascar, 4 spp. in Africa, 3 spp. in Asia-Melanesia); *Loeseneriella* (2 spp. in Madagascar, 12 ? spp. in Africa; 8 ? spp. in Asia-Melanesia); *Elachyptera* (1 sp. in Madagascar, 3 spp. in Africa, 3 spp. in America); *Pristimera* (4 spp.

in Madagascar, 5 spp. in Africa, 9 spp. in America); *Salacia* (2 spp. in Madagascar, 90 spp. in Africa, 30 spp. in Asia-Melanesia, 29 spp. in America).

Salvadoraceae, *Aquifoliaceae* (cf. Humbert, 1959).

Icacinaceae is a family of pantropical distribution with 58 genera and 400 species. It is represented in Madagascar by 8 genera, of which 4 Madagascan-African (*Cassinopsis*, 4 endemic spp., 2 spp. endemic to S. Africa; *Leptaulus*, 1 endemic Madagascan species, 2 species endemic to tropical Africa; *Desmostachys*, 1 species in Madagascar, Comores, S. Africa, 2 species endemic to Africa; *Raphiostyles*, 6–7 species in Africa, 1 species endemic to Madagascar; 3 palaeotropical (*Apodites*, *Iodes*, *Pyrenacantha*); 1 endemic, *Grisollea*, which contains 2 species, of which 1 is restricted to the Seychelles.

Dichapetalaceae is a small family (3 gen., near 100 spp.) nearly confined to the tropics. It is represented in Madagascar by 14 species, all of them endemic, belonging to genus *Dichapetalum*, a pantropical one that is by far the largest in the family, and which is abundantly present in Africa (⅔ of the whole—Breteler, 1969).

Buxaceae (5 gen., 50 spp.). The plants of this family occur mainly in temperate regions of the northern hemisphere, but also in tropical mountains. The family reaches the southern hemisphere with 2 genera: *Styloceras* (tropical S. America, perhaps a special family) and *Buxus* sensu lato. The latter is present in Madagascar with an isolated group of 2 species, *B. madagascarica* and *B. macrocarpa*, which is strongly related to species of E. and S. Africa.

Euphorbiaceae (300 gen., 7,500 spp.). This is a family of almost cosmopolitan distribution, mainly of the tropics, with two large centers of distribution: tropical America and Africa. The new taxonomic results that have been obtained for Madagascan Euphorbiaceae during the last twenty years, part of which are not yet published, provide some new insights (Léandri, oral comm.). In particular, we must cite the Webster's (1975) work, which has modified the former systematics and suggests new ways of approaching origins and affinities. Following this author, there would be 5 subfamilies in Madagascar: Phyllanthoideae (7 tribes), Oldfieldioideae (1 tribe), Acalyphoideae (16 tribes), Crotonoideae (7 tribes), Euphorbioideae (3 tribes). Thus, 34 (out of a whole of 52) tribes are present in Madagascar. Thanks in particular to Capuron, the number of Madagascan genera amounts now to 62, 14 of which are endemic. There are about 600 species, of which nearly 540 are endemic (J. Léandri, oral comm.).

Special mention must be made of the genera *Voatamalo* (2 spp., endemic to Madagascar) and *Androstachys* which are related to one another and represent a very singular group (Androstachyaceae Airy Shaw). *Androstachys* has several species in Madagascar, one of which (a kind slightly different) is also present in E. Africa. One monotypic genus, *Cordemoya*, is endemic to the Mascarenes.

This family is well represented in Madagascar, but its revision is not advanced enough to permit taxogenetic or biogeographical conclusions.

Rhamnaceae. This is a cosmopolitan family of 50 genera and 600 species which is represented in Madagascar by 10 genera and 22 species (Capuron, 1965a, 1966a). Four genera are pantropical: *Colubrina* (12 spp., 5 in Madagascar

with 1 endemic); *Guania* (60 spp., 5 in Madagascar with 3 endemic); *Scutia* (7–8 spp., 1 common to Madagascar, the Mascarenes, India, S. and E. Africa); *Ziziphus* (40 spp., 3 in Madagascar with 1 endemic). Two genera are palaeotropical: *Helinum* (3 spp., 1 in both Madagascar and S. and E. Africa); *Ventilago* (25 spp., 1 common to Madagascar and India). Three genera are common to Africa and Madagascar: *Lasiodiscus* (9 spp., 2 of which are endemic to Madagascar-Comores); *Phylica* (60 spp. in S. and tropical Africa, 1 in Mascarenes, 1 in Madagascar, both endemics); *Berchemia* (22 spp., 1 of which in Madagascar, endemic). The 1 endemic genus is *Bathiorhamnus* (3 spp.).

It is remarkable that the genera are relatively numerous but the species few, one genus, and 11 species (50%) only being endemics. Only one genus (*Bathiorhamnus*) is really Madagascan, the others (pantropical, Asian or African), it seems, have come there accidentally.

Leeaceae is a palaeotropical monogeneric family of 80 species with 2 species in Madagascar: one of which endemic, the other being African-Madagascan (Descoings, 1967).

Vitaceae. This family of about 12 genera and over 800 species, which ranges throughout tropical and warm temperate regions, is represented in Madagascar by 51 species belonging to 5 genera: 3 large pantropical ones (*Ampelocissus*, *Cyphostemma*, *Cissus*) with 47 species in all of them and but 1 of these species endemic; 1 palaeotropical (*Cayratia*) with 3 endemic species; 1 (*Rhoicissus*) with 10 species, primarily of E. Africa, but 1 of them reaching the Comores. There are no endemic genera (Descoings, 1967).

Connaraceae. This family of 25 genera and 200 species is of a particular interest because it principally covers a palaeotropical area and its main center of distribution is the African-Madagascan area where 16 genera occur, 11 of which are endemic. It is, however, poorly represented in Madagascar where only 5 genera occur, none being endemic. Some aspects, however, call for special mention: 1 African genus, *Byrsocarpus*, occurs there with 1 endemic species and 1 species common to Africa. There are 3 palaeotropical genera: *Ellipanthus* (1 sp.), *Agelaea* (3 spp.), *Cnestis* (4 spp.), and a pantropical one, *Rourea* = *Santaloides* (2 spp.). All of the Madagascan species are endemic.

Sapindaceae. This tropical and subtropical family is composed of woody plants which number 2,000 species distributed in 150 genera, 28 of which, with 89 species, are present in Madagascar, the Comores, and the Mascarenes (Capuron, 1969). Nine genera are endemic (*Conchopetalum*, 2 spp.; *Plagioscyphus*, 10 spp.; *Tsingya*, 1 sp.; *Beguea*, 1 sp.; *Chouxia*, 1 sp.; *Tinopsis*, 10 sp.; *Pseudopteris*, 2 spp.; *Tina*, 6 spp., *Neotina*, 2 spp.); *Doratoxylon* with 5 species occurs in the Mascarenes; *Hornea* with 1 species is endemic to the Mascarenes; *Molinea* with 6 species has 3 of them in the Mascarenes. One genus, *Stadmannia*, reaches the Mascarenes and E. Africa. Three genera are common to Madagascar and E. Africa: *Erytrophysa*, *Macphersonia*, and *Camptolepis*. Five genera are widespread in Africa: *Zanha*, *Majidea*, *Deinbollia*, *Crossonephelis*, *Haplocoelum*. Two genera are palaeotropical: *Filicium*, *Aphania*. Three genera are pantropical: *Allophylus*, *Dodonea*, *Cardiospermum*. One genus which is mostly

American, but also occurs in Africa, has 1 nonendemic species in Madagascar: *Paullinia pinnata* (probably recently introduced). Endemic to the Madagascan region are 79 species, and 4 species are endemic to Madagascar-E. Africa. It must be noted that the pantropical genus *Dodonaea*, highly developed in Australia, has a species endemic to Madagascar, *D. madagascariensis*. *Cossinia* (4 spp.) is only found in New Caledonia and Madagascar (Good, 1950).

The Madagascan Sapindaceae of which a detailed analysis on a biogeographical basis remains to be done seem to have no direct link with the American flora.

Burseraceae. This is a tropical, woody family of 20 genera and 550 species which is represented in Madagascar by 4 genera: *Canarium* (a palaeotropical genus of 100 spp.) with 2–3 endemic (?) species. *Protium* (a pantropical genus of 85 spp., mostly in tropical America) with 1 species in Mauritius and 1 species in Madagascar, these 2 species constituting a special section (Capuron, 1968c). *Commiphora* and *Boswellia*, with more than 200 species, are endemic to Africa and Madagascar occurring in arid or rather dry regions, particularly in northeastern Africa. There are more than 40 species of *Commiphora* in Madagascar, and only 1 of *Boswellia*: *B. madagascariensis* Capuron. This species must be considered as the type of a remarkable subgenus derived from African stock: it has unisexual flowers and valvate petals (besides, its stigma is sessile). The Madagascan Burseraceae are strongly linked to the African flora.

Anacardiaceae is a chiefly tropical family of 600 species distributed in 60 genera. It is represented in Madagascar by 9 indigenous genera, of which 3 are endemic: *Operculicarya* (3 spp.), *Faguetia* (1 sp.), *Micronychia* (5 spp.). There are 2 African-Madagascan genera: *Protorhus*, 16 species with only 1 outside Madagascar and endemic to South West Africa; *Sorindeia*, 1 species endemic to Madagascar, 1 Madagascan-African species. The other genera are: *Gluta*, 1 endemic species, 12 Indomalesian species; *Campnosperma*, 15 tropical species; *Poupartia*, 5 Madagascan species, 7 in Africa, 1 in India. *Poupartia caffra* is with *Maytenus* sp. a characteristic element of African-Madagascan savannas.

Simaroubaceae (30 gen., 200 spp.). This is a family of a special interest in the Madagascan region, with 5 genera, 2 of which are endemic. A closely related (if distinct) family, Ptaeroxylaceae, also occurs in Madagascar with 1 genus, while the other genus occurs in South Africa. The main center of distribution of Simaroubaceae is in tropical America, but there is a secondary center in West Africa (Nooteboom, 1962). The Madagascan genera are: *Perriera*, 2 endemic species; *Pleiokirkia*, 1 endemic species. The other 3 genera are represented each by one species: *Quassia indica*, *Suriana maritima* and, in the Seychelles, *Soulamea terminalioides*, an endemic species. This is a surprising distribution as *Soulamea* has 6 species endemic to New Caledonia, 1 in Fiji, whereas another ranges from Polynesia westwards to Borneo. As noted by Nooteboom "*Suriana* and *Soulamea*, both belong to the *Barringtonia* formation. The fruits are certainly dispersed by seawater and this seems to have been very effective." *Quassia indica* is a palaeotropical species dispersed throughout Asia to Australia.

The Madagascan Simaroubaceae have no link with America, a meaningless link with Asia, but a strong link to the African center.

Ptaeroxylaceae (2 gen., ca 4–5 spp.). This family, possibly a subfamily of Simaroubaceae, is special to the Madagascan region sensu lato: *Ptaeroxylon* is a monotypic genus endemic to E. and S. Africa. *Cedrelopsis* (3–4 spp.) is endemic to Madagascar (Leroy, 1959).

Rutaceae. This large family (150 gen., 1,000 spp.) is rather poorly represented in Madagascar and the Mascarenes with 9 indigenous genera, of which only 1 is endemic, and 65 species, but it offers some patterns of distribution of great interest. Since 1950, owing to Capuron's (1967b) work, our knowledge about the Madagascan Rutaceae has much advanced. In particular, he found 3 genera new for the Madagascan flora, 1 of which, *Evodia*, is endemic and contains 10 species. The remarkable genus *Chloroxylon*, considered until now as Asian, and monotypic, is present in Madagascar with 2 endemic species (Capuron, 1961). Thus, the subfamily Flindersioideae, composed of both *Chloroxylon* and the New Caledonian genus *Flindersia*, extends to Madagascar. This is a distribution that seems strongly relict and suggests the possibility of the existence of direct migration between Madagascar and New Caledonia via India, possibly through rafting.

Toddalieae is represented not only by a meaningless species of *Toddalia*, but also by the genus *Fagaropsis*, which contains 5 species: 3 in tropical Africa and 2 in Madagascar. It is closely related to the Asian *Phellodendron* and this pattern of distribution is to be classified with the precedent one (Capuron, 1961).

Regarding the Xanthoxyleae, we have to put aside the pantropical genus *Xanthoxylum*, although it is present in Madagascar with 8 endemic species. The remaining genera, *Evodia* and *Ivodea* have an interesting distribution. The large palaeotropical *Evodia* (130 spp.), which is absent from Africa, has 19 endemic species in Madagascar, and *Ivodea* is a Madagascan endemic (Capuron, 1961). This pattern of distribution is comparable to other two reported above.

The remainder, *Vepris* (40 spp.), *Diphasia* (5 spp.), and *Teclea* 25 spp.) represent a very natural group nearly confined to Madagascar-Africa, except for 1 *Vepris* species that extends to India. This genus is particularly well represented in Madagascar and the Mascarenes with some 30 species, while *Teclea* has only 1 species in Madagascar. *Diphasia* consists of 2 species, 1 African, 1 Madagascan.

Meliaceae (51 gen., 550 spp.—Leroy, 1977c). This is a pantropical family of woody plants divided into 5 subfamilies, all of them represented in Madagascar, and 3 of them monotypic and restricted to the "Grande Ile": Quivisianthoideae, Capuronianthoideae, Neomangenotioideae. The Melioideae is richly represented by the Trichilieae and Turraeeae, but 5 tribes out of 7 are lacking. The Trichilieae is composed of 10 genera, 9 of which are palaeotropical (3 restricted to Asia, 4 to Africa sensu stricto); there are 4 genera in Madagascar: *Malleastrum* (12 spp.) endemic to Madagascar-Comores-Aldabra; *Astrotrichilia* (14 spp.) endemic to Madagascar; *Lepidotrichilia* (4 spp.) restricted to Madagascar and E. Africa; *Trichilia* (50 spp. in America, 14 spp. in Africa, some spp. in Madagascar and the Indo-Malayan region). The palaeotropical tribe Turraeeae is best represented in this part of the world: only 1 genus (*Munronia*) is endemic to Asia; *Naregamia* has 1 species in India, 1 in Angola; *Turraea* has 24 species in tropical Africa, 30–40 species in Madagascar, Mauritius and the

Comores, and about 6 species in tropical Asia and Australia. There are 2 genera endemic to Madagascar: *Humbertioturraea* (6–7 spp.) and *Calodecaryia* (1 sp.) and 1 genus is endemic to S. Africa: *Nymania* (1 sp.). The Swietenioideae-Swietenieae (9 gen.) is represented by genera in Africa and Madagascar, all of the endemic: *Khaya*, *Entandophragma*, *Pseudocedrela* and *Lovoa* in Africa sensu stricto, *Khaya* and *Neobeguea* in Madagascar; there are 2 genera in Asia-Malesia: *Soymida*, *Chukrasia*, and 2 genera in America: *Swietenia*, *Schmardea*. The Xylocarpeae is composed of 2 genera: *Xylocarpus* (2 spp.), a genus of mangroves and swamps confined to Indian Ocean coasts, included in the Madagascan region, and one African-American genus, *Carapa* (2–3 spp.) (Pennington & Styles, 1975; Leroy, 1977b).

To conclude about Meliaceae, strong endemism exists, at the subfaminial and generic levels in Madagascar and at the generic level in Africa. The Meliaceae is an ancient family represented in Africa sensu lato by 24 genera—that is nearly 50% of the whole family—18 of which are endemic. One genus (*Lepidotrichilia*) is common to Madagascar and E. Africa. The tribe Turraeeae seems centered on the Madagascan region; here *Turraea* has its highest number of species, and 3 genera are endemic to this region sensu lato: 2 to Madagascar, one to S. Africa. Furthermore, there is a link between *Capuronianthus* and Xylocarpeae.

Zygophyllaceae is a family of 25 genera and 200 species (Hutchinson, 1967), is mostly woody, and is distributed in dry regions of the two hemispheres, often in semideserts. It is represented by 2 genera in Madagascar: *Tribulus*, a widely spread genus, which there has 2 nonendemic species; *Zygophyllum*, a large genus confined in the Old World, especially in southern Africa, with 2 species endemic to Madagascar, one of them *Zygophyllum madagascariense* (Baill.) Stauffer, with a peculiar drupaceous fruit, can be considered as the type of a special subgenus. The two species occur sympatrically in the South Domain, generally on sands next to the sea.

Erythroxylaceae is a family of 3(–4) genera, the largest of which is *Erythroxylum* with about 200 species. This pantropical genus has about 30 species in the Madagascan region, all endemics. The other genera are: *Aneulophus* (1 sp.) and *Pinacopodium* (2 spp.) in tropical Africa and *Nectaropetalum* (perhaps a special family) with 9 species, 5 of which are endemic to Madagascar and still undescribed, the other 4 being endemic to Africa. *Nectaropetalum*, whose Madagascan presence is known thanks to Capuron's work (1963c), is a remarkable plant with imbricate and persistent sepals and dry and dehiscent fruits. It occurs in the dry regions in the north and northwest parts of the western Domain in Madagascar. *Aneulophus* is sometimes put in the Linaceae.

Lepidobotryaceae. Following Hutchinson (1967), this palaeotropical family is composed of 3 genera: *Sarcotheca* (10 spp.) in tropical Asia, *Dapania* (3 spp.) in Malaya and Madagascar (Veldkamp, 1967); *Lepidobotrys*, in Africa (Léonard, 1950). Thus, it presents an interesting distribution, but its naturalness is questioned (Airy Shaw, 1966; Veldkamp, 1967). Whatever it may be, the Madagascan plant, *Dapania pentandra*, is a very interesting species sharply

distinct, with flowers perfect, 5-staminate, and deprived of interstaminate scales (Huynh, 1971). According to Raven & Axelrod (1974), *Dapania* might have reached Madagascar by long-distance dispersal around the Indian Ocean. Let us note that this hypothesis, rather convincing as regards a genus whose fruits are readily dispersed, is consistent with a great antiquity for the Madagascan species.

Geraniaceae. Following Humbert (1959), this family is represented by 3 nonendemic genera: *Geranium* (2 spp. of the African section *Simensia*, 1 of which endemic); *Pelargonium* (1 endemic sp. of the S. African section *Ciconium*; 1 endemic species of the section *Peristera*, which extends from S. Africa to Australia, New Caledonia); *Monsonia* (an African genus with 1 species in secondary vegetation).

Oxalidaceae. This unrevised family comprises 2 nonendemic genera and 21 species (according to Baron, quoted by Humbert): *Biophytum* and *Oxalis*.

Linaceae is represented by 2 nonendemic genera: *Linum* (2 endemic spp.) and the palaeotropical genus *Hugonia* (5 endemic spp.).

Balsaminaceae is a family of 2 genera, 1 of which, *Impatiens*, occurs abundantly in Madagascar where 100 species or so have been recognized.

Ixonanthaceae, considered by many authors as a subfamily of Linaceae, is present in Madagascar with an endemic species of the genus *Allantospermum* (= *Cleistanthopsis*), which is bitypic, the other species occurring in Borneo. These species which were described independently in the same year 1965 by Forman for Borneo and Capuron for Madagascar, are both very similar to one another and well distinct: each of them must be considered as a subgenus of its own.

It is surprising enough that the palaeotropical family Irvingiaceae consisting of 3 genera, 1 of which, *Irvingia*, occurs in Africa and Southeast Asia, the other two being endemic to Africa, is absent from Madagascar. But the related genus *Allantospermum* has a distribution parallel to that of *Irvingia*. Plants of the group Irvingiaceae—Ixonanthaceae are a fundamental link between Africa-Madagascar on one hand an Southeast Asia on the other. Hence, I fully agree with Raven & Axelrod (1974) that it must proceed from "an west Gondwanaland plexus."

Malpighiaceae. This family of woody plants consists of 5 tribes, 65 genera, and 1,200 species (Hutchinson, 1967), mostly of South America. Some outliers, perhaps 15 genera or so, occur far from America. There are 10 genera in Madagascar: *Acridocarpus* (30–50 spp.) extends from tropical and S. Africa, Arabia, Madagascar to New Caledonia. *Caucanthus* is an African-Madagascan genus of 25 species. The endemic genera are: *Trichomariopsis* (1 sp.), *Philgamia* (3 spp.), *Calyptostylis* (1 sp.), *Microsteira* (28 spp.), *Rhynchophora* (1 sp.), *Digoniopterys* (1 sp.). *Sphedamnocarpus* is a Madagascan-African genus (8 sp. in S. and E. Africa, 12 sp. in the Madagascan region). *Tristellateia* is a palaeotropical genus (40 spp., 20 spp. in Madagascar, 1 in E. Africa, none in Australia). All these genera belong to two tribes: Hiraeeae, which contains 20 genera, 10 of which are endemic to S. America, and Banistereae (15 gen.). If we consider the

wholly family, 48 genera are endemic to America, 3 to Africa, 3 to Asia, and 6 to Madagascar. All Madagascan genera are either endemic or palaeotropical.

On the basis of the present evidence one can retain the idea that a post-Oligocene improverishment intervened in Africa and perhaps in Asia to eliminate part of Malphigiaceae, Madagascar playing its well-known role as a center of survival.

Vochysiaceae and Trigoniaceae. Plants of this group are chiefly represented in South America with 8 endemic genera and many species. But 1 genus, *Erismadelphus*, is present in tropical Africa (with 2 spp.), 1 in Madagascar *Humbertiodendron* (1 sp.), and 1 in S.E. Asia *Trigoniastrum* (1 sp.). Judging from this pattern of distributions with wide disjunctions and unbalanced proportions concerning the number of species, we may suggest that Vochysiaceae originated in Gondwana, the extant, extra-American genera clearly being relicts.

Polygalaceae. This family with a wide and mainly pantropical distribution is an ancient one consisting of 17 genera, 50% of which are endemic to America; it is poorly represented in Madagascar with only 2 genera: 20 endemic species of *Polygala* and 1 endemic species of *Carpolobia*, a Madagascan-African genus of 7 species (Breteler, 1969).

Araliaceae is a family (still unrevised for Madagascar) of 600 species distributed in 50 genera, chiefly tropical, with two principal centers in Southeast Asia and America. Its representation in Madagascar and the Mascarenes and the Seychelles is very important and of special interest, with 9 genera, including 4 endemic, and over 50 species. Hutchinson considers the family to be composed of 7 tribes, 4 of which are present in Madagascar: Cussonieae: *Cussonia* (25 spp. in tropical and S. Africa, Madagascar, Comores, Mascarenes), *Botryopanax* (endemic to the Mascarenes with 6 spp.), *Cuphocarpus* (a monotypic genus endemic to Madagascar). Panaceae: *Polyscias* (palaeotropical genus of 53 spp.; 8 spp. in Africa, 35 spp. in Madagascar-Comores, 8 spp. in the Mascarenes, 1 sp. in the Seychelles, 1 sp. in Ceylon); *Gastonia* (10 spp. in tropical and E. Africa, Madagascar, Mascarenes, Borneo, New Guinea . . .); *Schefflera* (a pantropical genus with 15 spp. in Madagascar-Comores, 13 spp. in Africa, 1 in the Seychelles, some spp. in Ceylon); *Sciadopanax* (a monotypic genus endemic to Madagascar); *Geopanax* (1 sp.) endemic to the Seychelles. Hedereae: *Neocussonia* (5 spp. in tropical and S. Africa, Madagascar). Plerandreae: *Indokingia* (a monotypic genus endemic to the Seychelles).

Several facts have to be emphasized: (1) the distribution of the genera into 4 tribes, of which 2 have a single representative. (2) The pattern of endemism with one monotypic genus special to the Seychelles, and one polytypic to the Mascarenes. (3) The very large number of *Polyscias* species in the Madagascan region. (4) The absence of *Schefflera* species in the Mascarenes, while numerous in Madagascar. (5) Two-thirds of the genera are African-Madagascan.

These facts, some of which remain rather enigmatic, support the hypothesis of the Madagascan region not only as a center of refuge but at the same time as an active center of speciation. Moreover, the family as a whole is well rooted in the African region.

Umbelliferae (275 gen., 2,800 spp.). This family is represented in Madagascar

by only 9 genera, 2 of which are endemic: *Anisopoda* (1 sp.) and *Phellolophium* (1 sp.); 1 is African-Madagascan, *Heteromorpha* (8 spp. endemic to Madagascar and a few in Africa); 5 are widespread: *Carum*, *Pimpinella*, *Caucalis*, *Sanicula*, and *Peucedanum*. There are 22 species of which 19 are endemic (Humbert, 1959). The interesting recent discovery of a *Lilaeopsis* species in Madagascar, Raynal, (1977) is surprising enough. This genus, which until now had 26 species with 16 American and the others from Australia and New Zealand, is a typically Gondwanian genus, which is absent from Africa. So a new problem is raised which is worth thinking about and analyzing.

VI

Loganiaceae. This family (as circumscribed by Leenhouts, [1962] of 26 [28] gen., 600 spp.) is represented in Africa and Madagascan by 11 genera, 5 of which are endemic. The Madagascan representation is important with 6 tribes (the family consisting of 7), 8 genera, and 70 species.

The genus *Anthocleista* (Potalieae) is restricted to tropical Africa and Madagascar with 14 species (4 in Madagascar), but its nearest ally is *Fagraea* from Asia and the Pacific. *Nuxia* (Buddlejeae) consists of 15 species in Africa (Leeuwenberg, 1975a), 11 species in the Madagascan region, of which 10 are endemic (including 1 in the Comores and 1 in the Mascarenes); its closest affinities are with the monotypic genus *Peltanthera* from Central and South America, and also with the monotypic genus *Androya*, endemic to Madagascar (Leenhouts). *Buddleja*, a large genus of more than 100 species (belonging to the same tribe), widespread in the tropics, except for Australia and the Pacific, is highly differentiated in Madagascar (8 spp., 1 of which is endemic to the Reunion) (Leeuwenberg, 1975b). The tribe Loganieae from Malaysia and the Pacific, reaches the Mascarenes with 2 endemic species of *Geniostoma*: *G. borbonicum* and *G. pedunculatum*. The small genus (6 spp.) *Mitreola* (= *Cynoctonum*) (American-Asian tribe, Spigelieae), which has a very extended and discontinuous area, is present in Madagascar with 1 endemic species, *M. turgida* Jovet. Three other species are confined to Asia, 2 of which are local endemics (Vietnam, Sabah); 1 species is endemic to the southern United States, and the sixth, *M. petiolata*, occurs in N. America, Brazil, Asia, Australia, and West Africa (Leeuwenberg, 1974). One African species of *Mostuea* (Gelsemieae), a genus of 8 species, 7 of which are in tropical Africa, occurs in Madagascar; the eighth species is known from Brazil. The eighth genus, *Strychnos*, is widely distributed in the tropics and subtropics with about 200 species, 15 of which are in Madagascar.

All these facts form a complicated whole from which several ideas can be drawn. First, Loganiaceae is an old family with a worldwide distribution in the tropics and subtropics of both hemispheres. Second, we have to take care not to explain every case in terms of the old and discontinuous distribution of the family. There is one endemic species of *Mostuea* in Brazil, two endemic species of *Geniostoma* in the Mascarenes, and some vast gaps in the area of *Mitreola* species, but we think no general and single explanation of this is to be sought. With respect to *Geniostoma* species from the Mascarenes, one must have in

mind that an extremely close ally, the genus *Labordia*, with as many as 20 species, is endemic to the relatively young island Hawaii.

Gentianaceae (80 gen., 900 spp.). This family is represented in Madagascar by 9 genera (50 spp., ¾ of which endemic), of which 2 are endemics: *Tachiadenus* (10 spp.) and *Gentianothamnus* (1 sp.). The genus *Chironia* is endemic to Africa-Madagascar. The other genera are palaeotropical (*Exacum*, 15 spp., *Sebaea*, *Canscora*) or widely spread (*Swertia*, *Eniscostemma*, *Neurotheca*). Let us note that the genus *Neurotheca* is present in the Madagascan swamps, with the widespread species, *N. loeselioides* (Guyana, Brazil, tropical and E. Africa) (Raynal, 1968).

Menyanthaceae (5 gen., 33 spp.). The only genus present in Madagascar is *Nymphoides* with 3 endemic species.

Lentibulariaceae (4 gen., 170 spp.) is a family of insectivorous water herbs widely distributed over the Globe. It has 2 genera in Madagascar: *Utricularia* (13 spp., 10 ? endemic) and *Genlisea* (an African-American genus with 4 spp. in Madagascar, 3 endemic). Because these plants are readily dispersed, they do not provide good material for biogeographical analysis.

Apocynaceae (250 gen., 2,000 spp., according to Markgraf, 1976). This is a family of wide distribution but chiefly pantropical, which is composed of 4 subfamilies, all of them represented in Madagascar. There are 23 genera in Madagascar (10 endemic) and 146 species (140 endemic). One genus, *Oistanthera* is endemic to the Mascarenes. The palaeotropical genus *Carissa* (Plumerioideae—Carissinae) has 9 species in Madagascar (7 endemic). In the same subfamily, the Carisseae—Landolphiinae is mainly represented by the pantropical genus *Landolphia*, which has a total of 60 species (13 endemic) in Madagascar and over 40 in Africa. There are 2 genera in the Rauwolfieae (a tribe of 12 genera, mostly in Asia)—Rauwolfiinae (a subtribe of 3 genera with a disjunct distribution): the pantropical genus *Rauwolfia* (5 endemic species) and the endemic genus *Cabucala* (18 spp.). The Plumerioideae—Alstonieae is interestingly represented by 4 subtribes: the endemic monotypic genus *Craspidospermum* is one of 2 genera constituting the subtribe Craspidosperminae, the other inhabiting Malesia. *Stenophagia* (Aspidospermatinae, a subtribe of 3 genera: 1 in America, 1 in Africa), with 5 species, is endemic. *Catharanthus* (Catharanthinae) is an isolated genus with 7 Madagascan species and 1 species in India. Two genera out of 4 in the Plectaneineae inhabit Madagascar: *Plectaneia* (12 spp.) endemic; *Gonioma* with 1 species in S.W. of Madagascar and 1 species in S. Africa.

The Apocynoideae has 4 genera in Madagascar, 1 of which, *Roupellina* (1 sp.), is endemic; *Mascarenhasia* is an isolated genus with 12 species, 1 of which reaches E. Africa; *Pachypodium* is an isolated, xerophilous genus with 17 species in Madagascar (12 endemic) and a few in E. and S. Africa.

Stronger endemism is offered by the Tabernaemontanoideae, which contains 4 endemic genera and another one almost endemic with 1 species also in E. Africa (*Hazunta coffeoides*).

A fact of special interest is that two monotypic subtribes of Apocynoideae

(Mascarenhasiinae, Pachypodiinae) are restricted to the Madagascan-E. African area.

Asclepiadaceae (one monotypic genus, *Trichosandra*, is endemic to Mauritius), *Solanaceae*, *Hydrophyllaceae* (cf. Humbert, 1959).

Convolvulaceae (*Humbertiaceae* included) (55 gen., 1,400 spp.). This is a family of wide distribution, but mainly of the tropics and subtropics, that is particularly abundant in America. There are 11 genera in Madagascar, of which 3 are endemic (cf. Humbert, 1959).

Boraginaceae (100 gen., 2,000 spp.) (cf. Humbert, 1959).

Callitrichaceae (1 gen., 30 spp.). The genus *Callitriche* is represented in Madagascar by at least 3 endemic species. None of the African or European species exists in Madagascar. Two species seem to have some morphological characters of S. America taxa (H. Schotsman, pers. comm.).

Verbenaceae (91 gen., 3,000 spp.). This family is well represented in Madagascar with 12 indigenous genera and 130 species (123 endemics). There are 2 endemic genera: *Adelosa* (1 sp.) and *Acharitea* (1 sp.), the latter being very close to *Nesogenes*, which also has 1 endemic species in the Madagascan region while the others occur in E. Africa and Polynesia. Another genus, *Coelocarpum*, has 5 Madagascan and 1 Socrotan species. If we add another genus common to Madagascar and Africa, *Chascanum* (30 spp. with 2 endemic in Madagascar and 28 in Africa) and 2 palaeotropical genera, *Holmskioldia* (10 spp. with 5 endemic in Madagascar) and *Premna* (200 spp., of which 13 occur in Madagascar, all but 2 endemic), we see that 7 out of 12 genera can be considered to be palaeotropical. The other 5 genera, 2 of which, *Vitex* and *Clerodendrum*, have respectively 39 species (38 endemic) and 62 species (endemic) in Madagascar, are pantropical.

In contrast with these large genera, the other 3 are also large genera but small in their Madagascan representation: *Phyla* (1 cosmopolitan sp.), *Priva* (1 endemic sp., 1 sp. common to Africa, 1 sp. common to Asia), and *Callicarpa* (1 endemic sp.).

Some very interesting facts have to be emphasized. First of all is the presence of 2 monotypic endemic genera, 1 of which, *Acharitea*, is akin to *Nesogenes* (6 spp.), a genus with an extraordinary distribution in E. Africa-Comores-Seychelles-Mascarenes-Madagascar and Polynesia. The two genera belong to a group, a family of its own according to some authors (Dicrastylidaceae), which is essentially Australian (*Physopsis*, *Lachnostachys*, *Dicrastylis*, *Mallophora*, . . .). All of these genera are closely related to Verbenaceae—Stilboideae, a small subfamily of 5 monotypic genera, endemic to S. Africa. Therefore, there is a link, which seems ancient, between Madagascan and Australian Verbenaceae.

Another fact is that there is a littoral species of *Vitex*, *V. trifolia*, which covers a large area around the Indian Ocean from E. Africa to Japan and Australia. It represents, of course, a category different from that of *Calophyllum inophyllum*. The former has surely nothing to do with other species such as this one, which should be considered as a possible pioneer species. Another species, *Phyla nodiflora*, belonging to an American genus, occurs here and there, on sandy beaches and also at higher elevations, preferentially on calcareous soils.

Labiatae (in particular, one monotypic genus, *Mahya*, is endemic to Réunion), *Avicenniaceae*, *Plantaginaceae* (cf. Humbert, 1959).

Oleaceae. This family of 29 genera and 600 species is widespread over the World, especially in temperate and tropical Asia. There are 62 Madagascan species (60 endemic) and 5 genera, of which 2 are endemic to the Madagascan region: *Noronhia* (40 spp.) and *Comoranthus* (2 spp. in Madagascar and one in the Comores). The other genera are: *Olea*, an Old World genus with 20 species, of which 4 (3 endemic) occur in the Madagascan region. Two large tropical and subtropical genera: *Linociera* (1 sp. endemic to Madagascar and 1 endemic to the Comores), and *Jasminum* (9 spp., 8 endemic).

Scrophulariaceae (unrevised family; cf. Humbert, 1959; 2 genera, *Allocalyx*, 1 sp., *Bryodes*, 3 spp., are endemic to the Mascarenes).

Myoporaceae. This small family of Bignoniales deserves special attention. It is composed of 4–5 genera, 2–3 of which occur in S. Africa-Madagascar. Only one genus, *Myoporum* (30 spp.) has a wide distribution from Australia and the Pacific Islands to Japan and E. China and even the Mascarenes (1 sp., endemic). The other genera are: *Pholidia* (40 spp.), endemic to Australia; *Bontia* (1 sp.), endemic to the West Indies; *Ranopisoa* (1 sp.), endemic to Madagascar (Leroy, 1977d) and, when admitted in Myoporaceae, *Oftia*, 3 species endemic to S. Africa. *Ranopisoa* was described as *Oftia* by Capuron (1972a), but I have shown that it is distinguished from the latter by some characters. Whether or not *Oftia* belongs in this family or in Scrophulariaceae is not yet established, but in any case, it is at least an ally.

Thus, there is evidence from the pattern of distribution of the Myoporaceae, along with those from Cunoniaceae and other austral families, that their geographical origin might have been in any part of Gondwanaland. Moreover, the Myoporaceae, although having reached a high taxonomic level, might have originated before the breakup of Gondwanaland. However, the wide distribution of the genus *Myoporum*, obviously post-Gondwanian, might result from long-distance dispersal during Tertiary times.

Gesneriaceae (120 gen., 2,000 spp.). This is a family divided into 2 subfamilies, Gesneroideae and Cyrtandroideae, the former principally American (with some Australasian genera), and the latter principally tropical Asian and African and also European and even Australasian (*Cyrtandra*, . . .); it is represented in Madagascar by 3 genera: *Streptocarpus*, a genus endemic to Africa-Madagascar, with 41 species in Madagascar, all of them endemic and 90 species in Africa, almost all in S. and E. Africa; *Didymocarpus*, a genus widely distributed in warm regions (150 spp.) having 1–3 species in Africa and 3 endemic species in Madagascar; *Colpogyne*, an endemic monotypic genus (Burtt, 1971).

Bignoniaceae (120 gen., 650 spp.). In Madagascar this family, is represented by 2 tribes, out of 4 constituting the family (Schuman, 1895), and 10 genera. It displays an old distributional pattern of great interest with respect to the tribe Crescentieae, which is composed of 11–12 genera: 5–6 in Madagascar, all of them endemic, 5 in America, and 1 in Africa. This distribution is especially noteworthy as the 5–6 Madagascan genera form a homogenous group, with, it

seems, some distinctive evolutionary trends. If we put the genera with unilocular stamens aside (*Ophiocolea*, 5 spp. and *Colea*, 20 spp.), the other 3–4 genera, although well defined, are very close to one another. In my opinion, *Rhodocolea* might be the most primitive, particularly *R. perrieri* Capuron with its perfect actinomorph flowers and pentastaminate androecium (it even might be raised to the generic level). Next to *Rhodocolea* is *Phylloctenium*, then *Phyllarthron*, a plant whose leaves are reduced to an articulated rachis. Two species of the latter (discovered and described by Capuron, 1960, 1970a) offer such an extraordinary floral zygomorphism that I (Leroy, 1972) proposed to base a new genus *Paraphyllarthron*, upon them. Whether accepted or not as taxon by subsequent authors does not matter, what is important is that it descended from *Phyllarthron*, a taxon still in existence today in the same country. The genus *Phyllarthron* itself was possibly derived from a *Rhodocolea*-like taxon, now extinct. The Madagascan Crescentieae are possibly a group of closely related genera that have originated in Madagascar during post-Gondwanian time.

The tribe Tecomeae has 4 genera in Madagascar: *Perichlaena*, a monotypic and endemic genus very close to *Fernandoa*. *Fernandoa*, a genus of 6 species of which 3 are endemic to Madagascar and 3 endemic to tropical Africa (Gentry, 1975). *Rhigozum* (1 sp. in Madagascar, 3 spp. in South Africa). *Stereospermum*, a palaeotropical genus with 9 species in Madagascar (constituting a distinct section, confined to the western Domain).

The family Bignoniaceae in Madagascar seems to offer a typical case of post-Gondwanian evolution or taxogenesis from some ancestors, now extinct, common to Africa and South America.

Acanthaceae (250 gen., 2,500 spp.). In Madagascar there are 57 genera, of which 22 are endemic, and more than 400 species, 375 of which are endemic. Eleven genera are African-Madagascan with 47 species in Madagascar, 42 of which are endemics. Five genera are related to African genera. The other genera are palaeotropical or pantropical: *Justicia*, 95 species in Madagascar, 90 of which are endemic with African affinities; *Hypoestes* 80 species, 78 of which are endemics. On the whole, affinities with the African flora are obvious; those with the Asian and Malaysian floras are rather modest (Benoist, quoted by Humbert, 1959).

Several remarks deserve attention: The very high degree of generic endemism is noteworthy in Madagascar. Moreover, the distributional pattern of several genera is of a particular interest. The genus *Stenandriopsis* (5 spp. in tropical west Africa, 1 in E. Africa, 8 in Madagascar) is closely allied to *Aphelandra* (200 spp. in tropical America; Heine, 1963; Stearn, 1971). The genus *Mendoncia*, which is mostly S. American (90 spp.), has 4 species in Africa (Gabon & Ivory Coast) and 3 in Madagascar. It is closely related to the monotypic genus *Gilletiella*, endemic to Congo-Angola, so much so that Bremekamp proposed to link the two genera in the new family Mendonciaceae. The genus *Justicia* occurs likewise in S. America and Africa-Madagascar. *Oplonia* is Madgascan-American (9 spp. in the West Indies, 5 spp. in Madagascar), but absent from Africa (Stearn, 1971). All these factors indicate that the family, evolu-

tionarily advanced as it is, might have had a Gondwanian origin (perhaps by the close of the Cretaceous).

Pedaliaceae. This small family (12 gen.) is almost completely confined to warm regions of the Old World, especially Africa where 9 genera are endemic. *Uncarina*, endemic to Madagascar, is a genus of shrubs with thick branches and contains 9 species, all of them more or less xerophilous and occuring in the Occidental Domain (Humbert, 1962). Several species belonging to other genera have been introduced: *Dicerocaryum zanguebarium*, a monotypic genus of E. and S. Africa and Rhodesia, Angola; *Sesamum* sp.; *Martynia* (= Martiniaceae Stapf., an American family of 3 genera) *annua*, introduced from Mexico into Africa and Madagascar. An annual herb of African sandy beaches, *Pedalium murex*, is also in Madagascar and reaches Ceylon and India.

Campanulaceae (*Lobeliaceae* included) is a family (60 gen., 1,500 spp.) with worldwide distribution, but particularly in the Mediterranean region and S. Africa, and also in the Tropics. There are 30 species (26 endemic) and 7 genera (3 endemic) in the Madagascan region. Four genera belong to Lobelioideae: *Heterochaenia* (a genus consisting of 3 spp. endemic to Réunion), *Dialypetalum* (endemic to Madagascar, 5 spp.), *Monopsis* (a genus of tropical and S. Africa with 1 sp. on the Comores), *Lobelia* (a widespread genus [300 spp.], mostly tropical and subtropical, richly represented in Africa and America with 12 species in Madagascar [9 endemic] and 7 species in the Mascarenes [2 endemic]). There are 3 genera of Campanulaceae sensu stricto: *Berenice* (a monotypic genus endemic to the Reunion—Badré et al., 1975), *Gunillaea* (an African-Madagascar genus with 1 species endemic to Africa, 1 common to E. Africa and Madagascar), *Wahlenbergia* (a widespread genus but mainly of the S. hemisphere with 200 species 11 of which in Madagascar (4 endemic) (M. Thulin, unpublished paper, 1977).

It is of special interest that 2 genera are endemic to the Mascarenes, and monotypic: they seem, therefore, to be vestigial.

Goodeniaceae. This family of 14 genera and 300 species is almost exclusively austral but its Madagascan representation, 1 genus, *Scaevola*, with 2 species widespread along sea coasts all over the Globe, has no special significance.

Rubiaceae (500 gen., 5,000 spp.). This is a pantropical and subtropical family represented in Madagascar by its 3 subfamilies and about 21 tribes (Psychotrieae, Morindeae, Triainolepideae, Pauridiantheae, Craterispermeae, Knoxieae, Paederieae, Hedyotideae, Cruckshanksieae, Lathraeocarpeae, Anthospermeae, Spermacoceae, Rubieae, Naucleeae, Cinchoneae, Mussaendeae, Gardenieae, Ixoreae, Alberteae, Vanguerieae, Guettardeae). There are about 70–80 genera, 25–30 of which are endemic (2 new genera recognized by Capuron await description), and more than 600 species, nearly all of them endemic. As was emphasized by Bremekamp (Humbert, 1959), the Madagascan Rubiaceae have much stronger affinities with the African flora than with the Asian one. Some genera (*Triainolepis*, *Alberta*, . . .) are restricted to Madagascar and E. and S. Africa. Some tribes are particularly well represented in Madagascar: Psychotrieae (ca. 11 gen., 5 endemic), Hedyotideae (5 gen., 2–3 endemic), Spermacoceae,

Naucleeae (a tribe of 8 genera, 5 endemic in Madagascar), Ixoreae (8–12 genera, several of which endemic), Gardenieae (4 gen., 2 endemic—Leroy, 1974). There is one endemic genus in the Madagascan Cinchoneae, and another one in the Mussaendeae. Three genera are endemic to the Mascarenes: *Scyphochlamys* (1 sp.), *Neoschimpera* (1 sp., Seychelles), *Fernelia* (2 spp.).

Many data concerning the Madagascan Rubiaceae are contained in an important unpublished paper by Capuron, but it is, however, impossible to draw any serious conclusion before the revision of the family is completed.

Compositae (900 gen., 15,000 spp.). This is a very large family of cosmopolitan distribution. It ranks first in the S. African flora with 174 genera and 2,072 species (Goldblatt, this symposium). It is also first in Madagascar with 87 genera (13 endemic) and 550 species (500 endemic) distributed in 9 tribes (none of which endemic). Two monotypic genera are endemic to the Mascarenes (*Eriothrix*, *Cylindrocline*). The Madagascan Compositae are strongly linked with the E. and S. African ones (cf. Humbert, 1959).

VII

Concerning the Madagascan Monocots I shall be content with recalling some of the outstanding classical facts, supplemented with some recent results. It is well known, for example, that the Bambuseae, Palmae, Pandanaceae, and Orchidaceae have a particularly important Madagascan representation.

A. Alismatidae.—Among the represented families: Alismataceae, Aponogetonaceae, Scheuchzeriaceae, Najadaceae, Potamogetonaceae, Hydrocharitaceae, Triuridaceae, only the latter has an endemic Madagascan genus, *Seychellaria* (1 sp. in Madagascar, 1 sp. in the Seychelles). The Triuridaceae (7 gen., 80 spp.) are herbaceous terrestrial mycotrophic plants with apocarpous flowers and albuminous seeds.

B. Commelinidae.—The Bamboos are impressively represented in Madagascar with 10 genera, 6 of which endemic. One of the latter, *Nastus*, has 12 species in Madagascar, 1 in the Réunion. Three are monotypic: *Hitchcockella* (which is related to both *Nastus* and the American genus *Chusquea*), *Decaryochloa* and *Pseudocoix*. The other 2 genera are *Hickelia* (2 spp.) and *Perrierbambus* (2 spp.) (which would be related to an American genus [Humbert, 1959]).

The nonbambusoid tribes of grasses taken as a whole are represented in Madagascar by 132 genera, 15 of which are endemic, and 500 species. Two genera constitute by themselves two tribes apart: *Cyphochlaena* (Boivinelleae) and *Lecomtella* (Lecomtelleae) (J. Bosser, pers. comm.). Thus there is some indication of an active and ancient differentiation of grasses, perhaps since the Eocene. A study restricted to the Malagasy fodder grasses was published by Bosser (1969).

Cyperaceae (90 gen., 400 sp.). There are 29 genera and 350 species (60 endemic) in Madagascar (cf. Humbert, 1959). In particular, the genus *Costularia* is to be cited: it is composed of 14 species, 11 of which occur in Australia, and 3 in S. Africa and Madagascar.

Strelitziaceae (3 gen., 7 spp.). This is a family, formerly merged into

Musaceae, whose distribution is strictly austral and strongly discontinuous, with *Ravenala*, a monotypic genus, in Madagascar, *Strelitzia* (5 spp.) in S. Africa, and *Phenakospermum* (2 spp.) in S. America. One genuine species of the palaeotropical family Musaceae (*Ensete* sp.) inhabits Madagascar.

Commelinaceae (38 gen., 500 spp.). Two genera are of special interest: *Coleotrype* with 5 endemic species in Madagascar, 1 species in S. Africa, and 1 in W. tropical Africa; *Pseudoparis* (2 spp.), a very isolated endemic genus.

Eriocaulaceae (13 gen., 1,200 spp.) is a family of extreme biogeographical interest whose area is almost entirely confined to tropical and subtropical America. There are only 2 genera endemic to Africa-Madagascar: *Mesanthemum* with 2 species in Madagascar and 6 in Africa; *Moldenkeanthus*, a monotypic genus endemic to Madagascar. Aside from *Eriocaulon*, a large genus which has 19 species in Madagascar (10 endemic), the other 2 genera are American with only 1 or 2 species in Africa and Madagascar (*Paepalanthus*, *Syngonanthus*). The endemic genus *Moldenkeanthus* is very close to *Paepalanthus* and the strictly American genus *Leiothrix* (Morat, 1976).

Zingiberaceae (45 gen., 700 sp.). This family, especially well developed in Indo-Malesia, is represented by 6 nonendemic genera in Madagascar, 1 of which, *Aulotandra*, has 5 species (4 Madagascan and 1 in W. tropical Africa).

Typhaceae, Juncaceae (cf. Humbert, 1959).

C. Arecidae.—Palmae (220 gen., 2,500 spp.). The Palmae (Arecales), whose fossil material is known from the Upper Cretaceous, are one of most noteworthy features of the Madagascan flora. There are 18 indigenous genera, 15 of which are endemic, and 120 species, all but 2 endemic (Humbert, 1959).

The palms occur also in the Seychelles (6 endemic gen.: the famous Borassoid *Lodoicea* possibly related to the Malayan *Borassodendron*, and 5 spiny Arecoid gen.) and Mascarenes (6 endemic monotypic gen.) (Corner, 1966). According to Corner, Madagascar "acting as a small continent of long isolation has evolved new species of undergrowth palms from its Arecoid heritage, but it has not produced a subfamily or a new manner of palm life." However, such Borassoid genera as *Medemia*, *Latania*, and *Lodoicea* are Gondwanian relicts (Corner).

Pandanaceae (3 gen., 700 spp.). The abundance of *Pandanus* species is also a striking feature of the Madagascan flora which counts 30 species, nearly all of them endemic (Mascarene included).

Araceae (100 gen., 2,000 spp.) are of a particular interest with respect to taxogenesis for, aside from the pantropical genus *Pistia* and some introduced species (*Alocasia* sp., *Caladium* sp., *Zantedeschia* sp.), they are represented in Madagascar by two elements:

1. An autochthonous highly differentiated element composed of 2 endemic tribes and 4 genera: (a) Typhonodoreae (Philodendroideae): 1 genus, *Typhonodorum*, which reaches Pemba and Zanzibar. (b) Arophyteae (Aroideae), including *Carlephyton* (3 spp.), *Colletogyne* (1 sp.), and *Arophyton* (7 spp.).

2. An oriental element marked by the presence of an endemic species of

Amorphophallus (*A. hildebrandtii*), and secondarily by some natural, naturalized, and/or cultivated species (*Remusatia vivipara*—which reaches Africa, *Typhonium divaricatum*, *Pothos scandens*, *Amorphophallus campanulatus*, and *Colocasia esculenta*).

All in all, there are 13 endemic species.

Lemnaceae (cf. Humbert, 1959).

D. Liliidae.—Pontederiaceae (6 gen., 30 spp.) is represented in Madagascar by one monotypic genus, *Scholleropsis*. This genus had been considered to be a Madagascan endemic until 1967, when Letouzey and Bosser (Letouzey, 1967) reported its presence in Cameroon. The Pontederiaceae are easily dispersed water plants, however, *Scholleropsis* might be an ancient genus in its African-Madagascan area.

Liliales. Any serious biogeographical judgement on the Liliaceae, together with many other closely allied families, would need a careful review of a great many publications, among them that by Huber (1969). I only intend to give indications on some selected families.

The Herreriaceae (which is a subfamily of Liliaceae for many authors), close to Asparagaceae, is composed of 3 genera: 1 in Madagascar (*Herreriopsis*, 1 sp.), 1–2 in S. America (*Herreria*).

Asteliaceae is a family of some genera (*Yucca*, *Dracaena*. . .), 1 of which, *Cohnia*, with fleshy fruits, has 3 species ranging from the Mascarene Islands to New Caledonia.

Dianellaceae is an Australasian family with 2 genera: *Dianella* in Asia, Hawaii, and Madagascar (Raven & Axelrod, 1974) and *Excremis* in S. America.

Asphodelaceae. The genus *Arthropodium* has 1 species in Madagascar, the others in Australia and Pacific Islands. *Lomatophyllum*, an endemic genus with fleshy fruits, has 10 species in Madagascar, 3 species in the Mascarenes. *Aloe*, an African-Madagascan genus, chiefly developed in Madagascar, where it has 30 endemic species, and oriental and austral Africa.

Liliaceae-Scilloideae has 1 endemic genus: *Rhodocodon* (8 spp.).

Iridaceae. The endemic monotypic genus, *Geosiris*, is obviously a relict.

Velloziaceae (5–6 gen., 200 spp.) is a small, typically occidental-austral family composed of 2 genera: *Xerophyta* in Madagascar and Africa and *Talbotia* S. Africa and 4 in South and Central America (Smith & Ayensu, 1974). *Talbotia* is a monotypic genus. The genus *Xerophyta* is divided into 3 sections. One of these, section *Xerophyta*, is endemic to Madagascar with 2 species. The second section is common to Africa (1 sp. endemic to Madagascar, 10 endemic spp. in Africa, some of them reaching Zaïre and Ethiopia). The third section is endemic to Africa (14 spp.).

Dioscoreaceae (4 gen., 650 spp.) is represented in Madagascar by 2 genera: *Dioscorea* (over 30 spp., 27 endemic) and 1 monotypic endemic genus, *Avetra*, certainly primitive with a vestigial rhizome, which has completely disappeared in *Dioscorea*. Another genus, likewise monotypic but Indonesian, *Trichopus* (Trichopodaceae) is generally considered as related.

Taccaceae (cf. Humbert, 1959).

Orchidaceae (740 gen., 20,000 spp.). This is one of most important families

in the Madagascan flora with about 1,000 species and 56 genera, about 10 of which endemic. Some genera are widely distributed: *Bulbophyllum*, *Eulophia*, *Oecoeclades*, ... Certain others have a much higher number of species in Madagascar than in Africa: *Angraecum*, *Jumellea*, *Aeranthes*, *Cynorkis*, *Benthamia*. The Asian affinities are weaker than the African ones (J. Bosser, pers. comm.).

In conclusion, many data can be drawn from the analysis of the Madagascan Monocots to form the basis for certain useful conclusions. The occurrence of isolated and highly differentiated genera such as *Medemia*, *Latania*, *Lodoicea*, *Seychellaria*, *Geosiris* (a family of its own for some authors), *Avetra*, as well as that of endemic tribes, namely Boivinelleae and Lecomtelleae in nonbambusoid grasses, and Typhonodoreae and Arophyteae in Arales, appears to support the hypothesis of a Madagascan-African origin for many Monocots by, most likely, the close of the Godwanian epoch or early in the Tertiary. Further, the fact that such high level taxa as Bambuseae, Palmae, Pandanaceae, Orchidaceae, are particularly well represented in Madagascar might, in part, be explained by referring to a serious impoverishment of the African flora from Miocene times onwards. In many cases, of course, e.g., those of Orchidaceae (*Angraecum*, *Jumellea*, *Aeranthes*, *Cynorkis*, *Benthamia*), Palmae (the group including *Dypsis* with 21 spp., *Neophloga* with 30 spp., *Chrysalidocarpus* with 20 spp. . . .), and Poaceae, we do not deal with an ancient differentiation but with a secondary one: it is the young part of the Madagascan element. The genera *Dypsis*, *Neophloga*, and *Chrysalidocarpus* are closely allied and have certainly had a common ancestor in Madagascar. Others, such as those of the fan-leaved subfamily Borassoideae seem being genuinely Late Gondwanian elements: *Medemia* (1 sp. in Madagascar, 1 sp. in E. Africa); *Latania* (3 spp.); *Lodoicea* (1 sp.) related to *Borassodendron* of S.E. Asia (Corner, 1966); *Borassus* (5 spp. ? of which 2 in Madagascar, 1 in Africa, 1 in Asia, 1 in New Guinea); *Hyphaene* (more than 10 spp. in Africa and Madagascar). The ancestors of these Borassoid genera must have been dwellers of the Gondwanian Africa.

VIII

Pteridophytes (F. Badré, pers. comm.; Christensen, 1932).—Most of the genera are represented in the Mascarene region, except for the primitive ones such as *Matonia* (Malaysia, Borneo, Sumatra), *Dipteris* (Asia), and *Loxsoma* (New Zealand). The Mascarene region is known for its high number of endemic species: 200 out of a total of 550. The greater part of the Pteridophytes from the Mascarene region is related to representatives from Asia (and particularly from Indomalaysia). According to their affinities, Christensen (1932) recognized 7 groups of species:

(1) The Mascarene element: about 70 species, mostly belonging to groups of species within large genera such as *Cyathea*, which contains 37 species, almost all of them endemic. Several large genera have only 1 or a few endemic species. There are 2 endemic and monotypic genera: *Psammiosorus* (confined to Madagascar) and *Ochropteris*.

(2) The African element: about 92 species (Christensen). Here belongs also the genus *Mohria* (2 spp. in Africa, Madagascar, and Réunion). Let us cite also the genera *Blotiella* with 1 species in America and 16 in Africa, Madagascar and the Mascarenes, and *Actiniopteris*, which is however also present in India (2 spp. out of 5).

A markedly disjunct area is shown by *Elaphoglossum hirtum* (tropical America, Réunion, Madeira, Azores) and *Pellea calomelanos* (Spain, E. and S. Africa, N. India, Madagascar, Réunion).

(3) The Eastern (African-Malesian) element: represented by more than 150 species, that is, nearly ¼ of the total number. Examples include *Angiopteris* (from Madagascar and Réunion, with 1 species in Japan and Polynesia), *Drynaria* (about 20 spp. in Asia and Australia, 1 sp. in Madagascar and Mauritius), *Loxogramme* (35 spp. in Asia with 2 spp. in the Mascarene region, 1 of which also in Africa), *Microsorium*, particularly well represented in tropical Asia (4 spp. in the Mascarene region, 2 of which are endemic), *Davallia* (40 spp. mainly Asian and Polynesian, 1 in Africa, Seychelles, Rodrigues, Mauritius, and Madagascar). Several species are widely distributed, occuring also in Central and Eastern Asia. Examples include *Dryoathyrium boryanum* (Africa, Madagascar, Mascarenes, Asia, Polynesia), *Diplazium sylvaticum* (Mauritius, Asia, Philippines).

(4) The Western (American-African) element: about 85 species (18% of the total number of Pteridophytes). Here belong such genera as *Elaphoglossum* (400 spp., most of which occur in America, 40 spp. in the Mascarene region), *Doryopteris* (35 spp., mainly in S. America, 2 of which are endemic), *Pellea* (75 spp., most of which occur in S. America, 30 spp. in Africa and the Mascarene region), *Trachypteris* (2 spp., 1 of which occurs in S. America and the Galapagos Islands, the other in Madagascar).

(5) The Southern element: represented by 15 species belonging to such genera as *Blechnum*, *Schizaea*, *Gleichenia*, ...

(6) The pantropical element with about 20 species.

(7) The cosmopolitan element: about 15 species, including *Osmunda regalis*, *Lycopodium clavatum*, *Pteridium aquilinum*, *Pteris cretica*, *Pteris vittata*, *Equisetum ramosissimum*, *Cystopteris fragilis*, *Adiantum capillu-veneris*, *Hymenophyllum tunbrigense*. . . .

From that rather artificial classification it becomes clear that the palaeotropical element is best developed in the Mascarene flora. Also that the number of endemic species in the Mascarene region is proportionally high, whereas only a few of the genera are endemic. This is a general feature of the Mascarene flora which is characterized by a very strong specific endemism.

Gymnosperms.—Podocarpaceae (8 gen., 150 spp.). This family of Coniferales, almost confined to the tropical southern hemisphere, is represented in Madagascar by the only genus *Podocarpus* (100 spp.) with 6 endemic species. This genus was divided into 8 sections (Buchholtz & Gray, 1948), 1 of which is endemic to S. Africa. The Madagascan species belong to section *Eupodocarpus* (with transfusion tissue) which is present also in Africa, but also in S. America, Australia, South Pacific Islands and Asia.

Cycadaceae (1 gen., 10 spp.). The genus *Cycas*, confined to the Indian Ocean and western Pacific, is represented in Madagascar, the Comores, and E. Africa (Tanzania, Mozambic) by 1 special species (*C. thouarsii*) which grows along sea coasts, often in the *Barringtonia* formations.

General Conclusions

In every stage of its evolution, whether it be primitive, advanced, or intermediate, the Madagascan vascular flora is of outstanding originality. No doubt, this is due in part to extremely diversified ecological conditions, but also, and above all, to the fact that the island which was part of the Gondwanaland continent, was hardly modified in the course of time, at least since the early Cretaceous. In contrast, most of the same flora that occupied continental Africa became greatly impoverished, particularly from the Miocene on, due to climatic changes.

Therefore, Madagascar now appears to be an African fragment that has not only been an extraordinary area for the differentiation of taxa but above all both a refuge for every kind of immigrant and a center of survival for archaic autochthonous plants. Its relationship with East and South Africa is obvious and represents an especially interesting kind of affinity because it testifies to the peripheral character of this region compared to the African landmass; it also testifies to the antiquity of the Madagascan flora. That this relationship really exists is supported by many facts, by far the most convincing of which is the occurrence in the Madagascan region sensu lato of a close-knit group of two austral families with monosulcate or monosulcate-derived pollen, belonging to Magnoliales: the Winteraceae and Canellaceae. The former is divided into two subfamilies, one with 7 genera in the Pacific area and 1 in tropical America; the other subfamily is unispecific and endemic to Madagascar. The Canellaceae comprises 5 genera, 1 endemic to Madagascar, 1 to South Africa, and 3 to tropical America. Linked to these two families of Magnoliales, absent from the interior of Africa is the Monimiaceae which is likewise austral, and especially richly represented in Madagascar. Equally significant in the austral Magnoliales is the Hernandiaceae (4 gen.); *Hernandia* consists of several subgenera, 2 of which are most primitive, 1 of them is endemic to Australia, the other to Madagascar.

It is also noteworthy that the primitive Hamamelididae is represented in the same area by 2 endemic genera of Hamamelidaceae (none in the interior of Africa) and, if admitted in this subclass, by several special families such as the Myrothamnaceae and Didymelaceae.

Another striking fact is the very strong endemism of the Dilleniidae, not only at the generic level, but also at the familial one: 5 endemic families (Diegodendraceae, Sphaerosepalaceae, Sarcolaenaceae, Asteropeiaceae, Medusagynaceae); several families with an exceptional development (Malvales, Flacourtiaceae, Sapotaceae, Ebenaceae, . . .). The taxonomic level is roughly rather higher than that of Megnoliidae and in many cases speciation is active.

The Rosidae are also to be noted. Such families as Brexiaceae, Montiniaceae,

and Escalloniaceae are austral families and not or hardly represented in continental Africa sensu stricto. The Proteaceae, an austral family of 75 genera, is concentrated in Australia (45 gen.) and South Africa (14 gen.), but it has 3 genera in Madagascar, 2 of which are endemic. The Balanophoraceae, again an austral family, has been divided into 6 subfamilies, 2 of which are endemic to Africa, principally South Africa; the subfamily Helosioideae to which belongs the Madagascan genus *Ditepalanthus*, is absent from Africa and present in Asia (3 gen.) and America (3 gen.).

The Asteridae which is evolutionarily more advanced is also richly represented in Madagascar, but contrary to the facts mentioned above, its endemism is in general rather at a lower level. There is almost a rule: as one goes down taxonomic levels, speciation becomes more active. Perhaps not a single endemic family of Asteridae is present in Madagascar whereas such genera as *Clerodendron*, *Justicia*, *Coffea*, *Helichrysum*, *Vernonia*, *Senecio*, etc. have many endemic species.

With respect to Monocotyledons, it is difficult to draw any homogenous conclusion because the taxogenetic knowledge of this group is rather poor. Roughly, however, the facts are comparable. There is on the one hand, a very important archaic element including relictual endemic subfamilies, tribes, and genera and, on the other hand, a younger element with neo-endemic genera and a huge number of endemic species that result from an expectionally active speciation (Orchidaceae, Gramineae, . . .).

As a whole, the Madagascan vascular flora is considered here as an autochthonous flora that has differentiated principally from the original Gondwanian stock and has, in course of time, grown rich through evolution of its members and immigration of newcomers through long-distance dispersal.

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