

Fig. 20. Origins of the flora of Cuba (after ALAIN LIOGIER 1958, strongly modified). 1. Continents and islands, 2. Shallow seas (less than 1000 m deep), 3. Deep seas (depth more than 1000 m), 4. West-Cuban phytogeographical subprovince, 5. Middle-Cuban phytogeographical subprovince, 6. East-Cuban phytogeographical subprovince, 7. Main migratory routes of the flora, strong floristic affinities, 8. Important migratory routes, notable floristic relations, 9. Less important migratory routes of the flora, recognizable floristic relations

or varieties. This is, however, an illusory view formed under the influence of SCHUCHERT's theories discussed above. Given this knowledge, the first fundamental statements regarding the origin of the flora of Cuba were made by ALAIN (1958 pp. 33-34). He suggests that the flora is mainly of Neotropical origin and the elements immigrated from five different directions (Fig. 20). This problem will be considered later in more detail.

The influence of plate tectonics

The results of contemporary plate tectonics gave an impetus to the research of flora evolution. Several new hypotheses were created concerning the evolution and migration of primitive floras and the radiation of Gondwana elements, etc. At the same time, controversies among experts also revived. Several influential biologists, e.g., THORNE (1973) and VAN STEENIS (1962) in botany, maintain their conservative view. They claim that the division and drift of continents need not be assumed to understand the recent state of floras. As VAN STEENIS asserts, for example, the Pacific and the Indonesian flora may have been directly originated from Asia via land bridges that have now been covered by sea. Even if the land bridge theory is applicable to the Indonesian flora, there are still many paleogeographic and biogeographic problems that cannot be solved in this way. It is therefore obvious that most botanists call in the theoretical possibilities offered by plate tectonics, even though this field of geology has its own unanswered questions.

Plate tectonics of the West Indies

Despite many controversial details, most geologists agree that the Caribbean region is a separate tectonic unit. After ISACHS et al. (1968) and MORGAN (1958) the existence of a separate Caribbean Lithosphere Plate is generally accepted. As far as the origin and the characteristics of this plate are concerned, the views are varying. SCHUCHERT (1935), WOODRING (1954), EARDLEY (1954), BUTTERLIN (1956), TIKHOMIROV (1967), and KHT DOLEY and FURAZOLA (1971) think that the Caribbean Sea took the place of a land mass. H. A. MEYERHOFF (1954), HESS and MAXWELL (1953), WEYL (1966), A. A. MEYERHOFF (1967), DENGU (1968), MOLNÁR and SYKES (1969), and MACGILLAVRY (1970) presume the existence of a permanent basin in the ocean surrounded by island bends and geosynclinals.

Most experts (BALL and HARRISON 1969, DENGU 1969, MOLNÁR and SYKES 1969, MACGILLAVRY 1970, MALFAIT and DINKELMAN 1972, MATTSON 1973, and ITURRALDE 1975, 1978) explain the development of the Caribbean Plate on the basis of continental drift and, in general, of the dilatation of ocean floor.

The unanimous view of the above authors is that the Caribbean Plate was primarily oceanic. They exclude the possibility that the Antilles were connected to either part of the American continent up to the Middle Miocene. In the Upper Jurassic the Caribbean Plate may have been located at the northwestern edge of the Afro-American land mass in the Pacific Ocean at the western mouth of the Tethys Sea (where Nicaragua and Honduras are now found). In the Cretaceous, simultaneously with the process separating South America and Africa, the South American continent was significantly rotated causing the Caribbean Plate, which was connected to the Guyana Plate, to move eastward. Having moved about 800-1200 kilometres, the Caribbean Plate drifted away into the Tethys Sea. As from the Upper Miocene the Antilles exhibited a platform-like development. According to ITURRALDE, Cuba has been formed of six archaic isolated blocks, Hispaniola probably of three blocks, and Jamaica and Puerto Rico of one block each. In the Upper Miocene started the general vertical

movement leading to the emergence of the Cayman and Icaragua Ridge. Thus, the archipelago and Central America became connected. This process was completed in the Pliocene and then the islands started to get separated. Finally, the recent shape of the islands was formed in the Pleistocene.

The theory of a three-phase evolution of the West Indian flora

Although Caribbean Plate tectonics poses many unresolved problems (HOWARD 1980 p. 244) it is now attempted to outline the general history of the Antillean flora. Three major periods are recognized, each corresponding to a given geological stage:

1. Plate phase,
2. Land bridge phase, and
3. Archipelago phase.

Plate phase

The name of the first stage indicates that at this time the Caribbean Plate was an independent land mass in the sea. It is assumed that this period started in the Middle Jurassic and ended in the Upper Oligocene. Relatively few elements of the flora may be traced back with complete certainty to this phase. These important taxa are either phylogenetically old relicts, or endemics with distant relations, or genera with disjunct geographic distribution.

Relict cryptogams

As expected, the flora of this early period is mainly represented by cryptogams in the recent flora. Such plants are, for instance, the tree ferns. As many as seventeen endemic tree ferns occur in the Antilles. It is well-known that the family Cyatheaceae includes widely distributed species that are efficiently dispersed through spores. The fact that one of the evolutionary centres of the Schizaeaceae family, and its genus *Anemia*, is in Cuba (12 species of which seven are endemics) needs similar interpretation. In this respect, new bryogeographic results (REYES 1982, BORHIDI et PÓCS 1985) deserve particular attention as they indicate a definite relationship to Gondwanaland. For instance, there are many more liverwort species than mosses in Cuba. Such a partition of bryophytes is known to be typical of the islands in the southern hemisphere. The new studies by PÓCS and REYES revealed obvious relationships between the liverwort floras of the Guyana Highland and of the serpentine plateaux in Cuba, e.g. by the occurrences of *Plagiochila steyermarkii* Robinson and *Calypogeia venezuelana* Fulford. It is well-known that the Guyana Highland is one of the oldest block mountains in South America derived undoubtedly from Gondwanaland.

Relict phanerogams

The monotypical gymnosperm genus *Microcycas* is a "living fossil" representing the phanerogams of the plate phase. The assumption that at that time the Caribbean Plate was located at the border of the Pacific Ocean and the Tethys Sea has not only been justified by fossil Cretaceous faunas (western Cuba, Viñales) but has also been demonstrated by the close relationship between *Colpothrinax*, a Cuban-Central American genus, and the Pacific *Pritchardia*. These genera probably have a common ancestor.

Peri-Afro-American elements

The evolution of the specially distributed peri-Afro-American elements may also be dated back to the plate phase. Table 2 lists typical peri-Afro-American phanerogam genera that occur in the tropical America, East Africa and/or Madagascar but are absent from West and Central Africa.

Of the fifteen genera listed, eleven occur in Cuba, four genera (*Carpodiptera*, *Savia*, *Oplonia*, and *Stenandrium*) have their evolutionary centres in the Antilles (BORHIDI 1982).

According to STEARN (1971) this distribution type may have been developed as a result of drastic climatic changes. Many taxa became extinct in the interior of the "Afro-American" supercontinent due to the extreme continental climate. The flora of Central Africa became relatively poor in species. On the contrary, along the coasts of Madagascar, East Africa, North Africa and the northern part of South America an extensive coastal zone was formed which had a temperate climate. The abundance of diverse habitats in this region was advantageous for survival so that a very rich vegetation developed. Besides the Madagascar Plate, the Macaronesian and Caribbean Plates were probably also parts of this coastal zone.

In addition to the genera mentioned so far, a similarly close relationship is indicated for *Dracaena cubensis* from Cuba, *D. draco* from Macaronesia and *D. reflexa* from Madagascar. The primitive Cneoreaceae family may also be mentioned as a good example (BORHIDI 1982). It has only three living species, one in the Mediterranean of Europe, another in the Canary Islands and the third in eastern Cuba on the southern slopes of Sierra Maestra. Further evidence confirming the existence of these relationships is that amongst the cryptogams there are not only genera but also some species exhibiting peri-Afro-American distribution (e.g., liverworts).

Table 2
Examples of peri-Afro-American genera

Genus. Family	Total species	S. America, W. Indies	W. and Central Africa	E. Africa, Madagascar
<i>Desmanthus</i> (Fabaceae)	22	15	1	6
<i>Echinochlaena</i> (Poaceae)	7	6	—	1
<i>Ocotea</i> (Lauraceae)	400	380	3	18
<i>Oliganthes</i> (Asteraceae)	21	12	—	9
<i>Carpodiptera</i> (Tiliaceae)	6	5	—	1
<i>Oplonia</i> (Acanthaceae)	18	13	—	5
<i>Phenax</i> (Urticaceae)	28	25	—	3
<i>Piriqueta</i> (Turneraceae)	28	24	1	3
<i>Rhedia</i> (Clusiaceae)	50	37	—	13
<i>Ravenala</i> (Musaceae)	2	1	—	1
<i>Savia</i> (Euphorbiaceae)	25	15	1	9
<i>Stenandrium</i> (Acanthaceae)	25	22	—	3

It is assumed that some primitive angiosperms have also been present in Cuba since the plate phase. These are genera with bi- or trisectorial distribution, e.g., *Podocarpus*, *Magnolia*, *Talauma*, *Ocotea*, *Persea*, *Guatteria*, *Oxandra*, *Hedyosmum*, *Dorstenia*, *Bonnetia*, *Laplacea*, *Freziera*, *Lagetta*, *Linodendron*, *Myrcia*, *Spathelia*, *Purdiaea*, and *Calophyllum* and those listed in Table 2.

Land bridge phase

The second period which lasted from the end of the Oligocene up to the end of the Pliocene may be termed the land bridge phase. At the beginning of the Oligocene started the Caribbean Plate to emerge. As a result of this process the Greater Antilles became connected to the continent first via Honduras and the Yucatan peninsula and later via the newly emerged Lesser Antilles. This is the period of the large scale immigration of species into Cuba because apart from facilitating migration, the emerged lands offered extensive bare areas for the pioneer vegetation.

The broad-leaved tropical Honduras flora

During the Oligocene and the Lower Miocene a tropical flora consisting primarily of broad-leaved evergreen trees and shrubs may have immigrated into the Greater Antilles. In this period Cuba had been divided up into six isolated blocks: 1. Guane, 2. Isla de Pinos, 3. Villa Clara, 4. Camagüey, 5. Sierra Maestra, and 6. Moa-Baracoa. In the Middle and Upper Oligocene Guane was connected to the Yucatan peninsula. The Sierra Maestra block and Honduras were connected via the Cayman Ridge. The Moa-Baracoa block joined probably with Hispaniola and formed a part of the Honduras–Jamaica–Hispaniola–Puerto Rico range which was the main route of immigration. Obviously, the relatively small Guane block, that became separated earlier from the continent, accumulated a more limited gene pool than the larger Oriente blocks (Sierra Maestra and Moa-Baracoa) which had been connected to the other parts of the Greater Antilles for a longer period of time. The plants of the latter blocks comprise the so-called Honduras flora which might also be termed the *Swietenia-Trichilia-Zanthoxylum* flora after its typical genera. Most Neotropical elements of the Greater Antilles have been originated from the Honduras flora. According to my hypotheses, it is the phase when three main groups of tropical genera immigrated. These are:

1. Genera represented by few but widely spread endemic species in the recent flora (*Swietenia*, *Trichilia*, *Cedrela*, *Inga*, *Albizzia*, *Bursera*, *Dipholis*, *Pseudolmedia*, *Chlorophora*, and *Simaruba*).

2. Genera with secondary evolutionary centres evolved due to climatic and geological changes in the Antilles. These genera have many endemic representatives in the recent flora (*Pithecellobium*, *Cassia*, *Caesalpinia*, *Copernicia*, *Eugenia*, *Calypttranthes*, *Zanthoxylum*, *Pilea*, *Rondeletia*, *Psychotria*, *Guettarda*, *Miconia*, *Ossaea*, *Phyllanthus*, etc.), and

3. Presumably extinct genera that are ancestors of typical endemic genera or genus groups characteristic of the Antilles, e.g., the group *Portlandia-Cubanola-Thogsennia*; the group *Schmidtotia-Isidorea*; the group *Phialanthus-Ceratopyxis-Shaferocharis*; the group *Antillia-Urbananthus-Spaniopappus*; the group *Scolosanthus-Eosanthe*; the group *Pinillosia-Tetraperone-Koehneola*; and the group of *Espadaea-Goetzea-Henoonia*, etc.

The sclerophyllous broad-leaved Madro-Tethyan vegetation

AXELROD (1975) recognizes that the high similarity between the mediterranean vegetation of North America and Eurasia–N. Africa is not merely a physiognomic resemblance because most genera occurring are common to both regions. He shows that a sclerophyllous broad-leaved vegetation developed in the Eocene and Oligocene of Sierra Madre (Mexico) and the southern United States, and also in the Oligocene and Miocene of southern Eurasia, with many species in common. This vegetation, quite uniform in appearance, was named

the Madro-Tethyan vegetation after its westernmost limit, Sierra Madre, and the Tethys Sea, along the northern coast of which this vegetation type was spread. It was widely spread, too in the Upper Miocene of Central Europe. For example, the Sarmatian flora described from Hungary (ANDREÁNSZKY 1956, 1962*a, b*) is also designated by AXELROD as being parts of the Madro-Tethyan vegetation. This sclerophyllous broad-leaved vegetation, which was formed by plants highly adapted to the increasing summer droughts in the Tertiary, has now been split into remote, isolated stands living under very different ecological conditions. In California and Europe the summer is dry and the winter is wet, in Arizona and New Mexico there are two dry seasons. This vegetation type occurs under the dry winter and rainy summer climate of Mexico and the West Indies. Moreover, extensive stands are also found in places where the climate is wet throughout the year, but there are some sufficiently dry or nutrient poor habitats thanks to edaphic effects (e.g., white sand, serpentine, granite-gneiss domes, lava, limestone dog-tooth areas, etc.).

The southern link

AXELROD pointed out correctly that the laurel forests of the Canary Islands belong to the Madro-Tethyan vegetation, representing its southernmost portion. However, he did not think of the sclerophyllous communities of the Antilles which are also a part of that section. In the Miocene Honduras, the Yucatan peninsula and the Greater Antilles, which were connected to the first two, formed the southern coast of the Tethys Sea in America. These areas were similar in effect to the northern coast of Africa and the Canary Islands on the other side of the Tethys Sea. Accordingly, a special type of the sclerophyllous Madro-Tethyan vegetation, which should preferably be termed the *Peri-Tethyan* sclerophyllous vegetation, developed in the Greater Antilles. In addition to the Madro-Tethyan elements, this Antillean type is characterized by its richness in Neotropical sclerophylls and particularly in endemics, and also by its isolation. No doubt that the serpentine charraseals (dry evergreen shrublands), pine-oak woodlands, pine-laurel forests, and pine-*Dracaena* forests of Cuba are relicts left of the southern portion of the Madro-Tethyan vegetation.

The Madro-Tethyan flora in Cuba

The sclerophyllous broad-leaved Madro-Tethyan flora immigrated into the Antilles presumably in the Lower and Middle Miocene. It was probably a direct continuation of the former invasion of the Honduras flora. In this period an increasingly arid subtropical climate was predominant not only in the tropical zone but also in most parts of the warm temperate zone. More recently, this unusual expansion of the subtropical zone is attributed to a temporarily formed ring around the Earth, similar to that of the Saturn. This dry period displayed a strong influence on the evolution of the Cuban flora, in which the sclerophylls are still dominant, 75% of the endemic species are micro- or nanophanerophytes (2265 species), most of them (86%) being micro-, nano- and leptophylls. Many genera typical of the Madro-Tethyan vegetation immigrated into Cuba and became important elements of the flora supposedly in this period. These genera are: *Pinus*, *Juniperus*, *Quercus*, *Juglans*, *Buxus*, *Ilex*, *Lyonia*, *Vaccinium*, *Pieris*, *Kalmiella*, *Berberis*, *Celtis*, *Prunus*, *Myrica*, *Acacia*, *Calliandra*, *Erythrina*, *Karwinskia*, *Zizyphus*, *Reynosia*, *Colubrina*, *Thouinia*, *Dodonaea*, *Myrtus*, *Psidium*, *Euphorbia*, *Amyris*, *Helietta*, *Auerodendron*, *Sarcomphalus*, *Rhacoma*, *Forestiera*, *Sabal*, *Coccothrinax*, *Maytenus*, *Paepalanthus*, *Lachnocaulon*, *Syngonanthus*, *Eriocaulon*, *Chaetolepis*, *Befaria*, and *Garrya*.

Neotropical sclerophylls in the Madro-Tethyan vegetation of Cuba

The southern part of the Madro-Tethyan vegetation has its own typical features. Numerous species of the earlier established tropical broadleaf Honduras flora became adapted to the new arid climate, and several secondary evolutionary centres developed. Different Neotropical families and genera, represented by membranous leaved macrophylls and mesophylls in the continent, suffered a change so that new species groups or entire sections containing only sclerophylls and coriaceous leaved microphylls appeared in Cuba. Such genera are, for example, *Croton*, *Phyllanthus*, *Harpalyce*, *Miconia*, *Ossaea*, *Plumeria*, *Jacquinia*, *Plinia*, *Eugenia*, *Diospyros*, *Antirhea*, *Exostema*, *Rondeletia*, *Guettarda*, *Machaonia*, *Melocactus*, and *Gesneria*, etc. The endemic genera of the Antilles, Hispaniola and Cuba, that are typical of the sclerophyllous vegetation types, may also be considered as results of this climatic change. Examples are *Acrosynanthus*, *Phialanthus*, *Neomazaea*, *Ariadne*, *Phyllacanthus*, *Sarcophalus*, *Doerpfeldia*, *Pachyanthus*, *Scolosanthus*, *Catesbaea*, *Notodon*, *Nashia*, *Sauvallella*, *Leucocroton*, *Phidiasia*, *Lescaillea*, *Harnackia*, *Phania*, *Shafera*, *Moacroton*, *Hemithrinax*, *Ceuthocarpus*, *Schmidtottia*, *Roigella*, *Suberanthus*, *Kodalyodendron*, *Henoonia*, *Linodendron*, *Adenoa*, and *Tetralix*.

Drought resistant ecotypes

The numerous newly occurred sclerophyllous species and genera were only one indication of the adaptation to the dry climate of the Miocene. The membranous leaved trees of the Honduras flora became also adapted to aridity by developing drought resistant ecotypes. Although there are very little morphological differences between these ecotypes and the corresponding Central American populations the habitats of these species are apparently drier in Cuba than in the continent. Examples are: *Ceiba pentandra*, *Trichilia glabra*, *T. hirta*, *Cupania macrophylla*, *Bursera simaruba*, etc.

Archipelago phase

The third period is termed the archipelago phase. It came about in different points of time over the Greater Antilles. In Cuba it started at the end of the Miocene, when the Bartlett Trench, that separates Cuba from Jamaica and Hispaniola, was formed. Of these islands Jamaica had been connected to the continent for the longest time, as clearly indicated by the floristic composition of this island (ASPREY and ROBBINS 1953, ADAMS 1972). Changes typical of this period are the ecological specialization of floras isolated from one another and, as a consequence of this, the internal migration of species. In this phase the flora and fauna of Cuba were subjected to severe climatic and geological changes. In the Pliocene and the Pleistocene the wet climate frequently alternated with dry periods. The effects of this climate are clearly indicated by the stratification of ferritic soils in the Pipe Mts. Cooler periods, too, were frequent in the Pleistocene. Large scale tectonic events took place simultaneously with the climatic changes. The most effective of them was that the six, formerly separate land blocks emerged and joined together to form a single island with extensive bare areas. The colonization of these lands required further differentiation and migration of the flora and the adaptation of species to the new environmental conditions. Other external effects, independently of the geological changes, also influenced the flora of Cuba.

The broad-leaved rainforest flora of Guyana

The direct land connections between Cuba and Central America disappeared by the end of the Miocene. Later, in the early Pliocene, the climate became wetter. In the second half of the Pliocene the arch of many young volcanoes, i.e., the Lesser Antilles, emerged and the islands of the Greater Antilles also reached the maximum elevation. Presumably, this is the period when the South American elements immigrated into Cuba via the Lesser Antilles, although at that time land strips no longer existed. Yet, the genera *Carapa*, *Ochroma*, *Coussarea*, *Tocoyena*, *Paratheria*, *Phinaea*, *Proustia*, *Guarea*, and the *Myrsine guianensis* group must have been originated in this way.

The broad-leaved semi-deciduous Yucatan flora

It strikes one that there are numerous species common to the semi-deciduous forests of lowlands and hill-countries in western Cuba and Yucatan. Some of them occur solely in the Guanahacabibes peninsula and Yucatan. As examples the genera *Hirtella*, *Poiretia*, *Eriosema*, *Belotia*, *Luehea*, *Schwenckia*, *Chimarrhis*, *Calycophyllum*, *Elaeagia*, *Deherainia*, *Ateleia*, *Forchhammeria*, and *Neomacfadya* are worth mentioning. Although the presence of these elements suggests a direct relationship between the Miocene flora of Mexico and Cuba, there are neither geological nor biogeographical evidences supporting the existence of land connections in that period.

Elements from the temperate North America

The next most important region influencing the flora of Cuba, particularly western Cuba, is Florida and the southeastern United States. Several elements, such as *Pinus*, *Quercus*, *Fraxinus*, and many species of Ericaceae, Gramineae, and Cyperaceae, etc., of the temperate zone immigrated from the north and became predominant in some parts of western Cuba. ALAIN (1958 p. 19) presumes the existence of a former land connection between western Cuba and Florida, although according to geologists this possibility has been excluded since the Eocene Epoch. In my view, the flora from the temperate zone in western Cuba developed during the glacial periods in the Pleistocene, that took place simultaneously in the whole continent as pointed out by VAN DER HAMMEN (1961) and VAILLEUMIER (1971). Consequently, instead of assuming a land strip it is more reasonable to trace back the Florida–Western Cuba relationship to the Madro-Tethyan flora. As already seen, this sclerophyllous evergreen flora originally contained several genera from the families of the temperate zone. In addition, there was sufficient amount of time during the Miocene available for a fairly uniform vegetation to develop, first on the coast of the Tethys Sea and later, following the emergence of Central America, along the Gulf of Mexico. This flora was exposed to the cooler climatic periods occurring many times in the Pliocene and the Pleistocene. In particular, the coastal region of the Gulf of Mexico was affected, since the cold Labrador Current often reached this zone during the Pleistocene. The new environmental conditions, e.g., modified soil types, and the adaptive responses of plant populations generated by this cooling process were probably similar on both sides of the gulf. The standardization of the flora may have been furthered, too, by the strong northerly and westerly winds during the glacial periods and by the more intensive bird migration. In Cuba, the expansion of this flora was also promoted by the newly emerged lands and white sands that offered extensive bare areas for plants. Thus, the recent flora elements common to western Cuba and Florida are remnants of a Pleistocene

flora spread along the entire coast of the Gulf of Mexico. The continuity of this flora was broken in the postglacial period, when the Central American subtropical flora retreated to the western coast of the gulf, forcing back the remnants of the Madro-Tethyan flora to a north-western and northeastern direction.

Remarks on the driving forces of migration

In connection with the above discussion, it has to be emphasized that very little is known about the water and aerial dispersal of seeds. Seed dispersal is likely to be more important than generally thought, and the explanation of floristic relationships does not necessarily require a search for disappeared land strips. Only confirmed geological results may serve as a basis for hypotheses on the distribution, development and migration of the flora. Moreover, even undoubtful land connections may prove to be of no help in promoting dispersal. For instance, *Befaria cubensis*, *Microcycas calocoma*, and *Rhus copallina*, did not reach Isla de Pinos despite the direct terrestrial contact to Cuba in the Pleistocene. Although *Fraxinus caroliniana* ssp. *cubensis* produces easily flying seeds, it could not become established on moorlands outside the Zapata peninsula. Many genera (e.g., *Victorinia*) and species (e.g., *Omphalea commutata*) are still restricted to an area along the former contact line between Cuba and Hispaniola (Fig. 21) although the ecological conditions would allow a larger geographic range on both islands. Many elements of the Bahamas, that managed to get across the wide and deep Bahama Trench and became established on the reefs around northern Camagüey, Tunas and Holguín, were unable to penetrate into Cuba through the narrow and shallow bays and even via the former land strips. Consequently, a terrestrial contact may not necessarily be enough by itself and cannot be a single explanation for migration. The migratory activity of taxa does not always coincide in time with the possibilities. In other cases in-favourable ecological and cenological conditions, such as the saturation of the flora, may prevent otherwise feasible migration.

Flora migration in the interior of Cuba

The chorological groups reflecting the origin of the Cuban flora, the approximate time of their manifestation and the potential migratory routes have already been discussed. These are, however, only the initial steps toward



Fig. 21. Geographical distribution of *Omphalea commutata* Muell. Arg. and *Petitia Urbanii* Ekm. (after ALAIN 1972 and BORHIDI 1973)

a complete flora development. The actual floristic composition is a result of further differentiation, adaptation and internal migration. Two fundamental principles should be considered in this regard.

Two principles of internal floristic changes in Cuba

A. Oriente is the earliest cradle of the Cuban flora,³ a starting point for the most important migrations.

B. The floras of mountains are older than those in the lowlands. The flora and vegetation of plains are originated from the mountainous regions.

Three stages of internal migration

According to time, starting point and direction, three stages of internal migration can be distinguished.

a. *Migrations in the early Tertiary (Eocene to Miocene Epochs)*. The centre of these movements, that were directed from the east to the west, was the mountains of Oriente. The low differentiation and specialization level of the flora is typical of this stage. Several migratory waves may be recognized, these are associated with different periods. The radius of action was determined in each case by geological events, transgression and the emergence of lands, that actually happened. The serpentine and karst flora of western Cuba and then the montane flora of the Escambray Mts were originated in this way. Later, the submontane tropical flora, which subsequently colonized the rising plains, took refuge in the valleys.

b. *Migrations at the end of the Tertiary and in the Quaternary (Pliocene and Pleistocene Epochs)*. Starting from both tips of the island the migrations were directed toward the interior. As a result, a new flora in the central plains of Cuba became established at the end of the Pliocene. The migrations of alternate direction in the Pleistocene are also mentioned here. During cooler periods these migratory waves swept over Cuba from the west to the east, but in the warm periods the migration was of the opposite direction. This is the time of ecological and cenological adaptation and specialization. The vegetation zones and, among others, the formation of the endemic montane flora of Turquino may also be dated back to this stage. Furthermore, the homogenization of the flora and vegetation, that were originated from different mountains, may have been caused by the repeated "shake up" of the flora of plains.

c. *Migrations driven by anthropogenic forces during the historical ages*. The starting point for these migrations is usually western Cuba, so the direction is toward the east. The reason for this is that western Cuba was the sanctuary of many savanna and prairie elements in the Pleistocene, that found refuge particularly in the herb layer of coniferous forests. The migration of these plants was made possible by tropical deforestation, which is mainly responsible for secondary savannas and the recent landscape of Cuba. In addition to the migration of native plants, many species were introduced most recently by man. These elements, too, migrate usually from the west to the east.

Evolutionary centres and the migration of ecological groups

The evolutionary centres and the migratory characteristics of genera, families and sections may be explored by comprehensive morphological and microevolutionary studies at the given taxonomic level. However, only a few relevant works have been published, for instance, WEBSTER (1958) on *Phyllan-*

thus, JUDD (1982) on *Lyonia*, DAHLGREN and GLASSMAN (1963) on *Copernicia*, and HOWARD (1949) on *Coccoloba*. Of course, besides the analysis of taxonomic categories, the evolutionary centres and migratory pathways of life forms or vegetation types may also be revealed by thorough studies. For example, the mangrove communities reach the highest diversity in the Indonesian archipelago, which may be considered the evolutionary centre of the mangrove vegetation types (ANDREÁNSZKY 1954). The localization of the richest and the poorest stands of each vegetation type or plant community in Cuba may be readily determined based on phytosociological relevés and vegetation maps. In the present study relevés taken by BORHIDI, MUÑIZ, DEL RISCO, CAPOTE and SAMEK are used together with published (LEÓN 1936, 1939, MARIE-VICTORIN 1942, 1944, 1956, WEBSTER 1956–58, BORHIDI and MUÑIZ 1977, KLOTZ 1979, and BORHIDI 1972, 1981) and unpublished (BORHIDI) distribution maps.

Evolutionary centres and migratory routes of the serpentine vegetation

The distribution of some typical elements of the serpentine vegetation is shown in Figs 8, 9, 11, 22. The evolutionary centres and principal migratory routes are illustrated in Fig. 23. The section *Orbicularia* of the genus *Phyllanthus* is a typical serpentinophilous group that includes many species occurring on the old ferritic soils of northeastern Oriente. Of this section *Ph. orbicularis* is the only species that is found on all the serpentine outcrops of the island (Fig. 8). Like *Neobraccia valenzuelana* (Fig. 9), this species must have reached its suitable habitats along the route indicated by arrows in the figure. LEÓN (1946) and WEBSTER (1958) assumed that this migration took place along a continuous serpentine "axis" ("eje serpentinoso"). Such a serpentine strip could not have existed later than the Oligocene, due to the long transgression of central Cuba. It is doubtful, however, whether such a large continuous serpentine area could have been denuded by that time, although the distributions of vicarious genera (Fig. 10) and species (Figs 11–12) of the Nipe Mts and Cajalbana suggest that a direct relationship may have existed. Yet, according to our recent geological knowledge, it is more likely that the serpentine blocks were more or less separated all the time. The serpentinophilous species were presumably distributed either by wind (*Neobraccia*) or by animals (*Phyllanthus*). They may have had wider distribution earlier, but due to the depletion of habitats (KRÜCKENBERG 1954) they survived only on serpentines and became subjects of intensive speciation. It seems that there were several stages of the east-west migration of the serpentine flora. Taxa with strongly disjunct geographical range, e.g., *Anemia*, *Moacroton*, *Lescaillea*, and *Harnackia*, etc., were distributed during the earlier stages. Later, some serpentinophilous species, e.g., *Jacaranda cowellii*, *Coccoloba geniculata*, *Zanthoxylum nannophyllum* (Fig. 22), and *Platygyne parviflora* (Fig. 14), migrated replacing the above mentioned taxa in the plains of eastern Cuba. In these stages the species with continuous distribution, such as *Neobraccia valenzuelana* and *Phyllanthus orbicularis*, became also widespread. On the basis of all these, three evolutionary centres of the serpentine flora may be distinguished in Cuba (Fig. 23). The first and the oldest is Moa from which the serpentine flora of the entire island, and the flora of other ferritic soil areas in northeastern Oriente, the Baracoa-Jauco zone and the Cristal and Nipe Mts were originated. The second is Nipe, a migratory centre of a more xerophilous serpentine flora which was capable of being established in the arid lowlands and of migrating to the west. The third centre is Cajalbana in western Cuba. A part of its flora retreated

to the serpentine blocks risen later in central Cuba, especially to Habana and Matanzas. Many latosol elements of this flora became adapted to the acidic slaty habitats of Pinar del Rio and Isla de Pinos. In Fig. 23 the dotted line directed to the east indicates the secondary migration of serpentine elements from areas which subsequently became secondary savannas under the influence of man.

Evolutionary centres and migratory routes of the flora of limestone cliffs

The flora of limestone karsts has two primary evolutionary centres (Fig. 24). One of them is in the conical karsts of Sierra de los Organos in western Cuba, which is considered to be the oldest geological formation on the surface of that area. The majority of species found here remained endemics, although a portion of the flora spread to the younger Tertiary karsts in the Habana and Matanzas Heights, e.g., *Bombacopsis cubensis*, *Thrinax morrisii* (Fig. 14) and *Phania matricarioides* (Fig. 25). Certain elements managed to get dispersed as far as to the high-altitude mogotes and to the southern coast at the Escambray Mts. During the transgression, Cuba itself was an old coastal zone serving as a refuge of the vegetation of coastal karsts. This vegetation started to spread over the recent coastal zone at the end of the Tertiary. The other primary evolutionary centre is the mountains of Oriente. Here, the development of the karstic flora is not as clear-cut as in western Cuba, since the karsts of Oriente are younger than the serpentine formations and, also, a part of the limestone flora is originated from primary soils derived from serpentine (e.g., Nipe Mts, Monte Libano). Of the many isolated

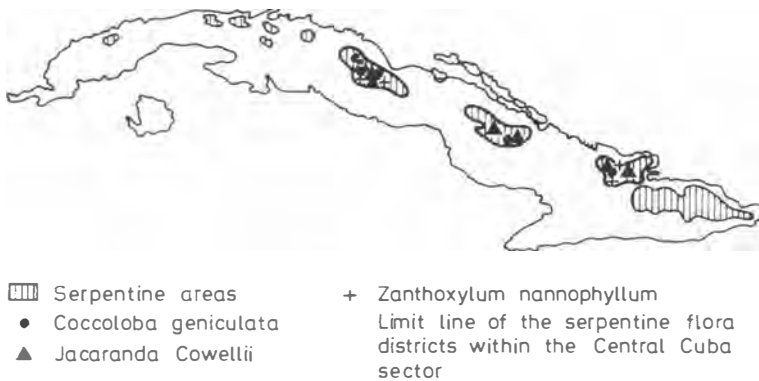


Fig. 22. Geographical distribution of *Cocoloba geniculata* Lindau, *Jacaranda cowellii* Britt. et Wils. and *Zanthoxylum nannophyllum* (Urb.) Alain (after BORHIDI 1973)



Fig. 23. Evolution centres and migratory routes of the serpentine flora in Cuba (after BORHIDI 1973)

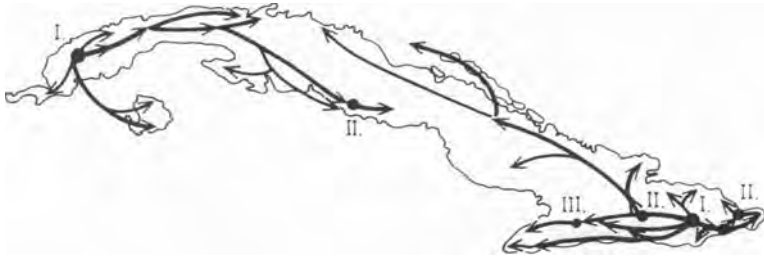


Fig. 24. Evolution centres and presumable migratory routes of the flora of limestone karsts in Cuba (after BORHIDI 1973)

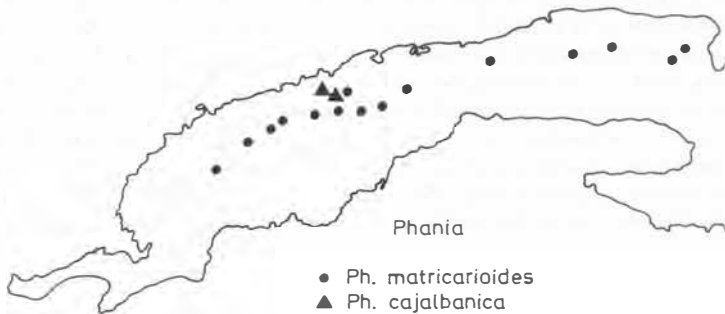


Fig. 25. Geographical distribution of the genus *Phania* (after BORHIDI 1973)



Fig. 26. Possible centres of evolution and migratory routes of the subdesertic, xero-megathermophilous elements of Cuba (after BORHIDI 1973)

karstic regions, the group of Monte Libano and Monte Verde appears the most peculiar evolutionary centre, so much the more because this area was crossed by many migratory paths of varying nature and direction. From this old coastal karstic zone spread the karst flora over the country, first along the coastline. In the westerly direction two secondary evolutionary centres developed: the karsts southwest of the Nipe Mts, and at the northern border of Sierra Maestra. In both areas the montane elements descending from the mountains were mixed with the karstic flora spread along the coast. The influence of this flora was extended to the east as far as the Yumuri karsts and Yunque de Baracoa, with a secondary evolutionary centre developed in the latter place. The rise of the terraces in southern Baracoa made possible



Fig. 27. Geographical distribution of the genus *Isidorea* A. Rich. (after BORHIDI 1973 modified)

for the flora of Monte Libano to spread over the semi-desert coastal zone. As a result of the migration, xero-megatherm species evolved. Some elements of the Oriente karstic flora migrated along the southern coast at the Sierra Maestra. The others spread to the west from the Nipe Mts via the former limestone block mountains along the northwestern coast of central Cuba, forming the flora of the Cubitas and Najasa Mts and, too, the flora of coastal shelves. The influence of this migration may be seen even in the mogotes of Caguagas (cf. the distribution of *Hemithrinax*, Fig. 13). This bidirectional distribution exhibited by karstic elements is an important characteristic of the recent flora, too, so it was considered in the delimitation of the flora regions of central Cuba.

Evolutionary centres and migratory routes of the xero-megatherm elements

Some semi-desert xero-megatherm elements are originated from central and southern Hispaniola (Fig. 26), to which the southeastern coast of Cuba was formerly connected. This relationship is proved by the distribution of several genera and species, e.g., *Omphalea commutata*, *Petitia urbani* (Fig. 21), *Victorini*, and *Isidorea* (Fig. 27), now restricted to the coastline. These elements, thanks to the gradual rising of the southern Baracoa coast, were intermixed with the endemic flora of karstic slopes. As a result, several centres of speciation developed, the richest of them being the Guantanamo Basin. The flora of Macambo-Imias and Maisi, and the Daiquiri-Siboney-Santiago area in the west are almost as rich as that of the Guantanamo Basin, so they can be considered as secondary and tertiary evolutionary centres, respectively. The number of xero-megatherm elements on the southern coast at Sierra Maestra, on the coasts of northwestern Oriente and northern Camagüey, in the southern foothills of Escambray Mts, on the northern rocky coast between Habana and Matanzas and on the southern limestone shores of the Guanahacabibes peninsula decreases in that order.

Evolutionary centres and migratory routes of the montane rainforest elements

The evolutionary centres and migratory routes of the flora in the montane rainforests are shown in Fig. 28. The distribution of *Hedyosmum* serves as an example (Fig. 7). Again, the main centre is the lower and old mountains in the Sagua-Baracoa Massif, especially the Moa-Toa area. According to my hypothesis, this region received its montane elements via Hispaniola, and served as a new centre for their further migration to Cristal, Ipe, Purial,

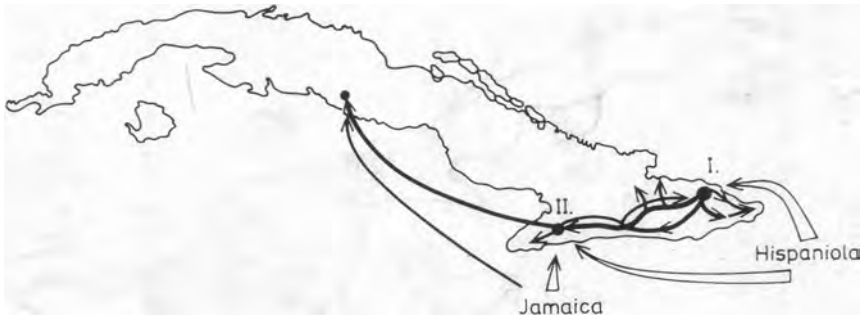


Fig. 28. Centres of evolution and possible migratory routes of the montane rain forest elements in Cuba (after BORHIDI 1973)

Imias mountains, and, in particular, to Sierra Maestra. The first stage of this process took place presumably in the mountain-range connecting Oriente and Escambray. The more permanent changes, however, are results of migrations in the cooler periods during the Quaternary between Sierra del Cristal and Gran Piedra through the Central Valley area which subsided later. At that time the lower border of montane rainforests may have run at a 2–300 m altitude. This montane flora was mixed with Jamaican and southern Hispaniolan montane elements and, during the cool stages in the Pleistocene, may have repeatedly retreated to the subalpine-alpine zone in the Turquino group. In this place a secondary centre of speciation developed. It is likely that even at that time some montane elements of Sierra Maestra got across to the Escambray Mts, which received elements from the montane flora of Jamaica, too.

Distribution centres and migratory routes of the semi-deciduous elements

The origin and migration of the elements of semi-deciduous forests and seasonal rainforests in the lowlands pose different problems. ALAIN (1958) traces the origin of some elements back to Mexico, assuming a west-east migration of these forests. It is my conviction that this flora survived in the refuge of valleys at the time of transgression, and subsequently spread over to every direction. Especially the mountains of Oriente, northern Camagüey, Pinar de Rio and the Escambray Mts should be mentioned as potential refuges. The high similarity between the characteristic composition of lowland and submontane forest formations also refers to this fact.

For cited references see the second part.