

PART III
FUNDAMENTALS OF
THE PHYTOGEOGRAPHY
OF CUBA

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PART III

Fundamentals of the phytogeography of Cuba

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The phytogeographic conditions of Cuba have not been overviewed or summarized in the literature as yet. Past contributions to this subject, the state of the art of research and future tasks have been mentioned in the Introduction and the long-needed relevant studies by the author and his co-workers are also outlined. In the sequel an attempt will be made to provide a comprehensive view of the subject using earlier results but relying primarily on our original research.

16 Life-forms and the biological spectrum of the flora of Cuba

Existing life-form schemes have been extensively and critically reviewed by Fekete and Szujkó-Lacza (1969–1972) in a paper consisting of four parts. The theoretical and practical problems of life-forms are not discussed here and repetitions will also be avoided so much the more because I share most of the views expressed by the authors referred to above.

16.1 Life-forms as a basis for the physiographic classification of vegetation

Raunkiaer's life-form categories play a role by far the most important in tropical vegetation surveys in both theoretical and practical respects (Richards *et al.* 1940, Richards 1952). Regardless (of the views of different phytosociological schools, the non-tropical plant communities are in fact characterized on the basis of relatively few species that are represented by many individuals. The floristic composition and the spatial and temporal structure of communities are maintained by the populations of characteristic species. In this regard the indicative role of life-forms is in fact indirect and the life-form spectra, as diagnostic tools, may only confirm the existence of the ecological trends recognized.

The situation is completely different in the tropical forest and scrub vegetation. Since the number of species is large and the number of individuals belonging to each species is small, the plant communities are primarily characterized by the spatial

structure. Due to the high floristic heterogeneity, the individuals of the majority of species are scattered within the stands to such an extent that populations cannot be defined in ecological terms. That is, most populations are 'dissolved' in the diverse community. At each stratum of the vegetation there are at least 6—8 species with the same life-form type. Regarding their ecological requirements, the individuals of these species can perfectly replace one another, not only in the visually observed structure of the community but also at the level of nutrient cycles and energy flow and even in the ecological niche space. An additional phenomenon is that similar vegetation types are completely different in species composition due to the presence of numerous endemic taxa and to the peculiarities in the evolution of the flora of different localities. In the tropical vegetation it is primarily the structure which repeatedly occurs as a consequence of ecological effects and sequences of habitats. The structure is determined by strata composed of similar life-form types and also by synusia composed of a single life-form type. Consequently, in the recognition and classification of tropical lignosa communities the mostly accidental and heterogeneous floristic composition is inevitably replaced by life-form spectra that are more stable in information content and diagnostic value. Thus, the indicator role of life-forms is of fundamental importance in any tropical vegetation survey no matter if that is a straight ecological study or a vegetation mapping.

16.2 Concerning the application of life-form categories

For the physiographic characterization of tropical vegetation types different improved versions of Raunkiaer's (1907) scheme have been used (e.g. Dansereau 1951, 1958, 1966, Cain and Castro 1959 etc.). The most detailed life-form classification is developed by Ellenberg and Mueller-Dombois (1967).

In analyzing the flora and vegetation types of Cuba we shall try to reach an ecological optimum regarding the information conveyed by the various life-forms. This is done according to the following considerations:

1. Any life-form exhibiting a significant indicator value of a given ecological pattern is treated as a separate category.

2. Furthermore, an effort is made to avoid the use of too few or too many categories. Therefore, certain morphologically or ontogenetically different groups that proved to be of no ecological distinctive value are combined.

16.3 A modified life-form scheme

The generally used life-form schemes are modified as follows:

- a) It is necessary to distinguish between tree ferns and other pachycaul trees. They are treated as separate life-form categories because tree ferns are different from both palms and pachycaul trees of the deserts and high mountains with respect to their ecological requirements and behaviour, and also in their role played within the communities.

b) Despite their pachycaulic character, the agaves are not assigned to the groups of rosulate phanerophytes, but rather to the succulent phanerophytes. The rationale is that they usually occur in similar vegetation types replacing one another depending on the characteristics of parent rocks and soil. This is a typical example of pseudovicariancy.

c) No distinction is made among the pachycaul elements (Corner 1964) for several reasons. One reason is that there are no reliable data concerning the early stages in the ontogenesis of several Cuban species and it is therefore difficult to decide if they are pachycauls. Furthermore, the group of known pachycaul forms appears to be ecologically heterogeneous. Consequently, it should have been divided into several groups in accordance with the ecological concept described above.

d) The grass-like lianes are removed from the group of tree-sized herbs (cf. Ellenberg and Mueller-Dombois 1967) and assigned to the woody lianes.

e) There is no doubt that the category of hemi-epiphytes is heterogeneous if the morphology and their role in the community are considered. The liane-like climbing species which, in my opinion, should preferably be termed the hemi-lianes, are assigned to the lianes. On the contrary, the true epiphytic stranglers (*Ficus*, *Clusia* species) are considered to have potentially alternating life-forms. Most of them may survive as an independent phanerophyte. Therefore, although this difference is occasionally indicated (actually in the phytosociological tables), it is ignored in the analysis of flora as being an uncommon feature. Thus, potential stranglers are assigned to the respective group of phanerophytes.

f) Three important ecological groups of epiphytes are distinguished:

1. Woody epiphytes (semi-parasites and myrmecophilous plants).
2. Shade tolerant (sciophilous), mainly obligate epiphytes (e.g., certain species of *Lycopodium sensu lato*, *Hymenophyllaceae*, moss-inhabiting orchids with creeping stalks and roots, broad-leaved hygrophilous bromelias).

3. Heliophilous, usually potential epiphytes, rosette ferns, orchids, narrow-leaved bromelias, epiphytic cacti).

16.3.1 Máthé's method for determining life-form spectra

The life-form spectrum was obtained based on Máthé's (1942) original method, used for the first time in tropical surveys. Not only the frequency of life-forms but their relationship to each area type was also examined. In this manner I was allowed to draw conclusions regarding the history and migration of the flora elements.

16.4 The life-form spectrum of the spermatophytes of Cuba

The life-form spectrum for the higher plants (including only Spermatophytes) of Cuba is given in Tables 17. The percentage distribution and the phytogeographic and phytosociological importance of life-form types are illustrated below with examples. 6375 species and subspecies are included in the analysis.

Table 17 The life-form

Flora elements	Mg— MsP	Mc— MsP	McP	N— McP	NP	Ms P _{tot}	Mc P _{tot}	LP	EP
<i>Group of endemic species</i>									
Pinar del Río endemics	2.0	4.7	15.8	1.5	28.7	2.9	0.9	1.7	1.5
Isla de Pinos endemics	1.8	3.6	7.1	—	10.7	—	1.8	3.6	—
Endemics to both Pinar del Río and Isla de Pinos	3.0	1.0	13.4	3.0	11.3	1.0	1.0	—	—
Species endemic to western Cuba	2.8	5.0	13.9	6.1	21.1	4.4	1.1	0.6	—
Habana endemics	—	3.1	21.8	3.1	34.4	—	3.1	—	—
Matanzas endemics	—	4.2	12.5	4.2	16.6	4.2	8.3	—	8.3
Las Villas endemics	3.6	6.4	19.3	1.4	25.7	2.9	3.6	1.4	0.7
Camagüey endemics	3.2	—	12.9	6.5	35.5	—	9.7	—	—
Species endemic to eastern Cuba	6.2	3.8	13.8	6.9	33.2	4.6	3.1	3.8	1.5
Oriente endemics	4.6	6.7	21.2	4.0	34.3	2.2	1.5	2.9	0.5
Pan-Cuban endemics	6.2	7.8	15.9	3.8	20.8	1.7	1.1	1.6	1.4
Total endemics	4.2	5.9	18.4	3.8	30.9	2.3	2.0	2.6	0.8
<i>Group of Caribbean species</i>									
Greater Antillean species	19.9	8.9	13.0	2.6	12.6	0.4	0.4	4.7	3.0
Antillean species	10.5	13.7	8.6	4.6	10.5	0.6	0.6	2.0	2.0
Antillean — Bahamean species	2.7	6.7	9.3	14.7	9.3	1.3	1.3	9.3	2.7
Bahamean species	7.1	15.7	10.0	—	25.8	—	—	1.4	1.4
Species of the Antilles, Florida and SE USA	5.7	9.1	2.3	1.1	2.3	1.1	—	2.3	—
Species of Cuba, the Bahamas and SE USA	—	14.6	12.2	3.7	7.3	—	1.2	—	1.2
Species of Cuba, Florida and SE USA	1.9	—	1.9	0.9	3.8	—	—	0.9	—
Northern Caribbean species	7.8	3.0	5.4	4.6	10.8	0.8	2.3	3.8	—
Southern Caribbean species	9.5	4.7	5.7	2.8	8.5	—	—	2.8	0.9
Pan-Caribbean species	7.6	11.2	9.5	2.6	8.2	—	0.8	3.9	—
Total Caribbean species	7.6	8.9	9.1	3.3	10.2	0.4	0.7	3.6	1.4
<i>Tropical species with wider distribution</i>									
Species of Cuba, the Antilles and South America	4.7	3.5	4.7	2.4	7.0	—	—	9.4	—
Species of Cuba, and South America	—	3.1	3.1	3.1	9.2	—	—	7.7	—
Neotropical species	4.7	5.1	4.1	2.0	6.5	0.4	—	5.4	0.8
Pan-tropical species	0.9	4.1	2.7	2.3	7.7	—	—	1.8	—
Total of widely distributed tropical species	3.6	4.6	3.8	2.1	7.0	0.3	—	5.1	0.6
Total of all tropical species	5.1	6.6	13.0	3.3	19.5	1.4	1.2	3.4	0.9
<i>Group of extratropical species</i>									
North and Central American species	2.4	—	—	—	—	—	—	—	—
American species	—	—	—	—	2.2	—	—	—	—
Cosmopolitan species	—	—	—	—	—	—	—	—	—
Amphiatlantic and circumpolar species	—	—	—	—	—	—	—	—	—
Total extratropical species	0.8	—	—	—	0.8	—	—	—	—
<i>Group of adventive species</i>									
Neotropical adventives	16.8	2.7	8.8	5.3	6.2	0.9	—	3.5	—
Palaeotropical adventives	17.1	4.4	3.8	—	9.3	1.1	—	5.5	—
Extratropical adventives	—	—	—	3.7	—	—	—	2.5	—
Total adventives	13.4	2.9	4.5	2.4	6.4	0.8	—	4.2	—
Total Cuban flora	5.5	6.2	12.2	3.2	18.3	1.3	1.2	3.4	0.8
Original flora of Cuba without adventives	5.0	6.4	12.7	3.2	19.2	1.3	1.2	3.3	0.9

spectrum of the flora of Cuba

SP	P _{Gr}	P	Ch	H	G	HH	Th	TH-H	L _H	E _H	E _{Co}	S ₀	Ch-E
1.5	—	60.0	6.1	16.3	1.2	3.5	3.5	0.9	7.0	6.9	0.6	—	40.0
—	—	28.6	7.1	49.9	3.6	1.8	3.6	—	3.6	1.8	—	—	71.4
—	—	33.7	12.2	36.9	2.0	6.1	6.1	1.0	2.0	—	—	—	66.3
1.7	—	56.7	2.8	21.6	3.7	4.4	1.1	1.1	7.8	0.6	—	—	43.3
6.3	—	71.8	6.3	6.3	—	—	3.1	3.1	9.4	—	—	—	28.1
4.2	—	62.5	4.2	24.9	4.2	—	—	—	—	4.2	—	—	37.5
2.1	—	67.1	3.6	17.2	4.3	—	5.0	0.7	1.4	—	0.7	—	32.9
3.2	—	71.0	16.1	—	—	—	9.7	3.2	—	—	—	—	29.0
3.1	—	80.0	3.8	13.2	—	—	0.8	—	2.3	—	—	—	20.0
0.8	—	78.7	4.0	7.8	1.4	0.1	0.7	0.2	3.1	3.6	0.3	0.1	21.3
1.1	—	64.4	2.4	13.5	2.7	0.9	3.0	0.5	8.6	3.0	—	—	35.6
1.2	—	71.9	4.4	12.3	1.8	1.2	1.9	0.5	4.4	2.6	0.2	0.03	28.1
1.4	0.2	57.0	4.1	16.8	3.2	1.0	3.2	0.6	5.5	6.4	2.2	—	43.0
1.3	0.6	55.0	1.3	20.3	3.9	2.0	3.9	0.6	5.9	7.2	—	—	45.0
1.3	—	58.6	2.7	13.4	2.7	4.0	5.3	—	8.0	5.3	—	—	41.4
1.4	—	62.8	1.4	14.3	1.4	1.4	2.9	—	8.7	5.7	—	1.4	37.2
—	—	23.9	2.3	44.2	9.1	8.0	3.4	3.4	3.4	2.3	—	—	76.1
—	—	40.2	2.4	20.7	9.8	4.9	9.8	1.2	11.0	—	—	—	59.8
0.9	0.9	11.2	1.9	56.0	2.9	15.8	6.5	1.9	1.9	1.9	—	—	88.8
1.5	—	40.0	6.9	26.2	1.5	4.6	10.0	2.3	4.6	0.8	2.3	0.8	60.0
1.9	—	36.8	2.8	17.0	4.7	1.9	4.7	—	10.4	15.1	6.6	—	63.2
1.0	0.3	45.1	3.9	22.1	3.6	0.3	7.2	1.6	3.6	7.7	4.6	0.3	54.9
1.2	0.2	46.6	3.5	22.8	3.8	3.0	5.3	1.1	5.6	5.9	2.2	0.2	53.4
—	2.4	34.1	4.7	30.7	9.4	9.4	3.5	—	3.5	4.7	—	—	65.9
—	—	26.2	6.1	32.3	7.7	7.7	6.1	—	6.2	4.6	3.1	—	73.8
0.3	0.8	30.1	3.0	32.9	2.0	7.1	11.0	1.4	6.5	4.2	1.8	—	69.9
—	0.4	19.9	1.4	32.2	4.1	5.4	20.8	1.8	14.0	0.4	—	—	80.1
0.2	0.8	28.1	3.0	32.5	3.3	7.0	12.1	1.3	7.8	3.5	1.4	—	71.9
1.0	0.2	55.3	3.9	19.5	2.7	2.8	4.8	0.8	5.4	3.7	1.0	0.1	44.7
—	—	2.4	—	46.4	—	34.2	14.6	2.4	—	—	—	—	97.6
—	—	2.2	2.2	50.0	4.3	21.8	15.2	4.3	—	—	—	—	97.8
—	—	—	6.9	27.6	—	37.9	20.7	6.9	—	—	—	—	100.0
—	—	—	—	100.0	—	—	—	—	—	—	—	—	100.0
—	—	1.6	2.5	45.5	1.7	28.9	15.7	4.1	—	—	—	—	98.
7.1	0.9	52.2	1.8	15.0	5.3	1.8	15.2	1.8	8.0	—	0.9	—	47.8
0.5	4.4	46.1	1.1	24.9	2.7	1.1	14.3	1.1	8.2	0.5	—	—	53.9
—	—	6.2	3.7	28.4	3.7	1.2	45.7	11.1	—	—	—	—	93.8
2.4	2.4	39.4	1.9	22.6	3.7	1.3	20.6	3.5	6.4	0.3	0.3	—	60.6
1.1	0.4	53.3	3.7	20.3	2.7	3.2	6.0	1.0	5.4	3.4	0.9	0.1	46.7
1.0	0.2	54.2	3.8	20.0	2.7	3.4	5.0	0.9	5.3	3.6	1.0	0.1	45.8

16.4.1 Phanerophytes (P)

These are plants with woody stalk or trunk and tree-sized herbs. 3493 species in Cuba (53.3% of the total flora).

Megaphanerophytes (MgP) Giant trees over 30 m. Two species in the Cuban flora (0.0003%): the pantropical *Ceiba pentandra* and the Neotropical *Carapa guianensis*, both characteristic of rainforests. *Ceiba* is an element of seasonal evergreen forests and semi-deciduous forests of lowlands. Under extremely favourable conditions some individuals of mesophanerophytes, such as *Hildegardia cubensis*, *Guarea guara*, *Dipholis jubilla*, *Cupania americana*, *Cedrela mexicana* and *Spondias mombin* may also reach the height of giant trees in Cuba.

Mesophanerophytes (MsP) Trees of 15–30 m height. Their number in Cuba is 360 accounting for 5.5% of the total flora. These trees compose the second canopy level in submontane rainforests and the upper canopy level in seasonal evergreen forests, montane forests and semi-deciduous forests. Most of them (147) are endemics. The mountainous regions of Oriente are the richest in endemic species (91). The distribution of other species is Greater Antillean (50), Neotropical (33) and Caribbean (23). The number of introduced and successfully established species is also large (50), most of them (31 species) being timber or ornamental trees of paleotropical origin. Besides those listed in the previous paragraph it is worth mentioning the following species: *Mastichodendron foetidissimum*, *Swietenia mahagoni*, *Calophyllum antillanum*, *C. utile*, *Bursera simaruba*, *Pseudolmedia spuria*, *Matayba oppositifolia*, *Zizyphus rhodoxylon*, *Magnolia cubensis*, *Myrsine coriacea*, *Laplacea angustifolia*, *Sloanea curatellifolia*, and several species of *Hyeronima*, *Ocotea*, *Cinnamomum* and *Cordia*.

Micro-Mesophanerophytes (Mc-MsP) Small or medium-sized trees of 8–15 m height 381 species in Cuba represent 6.2% of the flora. The third level of submontane rainforests, the second canopy level of seasonal evergreen and deciduous forests, and the upper tree layer of dry evergreen forests and montane rainforests are composed of these species. Examples are: *Tabernaemontana amblyocarpa*, (Fig. 77.) *Celtis trinervia*, *Hebestigma cubense*, *Ehretia tinifolia*, *Chrysophyllum oliviforme*, *Oxandra lanceolata*, *Guajacum sanctum*, *Acacia*, *Erythroxylum* and *Pithecellobium* species and many representatives of genera *Persea*, *Pera*, and *Tabebuia*.

Microphanerophytes (McP) Small trees of height ranging from 5 to 10 m. 798 species, accounting for 12.2% of the flora. These species occur in dry evergreen forests, karstic woods, shrublands on serpentine and ferritic soils, semi-dry montane forests and mossy forests. 72% of them (593) are endemic to Cuba, 45% (346) to the former province of Oriente, 59 species to the entire country and 58 to Pinar del Rio. 65 species are Greater Antillean, 29 species each are Neotropical and Caribbean. For example, many species belonging to the genera of families Myrtaceae and Melastomataceae, such as *Eugenia*, *Calyptranthes* and *Psidium*. Also, many species of *Bourreria*, *Psychotria*, *Guettarda*, *Rondeletia* and *Tabebuia*, and *Ateramnus lucidus*, *Polygala cuneata* and *Guajacum officinale*, etc.

Micro-nanophanerophyta (N-McP) Woody plants of 2–5 m height. Both shrub and tree-sized individuals may occur. Their number is 194 (3.2% of the flora).



Fig. 77 *Tabernaemontana amblyocarpa* Urb. a Pan-Cuban endemic tree, characteristic of the semi-deciduous and seasonal evergreen forests (Photo: A. Borhidi)

These are the plants of evergreen shrublands, other scrub formations and semi-deserts. The majority of species belonging to this life-form are endemics, most of them (62) endemic to Oriente, 14 to the entire country and 11 to western Cuba. Examples are *Byrsonima crassifolia*, *Kodalyodendron cubense*, *Schaferocharis multiflora*, *Ouratea illicifolia*, *Maytenus buxifolia* and *Rondeletia odorata*.

Nanophanerophytes (NP) Shrubs between 0.5 and 2 m. 1249 species accounting for 18.3% of the flora. This life-form is the richest in species in Cuba. They are particularly widespread in woods, shrublands, scrub formations, semi-deserts, karstic woods and montane thickets. 76% of them are endemics, especially in Oriente (611), in Pinar del Rio (103) and in the entire country (78). There are 64 Greater Antillean and 46 Neotropical species. Most of them belong to the genera *Buxus*, *Ilex*, *Eupatorium*, *Vernonia*, *Lyonia*, *Ossaea*, *Gochnatia*, *Eugenia*, *Phyllanthus*, *Croton*, etc.

Rosulate mesophanerophytes (MsPros) Tall, rosulate trees between 8 and 30 m 81 species (1.3%). They are most abundant in different hygrophilous and mesophilous forests, semi-deciduous and karstic forests. 85% of them (69 species) are endemics, 40% (30 species) exclusively in Oriente. Only 6 species are present in the other regions of the Antilles, 3 are Neotropical. Typical representatives are *Roystonea regia* and *Prestoea montana* with pinnate leaves, *Gaussia princeps* and *Gastrococos crispa* with barrel-like trunks. Examples of fan palms are *Sabal parviflora*, *Thrinax radiata*, *Copernicia gigas*, *C. baileyana*, *C. vespertilionum*, *C.*



Fig. 78 The tree-fern-shaped Rutaceae: *Spathelia brittonii* P. Wils. an endemic of the conical karsts of West Cuba. (Photo: A. Borhidi)

fallaensis, *Coccothrinax yuraguana*, *C. munizii* and *C. allexandri*, as well as *Colpotherinax wrightii* with barrel-like trunks, etc. Dicotyledonous trees are several species of *Ficus* and *Zanthoxylum*, *Didymopanax morototoni*, the endemic *Megalopanax rex* and *Dendropanax cuneifolius*. Also, *Spathelia brittoni*, (Fig. 78) an endemic of mogotes and *Bombacopsis cubensis* with bottle-shaped trunks.

Rosulate microphanerophytes (McPros) Small, rosulate trees between 1 and 8 m in height. Their number is 75, 1% of the flora. Some representatives of this group, the so-called small or dwarf 'savanna palms', are actually found in sclerophyllous shrublands and scrub vegetation and karstic woods. 65 (83%) of them are endemics. In particular, Oriente (28), Las Villas (6) and eastern Cuba (9) are rich in endemic small palms. The 1–2 m tall dwarf palms growing on serpentine in Camagüey are notable (4 species). A further 5 species are in common in the Antilles, another 5 in the Caribbean region. Dicotyledonous trees are the species of *Comocladia*, *Plumeria* and *Spathelia*, and the Neotropical *Carica papaya*. Of the monocotyledonous species the relict *Dracaena cubensis*, *Yucca aloifolia* and fan palms, e.g., *Copernicia cowellii*, *C. curtissii*, *C. macroglossa*, *C. yarey*, *Coccothrinax miraguama*, *C. pseudorigida*, *C. hiorami*, *C. garciana*, etc., belong to this category. An ancient gymnospermous relict, *Microcycas calocoma* is also to be included here.

Woody epiphytes (EP) Plants with ligneous stalks living on trees. 53 species (0.8%). A common life-form in hygrophilous forests, particularly montane rainforests. Only 23 species (44%) are endemic. The number of Caribbean species is 23, most of them being Greater Antillean (15). Eight species are endemic to Oriente, six are Neotropical. The majority of these parasitic or semi-parasitic plants belong to the family Loranthaceae (*Dendropemon*, *Dendrophthora*, *Phoradendron*). *Hillia parasitica* and *Psychotria nutans* from the Rubiaceae are also to be mentioned.

Woody lianes (LP) their number is 209, 3.4% of the flora. These are present especially in semi-deciduous forests with relatively open canopy layer, karstic woods and evergreen shrub woods and also in montane rainforests. Only 80 species (38% of this category) are endemic, most of them in the highlands of Oriente (46). The distribution of many species is Neotropical (38), Greater Antillean (24) and Caribbean (12). Usually entire genera, such as the endemic *Lescaillea*, *Platygyne*, *Feddea* and *Harnackia*, and also *Serjania*, *Cissus*, *Bauhinia*, *Marcgravia* and *Triopteris* belong to this life-form category. Spiniferous lianes are *Caesalpinia bonduc* and *C. crista*, and succulent cacti, as *Hylocereus undatus* and *Selenicereus grandiflorus*. The graminoid lianes of montane rainforests and mossy forests (e.g., *Chusquea abietifolia*) may be also included.

Succulent phanerophytes (SP) Plants with succulent trunks and height up to 15 m 68 species (1.1%). These species are found in the shrub vegetation of semi-deserts, and in a lower number in scrubs, shrub woods, deciduous and semi-deciduous forest communities. 55% of them are endemic (38 species), most of those in Oriente (13). Many introduced Neotropical species (8). Seven species are Greater Antillean. Several cacti belong to this group that are either arborescent, such as *Dendrocereus nudiflorus* and *Consolea macracantha*, or columnar, for example, *Ritterocereus*, *Pilosocereus* and *Harrisia*, etc. The *Agave* species may also be assigned to this category.

Arborescent forbs and grasses (GrP) Mostly tall species of grasses and bananas. Their number is only 22, 0.4% of the flora. Most of them are introduced from the Old World and established, e.g., *Bambusa vulgaris*. Further representatives of this life-form group are the Neotropical species of swamps (6), e.g., *Gynerium sagittatum*. *Heliconia caribaea*, a relative to bananas characteristic of submontane rainforests, is also noted.

16.4.2 The pachycauly in Cuba

Despite the problems discussed earlier in 16.2/c, the role of pachycaul elements (Corner 1964) will be dealt with. Corner showed that these are archaic elements in the development of flora, having a potentially significant role in the ancient floras of tropical islands, and also in the isolated tropical highlands, as pointed out by Mabberley (1975a, b) and Pócs (1976a, b) as well. In Cuba, pachycauls are found especially among small trees and shrubs, particularly in genera *Senecio*, *Gesneria*, *Rhytidophyllum*, *Tabebuia*, *Plumeria* and *Coccoloba*. The number of pachycaul elements recognized so far in Cuba is 327 (5.3% of the flora), including trunk succulents. 79% (259 species) of them are endemics. This group is represented in Cuba partly by very old relict elements (*Microcycas*, *Dracaena cubensis*), partly by species of highly specialized but still very adaptable genera at the highest evolutionary level (*Tabebuia*, *Gesneria*). The percentage distribution of pachycauls in the chorological categories is shown in Table 18.

Table 18 Percentage distribution of pachycauls in the distribution categories

Endemic species	No. of species	%
Pinar del Río	26	8.0
Pinar del Río + Isla de Pinos	4	1.2
Western Cuba	34	10.4
Las Villas	17	5.2
Eastern Cuba	22	6.7
Oriente	134	41.0
Cuba	22	6.7
Total:	259	79.2
Non-endemic species		
Greater Antillean	18	5.5
Antillean	7	2.1
Cuban – Bahamean	3	0.9
Antillean – Bahamean	4	1.2
Northern Caribbean	9	2.8
Southern Caribbean	3	0.9
Caribbean	5	1.5
Neotropical	7	2.1
Adventive	12	3.8
Total:	68	20.8

16.4.3 Non-woody plants

The different types of subshrubs and herbs are represented by 2882 species accounting for 46.7% of the flora.

Chamaephytes (Ch) Subshrubs. 230 species (3.7%). Plants present particularly in pine forests, montane and elfin thickets, rocky forests and serpentine shrublands. 57% (132) species are endemic, most of them to Oriente (61) and to the pine forest belts of Pinar del Rio and Isla de Pinos (36). Many species are Neotropical (21) and Greater Antillean (22). Several species of *Gesneria*, *Vernonia*, *Hypericum* and *Phyllanthus*, and *Phania cajalbanica*, *Croton nummulariifolius* and *Evolvulus arbuscula* belong to this group.

Hemicryptophytes (H) Perennial herbs with buds at the soil surface, 1251 species, 20.3% of the flora. Very common life-form, mainly in pine forests and woodlands, xerophilous forests, swampy and boggy meadows, natural and secondary savannas. Only 30.5% (389 species) are endemic, mostly in the coniferous zone of Oriente (130), Pinar del Rio and Isla de Pinos (123). Other common flora elements are: Neotropical (233), Greater Antillean and Antillean (116) and the species of the steppe zone of the southern United States (116). The number of introduced species of various origin (85) and that of the extratropical species (55) are also relatively high. The families Gramineae and Cyperaceae are to be mentioned with the largest genera being *Aristida*, *Andropogon*, *Paspalum*, *Panicum*, *Cyperus* and *Rhynchospora*. Of the dicotyledonous plants the endemic *Heptanthus* and the species of *Stenandrium*, *Justicia* and *Hyptis* belong to this group.

Geophytes (G) Perennial plants with buds that are buried in the soil during the dormant period. 168 species (2.7%). Their role in vegetation is negligible, they occur mainly in the herb layer of rainforests. Only 32% of them are endemic, especially to Oriente (20) and to the entire country (10). The number of Neotropical species (27), including 13 species with disjunct geographical distribution, and of the Greater Antillean-Antillean (22), Caribbean (18) and Pan-tropical (9) species is surprisingly large. Most of the geophytes are terrestrial orchids or belong to the family Amaryllidaceae, for example, species of *Crinum*, *Hymenocallis*, *Habenaria*, *Spiranthes*, *Ponthieva* and *Corymborchis*, *Phaius tankervillae*, etc.

Helo-hydatophytes (HH) Water and swamp perennials with reproductive organs either below the water surface or in the mud, 199 species (3.2% of the flora). The percentage of endemics is just 18% (35 species), many of them (27) endemic to western Cuba. Most species of this category are Neotropical (50), extratropical American (42), Pan-tropical (12), cosmopolitan (11) or originated from the southern United States (28). These are floating freshwater weeds (*Eichhornia azurea*, *Utricularia*, sp.), submerged rooted pondweeds (*Potamogeton* sp. *Vallisneria neotropicalis*). Others have emerged leaves (*Nymphaea ampla*, *Nelumbo lutea*, *Nymphoides grayanum*). *Thalassia testudinum* is a submerged saltwater weed

Therophytes (Th) Annuals. 370 species (6.0%). These are characteristic of sandy beaches, dry, loose soils and degraded habitats. The geographic distribution of numerous therophytes is Neotropical (78). Many introduced (78), Pan-tropical (46), Caribbean (40) and Greater Antillean (16) species. The proportion of

endemics is just 15% (56), most of those from the coniferous forests in western Cuba (20). Many species of *Eragrostis*, *Paspalum*, *Pilea*, *Mollugo*, *Chamaesyce* and *Polygala* and many *Compositae* sp. have this life-form.

Hemi-Therophytes (TH-H) Species exhibiting both biennial and perennial life-form represent an intermediate category. The life-form of an actual individual is determined by edaphic conditions and the intensity of anthropogenic effects. A total of 64 species (1% of the flora) show such a feature. Many of them are introduced (13), Neotropical (10) and Caribbean (8). The number of endemics is relatively low (14), accounting for 22% of this life-form class. Some characteristic examples are *Ageratum maritimum*, *Gnaphalium attenuatum*, *Epaltes matfeldii*, *Pectis leptoccephala*, *Sida rhombifolia*, *S. linifolia*, *Raphanus raphanistrum* and *Coronopus didymus*.

Herb lianes (LH) This group includes herbaceous lianes of either hemicryptophyte, geophyte or therophyte character. 329 taxa (5.4% of the flora). These plants are usually present in the communities of open, sunny and dry habitats including coastal and serpentine scrubs, shrublands and karstic woods. Approximately 40% of them are endemics (130 species), 48 being endemic to Oriente, 32 to the entire country and 24 to Pinar del Rio. Most of the widely distributed species are Neotropical (46), Pan-tropical (31) and Greater Antillean (28). Many paleotropical adventives. Entire genera with many species belong to this category, e.g. *Aristolochia*, *Dioscorea*, *Rajania*, *Cynanchum*, *Passiflora*, *Ipomoea*, and many species, such as *Anguria* and *Melothria*, etc.

Hygrophilous, mainly obligate epiphytic herbs (E_{G-H}). 208 taxa (3.4% of the flora). Epiphytes living on trunks and branches in the lower, shade tolerant epiphyte level of rainforests and mossy forests in high mountains. 35% (73 species) are endemics. 56 species are endemic to the mountain regions of Oriente. Other flora element types represented by numerous species are: Greater and Lesser Antillean (44), Caribbean (40) and Neotropical (30). Most representatives of this group are orchids, e.g., *Pleurothallis*, *Lepanthes*, *Maxillaria*, *Stelis*, *Epidendrum* s.l., *Polystachya*, *Dilomilis* and *Dichaea* spp.

Drought-resistant, mainly facultative epiphytic herbs (E_{ch}). 59 taxa (0.9% of the flora). These are found in the upper level of submontane rainforests, in particular, and also in seasonal-evergreen forests, semi-deciduous and deciduous forests and dry evergreen forests. These are often abundant on emergent deciduous trees. In karstic woods they also inhabit the soil and rocks. The overwhelming majority of them are widely distributed Caribbean (24), Neotropical (13), and Greater Antillean (11) species. The percentage of endemics is just 12% in this life-form category. Drought-resistant orchids, such as *Ionopsis utricularioides* and *Cattleyopsis lindenii*, and many bromelias, e.g., most *Tillandsia* spp. and *Hohenbergia penduliflora* comprise this category.

Dwarf succulents of chamaephytic character (S_{ch}). The four species belonging to this group play a negligible role in the communities. All of them are sparsely distributed in rocky forests and arid scrubs. One species, *Neobesseyia cubensis*, is endemic. The others are either Caribbean or Bahamean.

16.4.4 A simplified ecological spectrum of the flora of Cuba

Based on the life-form analysis discussed above a simple ecological spectrum may be derived by combining related categories. The resulting spectrum is compatible with the earlier analyses. A comparison of Raunkiaer's spectrum generalized for the tropics yields a remarkable similarity (Table 18) with relatively significant differences occurring only in case of hemicryptophytes and therophytes. The reason for this discrepancy is presumably that the arid habitats favourable for therophytes are limited to a very small area in Cuba whereas the coniferous forests and the occurrence of serpentine bedrocks are advantageous for hemicryptophytes. The proportion of chamaephytes is lower than usual due to the lack of an alpine zone.

Table 19 The life-form spectrum of Cuba with that of an average tropical flora

	P	Ch	H	K	Th	E
Cuba (Borhidi)	53	4	20	6	7	10
Tropical regions (Raunkiaer)	51	6	12	5	16	10

16.5 The life-form analysis of the pteridophytes of Cuba

The pteridophytes may also be included in the life-form and flora element analysis of Cuba. However, a synthetic evaluation of the pteridophytes of Cuba has not yet been published. The first relevant studies were done as a preparation for this monograph (Borhidi and Acuña 1972, unpublished). It was found that 500 species occur in this country. The life-form and distribution types of these were also analyzed with results summarized in Table 20.

16.5.1 The life-form categories for the pteridophytes of Cuba

The life-form groups recognized for the pteridophyte species of Cuba are as follows:

Phanerophytic pteridophytes (P_{pt}), tree ferns. 39 species (7.8%). This life-form type has been established for ecological and cenological reasons. The tree ferns were assigned by Ellenberg and Mueller-Dombois (1966*b*) to the group of rosulate trees together with palms on the basis of their morphological similarity. In addition to their similar appearance, however, the only "character" they share is that palms and tree ferns cannot be assigned to any of Raunkiaer's leaf-size categories (Webb 1959). My field experience in Cuba suggests that due to ecological differences palms and tree ferns should be regarded as mutually exclusive, ecologically vicarious life-form types. Tree ferns are found almost exclusively in montane rainforests and mossy forests characterized by gently humid, regulated climate. On lowlands tree

Table 20 Life-form and chorological type analysis of Cuban pteridophytes

Life-forms	Chorological types												Total
	Endem.	G-Ant.	Ant.	N-Car.	S-Car.	Car.	Car.Amer	Neotr.	Amer.	Pan tr.	Cosmop.	Adv. Paleotr.	
Mesophanerophyte (MsPpt)	3	1	—	1	—	1	—	2	—	—	—	—	8
Microphanerophyte (McPpt)	2	4	2	2	—	1	1	2	—	—	—	—	14
Nanophanerophyte (NaPpt)	—	3	2	—	—	1	—	10	—	1	—	—	17
Chamaephyte (Ch)	3	11	5	2	1	3	—	11	1	12	4	—	57
Hemicryptophyte (H)	19	22	6	9	1	9	—	51	—	15	1	—	133
Geophyte (G)	13	19	12	8	2	6	2	48	—	15	5	1	131
Helo-hydatophyte (HH)	1	—	—	—	—	—	—	3	1	1	2	—	8
Lianes(L)	5	4	2	1	—	2	—	12	—	—	—	—	26
Epiphyte (E)	7	13	9	4	1	5	6	50	—	10	1	—	106
Total of Cuban pteridophytes	53	77	38	27	5	28	9	189	2	54	13	1	500

Life-form pattern of Cuban pteridophytes in percentages according to chorological types

Mesophanerophyte (MsPpt)	37.5	12.5	—	12.5	—	12.5	—	25.0	—	—	—	—	100%
Microphanerophyte (McPpt)	14.3	28.6	14.3	14.3	—	7.1	7.1	14.3	—	—	—	—	

Nanophanerophyte (NaPpt)	—	17.6	11.8	—	—	5.9	—	58.8	—	5.9	—	—	100%
Chamaephyte (Ch)	5.3	19.3	8.8	3.5	1.7	5.3	—	19.3	1.7	21.1	7.0	—	100%
Hemicryptophyte (H)	14.3	16.5	4.5	6.8	0.8	6.8	—	38.3	—	11.3	0.7	—	100%
Geophyte (G)	9.9	14.5	9.2	6.1	1.5	4.6	1.5	36.7	—	11.4	3.8	0.8	100%
Helo-hydatorphyte (HH)	12.5	—	—	—	—	—	—	37.5	12.5	12.5	25.0	—	100%
Lianes (L)	19.2	15.4	7.7	3.8	—	7.7	—	46.2	—	—	—	—	100%
Epiphyte (E)	6.6	12.3	8.5	3.8	0.9	4.7	5.7	47.2	—	9.4	0.9	—	100%
Total of Cuban pteridophytes	10.6	15.4	7.6	5.4	1.0	5.6	1.8	37.8	0.4	10.8	2.6	0.2	100%

Chorological patterns of Cuban pteridophytes in percentages according to the life-form categories

Mesophanerophyte (MsPpt)	5.7	1.3	—	3.7	—	3.6	—	1.1	—	—	—	—	1.6%
Microphanerophyte (McPpt)	3.8	5.2	5.3	7.4	—	3.6	11.1	1.1	—	—	—	—	2.8%
Nanophanerophyte (NaPpt)	—	3.9	5.3	—	—	3.6	—	5.3	—	1.8	—	—	3.4%
Chamaephyte (Ch)	5.7	14.3	13.2	7.4	20.0	10.7	—	5.8	50.0	22.3	30.7	—	11.4%
Hemicryptophyte (H)	35.8	28.5	18.5	33.4	20.0	32.1	—	27.0	—	27.8	7.7	—	26.6%
Geophyte (G)	24.5	24.7	31.5	29.6	40.0	21.4	22.2	25.4	—	27.8	38.5	100.0	26.2%
Helo-hydatorphyte (HH)	1.9	—	—	—	—	—	—	1.6	50.0	1.8	15.4	—	1.6%
Lianes (L)	9.4	5.2	5.3	3.7	—	7.1	—	6.3	—	—	—	—	5.2%
Epiphyte (E)	13.2	16.9	23.6	14.8	20.0	17.9	66.7	26.4	—	18.5	7.7	—	21.2%
	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0%

ferns grow only in gallery forests along water courses. Most tree ferns are widely distributed Neotropical (14, 36%) and relatively narrowly distributed Greater Antillean (8, 21%) elements. The number of endemics is surprisingly high (5, 13%) as a result of the early isolation of high mountains. This group is subdivided as follows:

Mesophanerophytic pteridophytes (MsP_{pt}). Tall tree ferns (5–12 m), e.g. *Alsophila aspera*, *Cyathea araneosa*, *C. arborea*, *Hemitelia horrida*, and *Lophosoria quadripinnata*.

Microphanerophytic pteridophytes (McP_{pt}). Small tree ferns (2–5 m). Examples are *Alsophila aquilina* and *Cyathea tenera* etc.

Nanophanerophytic pteridophytes (NaP_{pt}). Dwarf tree ferns (< 2 m), such as the *Diplazium* spp.

Chamaephytic ferns (Ch). 57 taxa (11.4%). They are present in montane rainforests and mossy forests, elfin thickets coniferous forests and occasionally in semi-arid habitats on rocks. Some species, for example *Gleichenia bifida*, may occur in great abundance forming a secondary community after destruction of the original vegetation. Most of them are Pan-tropical (12, 21%), Neotropical (11, 29%), Greater Antillean (11, 19%) and Antillean (5, 9%). Only three endemics occur (5%). Almost all species of *Lycopodium*, *Selaginella*, *Marattia* and *Pteris* belong to this life-form class.

Hemicryptophytes (H) Perennial ferns with buds above the soil surface. 133 species (26.6%). They are especially common in the herb layer of rainforests, seasonal-evergreen forests, karstic forests and coniferous forests. Some species appear in very dry rocky habitats. The most common type of geographical distribution is Neotropical (51, 38%), Greater Antillean (22, 17%) and Pan-tropical (15, 11%). This group includes a remarkably large number of endemics (19, 14%), most of them living on serpentine and laterite, such as the *Anemia* and *Polystichum* spp. In addition, most species of *Asplenium*, *Blechnum*, *Bolbitis*, *Lindsaya*, *Nephrolepis*, *Pityrogramma*, and *Tectaria* are of this life-form type.

Geophytes (G) Perennial ferns with rhizomes. 131 taxa, 26.2%. In ecological requirements these are similar to the hemi-cryptophytes. However, geophytes are more abundant in humid, shade habitats on rocks. Where humidity is high enough some species, e.g. *Polypodium astrolepis*, *P. capillare*, *P. lycopodioides*, *P. polypodioides*, etc. become facultative epiphytes. Most of the geophytic ferns are Neotropical (48, 37%), Greater Antillean (13, 12%), Pan-tropical (15, 11%) and Antillean (12, 9%). The number of endemics is also high (13, 10%). This category includes almost all species of *Botrychium*, *Ophioglossum*, *Adiantum*, *Osmunda*, *Polypodium* and *Thelypteris* occurring in Cuba.

Helo-hydatoxytes (HH) Aquatic and uliginal ferns. 8 species, 1.6%. These are categorized as follows: floating freshwater ferns (*Azolla caroliniana*, *Salvinia auriculata*, *S. natans*), rooted aquatic ferns (*Marsilia polycarpa*) and saltwater ferns of mangrove forests (*Acrostychnum aureum*, *A. danaifolium*). All aquatic ferns are widely distributed being either Neotropical (3), cosmopolitan (2), Pan-tropical (1) or American (1). The only exception is the endemic *Isoetes cubana*.

Lianes (L) 26 species (5.2%). This life-form occurs in fairly diverse habitats including montane rainforests and mossy forests (*Dennstaedtia* and *Gleichenia*)

where lianes are most abundant, and also in coniferous forests (*Odontosoria*) and dry shrublands (*Lygodium cubense*). Having very strong stems, they are most similar to the graminoid lianes. Although their stems are not woody, they should be assigned to the phanerophytic lianes as in Table 24 (see Suppl. 7). Twelve species are Neotropical (46%). Most of the others are endemic (5, 19%) and Greater Antillean (4, 15%).

Epiphytic ferns (E) A remarkably large number of species (106, 21.2%) are included. These are abundant especially in submontane and montane rainforests, mossy forests, karstic forests and in the elfin thickets. The majority of species are Neotropical (50, 47%). The others are Pan-tropical (9, 8%), Greater Antillean (13, 12%) and Antillean (9, 8%). Only a few endemics occur (7, 7%). Most epiphytic ferns belong to the genera *Elaphoglossum*, *Hymenophyllum sensu lato* and *Trichomanes sensu lato*, and also to *Polypodium*, such as *P. duale*. *Lycopodium uniforme*, *Peltapteris peltata* and *Rhipidopteris peltata* are noted representatives of other genera.

16.5.2 A classification of epiphytic pteridophytes

For practical purposes, two types of epiphytic ferns can be distinguished. These are:

Membranous-leaved epiphytic pteridophytes (mE_{pt}) Film-ferns of the family Hymenophyllaceae. These are particularly characteristic of rainforests and mossy forests. Pócs (1976) observed a definite relationship between humidity and the number of species from this family in the rainforests of the Uluguru Mountains in East Africa.

Non-membranous epiphytic pteridophytes (nE_{pt}). Club mosses (*Lycopodium*), spike mosses (*Selaginella*) and ferns belonging to various families. These are less sensitive to humidity. Due to their hard or coriaceous leaves some species are explicitly drought-resistant.

Table 21 Geographical distribution of membranous-leaved (m E_{pt}) and non membranous-leaved (n E_{pt}) pteridophytes of Cuba

Flora element	m E _{pt} %		n E _{pt} %	
Endemic to Cuba	1	2.3	6	9.7
Greater Antille	1	2.3	12	19.4
The Antille	4	9.1	5	8.1
Northern Caribbean	1	2.3	3	4.8
Southern Caribbean	1	2.3		
Pan-Caribbean	2	4.5	3	4.8
Central American	3	6.8	3	4.8
Neotropical	23	52.2	27	43.6
Pan-tropical	7	15.9	3	4.8
Cosmopolitan	1	2.3		
Total:	44	100.0	62	100.0

The geographical distribution of the above groups is shown in Table 21. It is seen that Hypenophyllaceae usually have larger geographic range than the other epiphytic pteridophytes.

16.5.3 The ecological spectrum of the pteridophytes of Cuba

Table 22 shows the ecological spectrum for the pteridophytes of Cuba obtained by combining related life-form categories. This spectrum corresponds to a typical tropical flora. The high percentage of phanerophytic and epiphytic species indicates the abundance of humid habitats in Cuba.

Table 22 The ecological spectrum of the pteridophytes of Cuba

	P	Ch	H	K	E	L
Cuban pteridophytes	7.8	11.4	26.6	27.8	21.2	5.2

16.6 Growth types and leaf-size classes

In addition to the analysis of life-forms, the growth types of plants are also worth examining. In tropical vegetation surveys the different crown types, leaf-size classes, trunk and bark forms of trees, and also the presence or absence of spinose structures are commonly used for forest typification. In the present study only leaf-size classes were analyzed. These classes proved to be meaningful in reflecting the ecological conditions of various habitats and communities.

16.6.1 Leaf-size classes

The different leaf-size classes were constructed following Raunkiaer (1908), Richards, Tansley and Watt (1940) and Webb (1959). These categories, together with their serial numbers to be used in the sequel are listed in Table 23.

Table 23 The leaf-size categories

Category	Abbreviation	Area cm ²
1 megaphyll	mg	>1640.20
2 macrophyll	ma	182.25—1640.20
3 mesophyll	ms	45.00—182.25
4 notophyll	nt	20.25—45.00
5 microphyll	mc	2.25—20.25
6 nanophyll	na	.25—2.25
7 leptophyll	lp	<0.25
8 aphyll	ap	0

16.6.2 Some remarks on the leaf-size classes

As suggested by Webb (1959), only the leaves of phanerophytes *sensu stricto* were examined. Life-form types, such as palms, rosulate trees, tree ferns and lianes, for which the classification is ambiguous, were excluded from the analysis. In case of compound leaves the class membership was determined by the size of leaflets. The leafless trunk-succulents were assigned to the group of aphylls.

Contrary to Aubréville's (1965) opinion, the notophyll category (Webb 1959) proved to be useful especially in distinguishing among the vertical belts of rainforests and between the vicarious vegetation types of limestone and serpentine.

16.6.3. A general leaf-size index

The average leaf size, I_f , was applied to the ecological characterization of vegetation types and plant communities. This index is obtained as follows. The number of occurrences in each class is multiplied by the serial number of the corresponding class (see Table 23). The sum of these products is then divided by the total number of occurrences as shown below:

$$I_f = \frac{I_1p_1 + I_2p_2 + \dots + I_8p_8}{p_1 + p_2 + \dots + p_8} = \frac{\sum I_i p_i}{\sum p_i}$$

where p_1, p_2, \dots, p_8 indicate the number of occurrences in leaf-size classes 1, 2...8, and I_1, I_2, \dots, I_8 are the serial numbers of the corresponding classes. It was found that there is a definite relationship between climate and the I_f value for each vegetation type and community (see Chapter 17. for details).

17 Life-form affinities and the dynamics of the life-form composition along environmental gradients

17.1 Introduction

Although tropical vegetation types are commonly characterized using life-form categories, the affinity of life-forms and growth types to the different vegetation types is largely ignored in most surveys. There are no data illustrating the change of life-form and growth type spectra as influenced by vegetation changes along geographic or climatic gradients. This insufficiency may be explained as follows.

In most tropical studies no data are available on climatic or vegetation gradients, or very often on both. The lack of appropriate vegetation data is due to the fact that mapping surveys and ecological studies are usually performed independently by different research teams. While the change of vegetation types is mapped without quantitative analysis of vegetation structure, ecological studies are restricted to a

single vegetation type. Furthermore, any field work in the tropical environment presents numerous methodological problems and difficulties, making gradient analysis a troublesome task.

17.1.1 Affinity of life-form to vegetation types

Forty forest and shrubland communities and formations in Cuba (Table 24) were subjected to a comparative physiognomic and phytosociological analysis. Of the 40 vegetational noda 18 are considered to be climax, representing all climax formations of the island. (For composition of the communities see Table 25 in the Appendix)

Table 24 Major lignosa formations of Cuba

A. Western pine forests	
1.	<i>Paepalantho-Pinetum tropicalis</i> (Isla de Pinos, 11 plots) V. Samek
2.	<i>Pinetum tropicalis-caribaeae</i> (Isla de Pinos, 10 plots) V. Samek
3.	<i>Quercu sagraeanae-Pinetum</i> (Pinar del Rio, 5 plots) A. Borhidi
4.	<i>Neomazaeo-Pinetum</i> (Cajalbana, 5 plots) A. Borhidi
5.	<i>Agavo cajalbanensi-Pinetum</i> (Cajalbana, 5 plots) Borhidi, Borhidi and Muñiz
B. Eastern pine forests	
6.	<i>Anemio-Pinetum cubensis</i> (Sierra de Nipe, 10 plots) Borhidi and Muñiz
7.	<i>Rhynchosporo-Pinetum cubensis panicetosum</i> (Sierra de Nipe, 10 plots) Borhidi and Muñiz
8.	<i>Rhynchosporo-Pinetum cubensis typicum</i> (Sierra de Nipe, 10 plots) Borhidi and Muñiz
9.	<i>Agavo shaferi-Pinetum cubensis</i> (Sierra de Nipe, 5 plots) Borhidi and Muñiz
10.	<i>Rhynchosporo-Pinetum cubensis euphorbietosum</i> (Sierra de Nipe, 5 plots) Borhidi and Muñiz
11.	<i>Euphorbio helenae-Pinetum cubensis</i> (Moa: Cayo Chico, Cupeyal, Monte Libano, 5 plots) Borhidi and Muñiz
12.	<i>Shafero-Pinetum cubensis</i> (Moa: Cupeyal, 10 plots) Borhidi and Muñiz
13.	<i>Dracaeno-Pinetum cubensis</i> (Baracoa — Moa, 5 plots) Borhidi and Muñiz
C. Semi-arid montane rainforests	
14.	<i>Cyrillo nipensi-Pinetum</i> (Moa: Cupeyal, 5 plots) Borhidi and Muñiz
15.	<i>Podocarpus-Bonnetietum cubensis</i> (Moa: Cupeyal, Iberia, Jaguani, 10 plots) Borhidi and Muñiz
D. Semi-arid serpentine shrubwoods	
16.	<i>Ilici-Laplaceion moaensis</i> (Moa: Iberia, Mina Delta, Jaguani, 5 plots) Borhidi and Muñiz
17.	<i>Ariadno-Phyllanthion</i> (Moa: Playa Vaca, Yamanigüey, 5 plots) Borhidi and Muñiz
18.	<i>Spathelio-Bourrerietum</i> (Sierra de Nipe, 5 plots) Borhidi and Muñiz
E. Submontane tropical rainforests	
19.	<i>Calophyllo-Carapetum guianensis</i> (Moa: Jaguani, 5 plots) Borhidi and Muñiz
F. Moist montane rainforests	
20.	<i>Magnolio-Laplaceum angustifoliae</i> (Sierra Maestra, 10 plots) Borhidi and Muñiz, Borhidi
21.	<i>Magnolio-Cyrilletum racemiflorae</i> (Sierra de Escambray, 5 plots) Borhidi and Muñiz, Borhidi
G. Cloudforests	
22.	<i>Myrsino-Nectandretum reticularis</i> (Sierra Maestra, Turquino, 5 plots) Borhidi and Muñiz
H. Moist high mountain shrubwoods	
23.	<i>Ilici-Myricion cacuminis</i> (Sierra Maestra, Turquino, 5 plots) Borhidi and Muñiz

I. Submontane seasonal rainforests

24. *Oxandro-Dipholietum jubillae* (Sierra Maestra, 5 plots) Borhidi and Muñiz

J. Karstic forests or mogotes

25. *Coccothrinaci-Tabebuietum bibracteolatae* (Sierra Maestra, 5 plots) Borhidi and Muñiz
26. *Ceratopyxidi-Gaussietum principis* (Sierra de los Organos, 5 plots) Borhidi and Muñiz, Borhidi et Capote,
27. *Tabebuio sauvallei-Garryetum* (Sierra de Escambray, 5 plots) Borhidi and Muñiz, Borhidi

K. Semi-deciduous seasonal forests

28. *Bombacopsi-Catalpetum* (Guanahacabibes, 5 plots) Borhidi and Muñiz, Borhidi et Capote,
29. *Coccolobo diversifoliae-Burseretum* (Isla de Pinos, 5 plots) Borhidi and Muñiz
30. *Zanthoxylo-Burseretum* (Habana, Zapata, Las Villas, Camagüey, 5 plots) Borhidi and Muñiz

L. Arid lowland serpentine shrubwoods

31. *Coccothrinacio-Tabebuion lepidotae* (Campo Florido, Canasi, 5 plots) Borhidi and Muñiz, O. Muñiz, A. Borhidi
32. *Rondeletio-Guettardetum clarensis* (Las Villas, 10 plots) Borhidi and Muñiz, Borhidi
33. *Copernicio-Tabebuietum trachyphyllae* (Camagüey, 5 plots) Borhidi and Muñiz
34. *Guettardo-Jacarandion cowellii* (Holguin, 5 plots) Borhidi und Muñiz, Borhidi and Capote

M. Evergreen oakwoods

35. *Quercion sagraeanae* (Pinar del Río, 5 plots) A. Borhidi, Borhidi and Capote,

N. Swampy forests

36. *Chrysobalano-Annonion palustris* (Isla de Pinos, Zapata, 5 plots) Borhidi and Muñiz, Borhidi and Del-Risco

O. Arid evergreen forests

37. *Bursero-Lysilometum bahamensis* (Guanahacabibes, Isla de Pinos, Zapata, Cienfuegos, 5 plots) Borhidi und Muñiz, A. Borhidi,
38. *Swietenio-Metopietum brownei* (Isla de Pinos, Zapata, Cienfuegos, 5 plots) A. Borhidi, Borhidi and Muñiz,

P. Spinose evergreen limestone scrubs

39. *Pseudocarpidio-Cordion* (S. Oriente, 10 plots) Borhidi, Borhidi and Muñiz

R. Semi-desert scrubs with columnar cacti

40. *Consoleo-Ritterocereion hystricis* (S. Oriente, 10 plots) Borhidi, Borhidi and Muñiz
-

The spatial arrangement of my phytosociological plots allows for the study of actual vegetation transects both in vertical and horizontal direction. Having the bioclimatological results discussed in Part I, it was attempted to find explicit, quantitative relationships between different ecological and vegetational gradients by summarizing structural changes in an appropriate meteorological formula.

The phytosociological classification of the forty lignosa noda examined (see Chapter 23) was carried out using alternative input data sets. One of these analyses was based on the life-form structure of communities. The clustering algorithm used was the sum of squares agglomeration technique (Orlóci 1978). The classification was repeated several times using a different random selection of species in order to obtain a general view on the life-form structure of lignosa communities in Cuba.

The computations were based on the frequencies of life-form classes as input variables. The results obtained support the view by Fekete and Szujkó-Lacza (1971) that climatic conditions are clearly reflected by simple frequencies, rather than when cover or abundance is also considered. It is to be noted, however, that with the exception of marshes and coniferous forests, frequency data also indicate abundance because as the number of individuals increases the number of species usually also increases.

17.2 The affinity of life-forms to the different tropical forest communities of Cuba

The affinity of life-forms to the 40 *lignosa noda* examined is shown in Fig. 119 (see Table 25 for symbols of life-forms). Eight life form groups can be distinguished in the diagram.

a) The first group (B_2-M) contains the giant trees (A_3), macrophyll and mesophyll trees (B_2B_3) and tree-sized forbs (M), i.e., the characteristic structural elements of seasonal-evergreen forests and of the submontane rainforests with three canopy layers.

b) The second group is composed of tree ferns (N) and hygrophilous epiphytes (U). These life-forms are characteristic of montane rainforests and mossy forests. Tree ferns are scarcely found elsewhere, and the hygrophilous epiphytes are also most abundant in these formations.

c) The third group ($J-I$) includes life-forms with broad ecological tolerance. These occur in every kind of high forests, such as rainforests. The ecological optima of these life-forms are the semi-deciduous and karstic forest habitats, although they are also present to a smaller extent in all relatively arid vegetation types. The woody lianes (J), xerophilous epiphytes (X), geophytes (P), mesophyllous small trees and shrubs (D_3, E_3), tall palms (G) and the woody epiphytes (I) belong to this group.

d) The fourth group contains the ubiquitous woody life-forms. These are the notophyllous and microphyllous small trees and shrubs (D_4, D_5, E_4, E_5), very abundant in all *lignosa noda*.

e) In the fifth group the life-forms characteristic of pine forests, karstic forests and xerophilous shrublands are included. In particular, the annuals composing the herb layer (R), the perennial herbs (O), subshrubs (V), herbaceous lianes (T) and dwarf palms (H) are to be mentioned.

f) The helo-hydatophytes (Q) form the sixth group. This life-form is characteristic of swamps, gallery forests, and mangrove stands.

g) The seventh group contains trees composing seasonally dry forests. The notophyllous, microphyllous and nanophyllous tall trees and the notophyllous, microphyllous and leptophyllous microphanerophytes are dominant in the canopy layer of semi-deciduous forests, karstic forests and evergreen shrublands.

h) Finally, the eighth group includes the extremely drought-tolerant species of serpentine shrublands, thorny scrubs and semi-desert shrublands. These are nanophyllous emergents (C_6), nanophyllous and leptophyllous small trees and shrubs (D_6, D_7, E_6, E_7) and succulents (K_1, Y).

17.2.1 Conclusions

General relationships shown in Fig. 119 are as follows.

a) Rainforests are strikingly separated from all other seasonally dry vegetation types. There are eight life-form types in rainforests, that are not found in the other formations.

b) Every other life-form, except the helo-hydatophytes, is more or less abundant in all seasonally dry vegetation types, some of them in rainforests. The sequence of life-forms from left to right shows a continuously lessening affinity to rainforests.

c) Clearly, the cenological affinity between life-form classes which constitute corresponding vegetational strata is often very low, e.g., between hygrophilous epiphytes and lianes, between hygrophilous and xerophilous epiphytes, and between tree ferns and small palms, etc.

17.3 Life-form vicariancy

The vicarious life-forms and growth types may replace one another in a given layer of communities along geographic and climatic gradients. In this case, vicariancy refers to taxonomically heterogeneous groups rather than to the populations of two species. Therefore, there is an overlap between vicarious groups so that one life-form dominant in a given layer is continuously replaced by the other along the gradient.

17.3.1 Vicariancy between epiphytes and lianes

There is an obvious vicariancy between lianes and epiphytes constituting the trunk and branch layers. It was observed that lianes and xerophilous epiphytes are dominant in relatively open xeric communities with loose canopy layer. On the contrary, the hygrophilous epiphytes are dominant in more closed and more humid communities. For the comparison of the climatic conditions of communities a new index is suggested. This is Thornthwaite's humidity/aridity index (1948) modified such that PE is replaced by the mean annual temperature (T) in the denominator. The general humidity index is given by,

$$Qg_h = \frac{P - E_v}{T}$$

where P is the annual precipitation and E_v denotes the annual evaporation. The diagram in Fig. 80 shows the relationship between Qg_h and the sum of frequencies for lianes and hygrophilous epiphytes in all important climax formations and community types including semi-desert scrubs, semi-deciduous forests, rainforests, mossy forests and elfin thickets. It is seen that the rainforests and mossy forests have the most diverse trunk and branch layers. The general trend that dry climate is

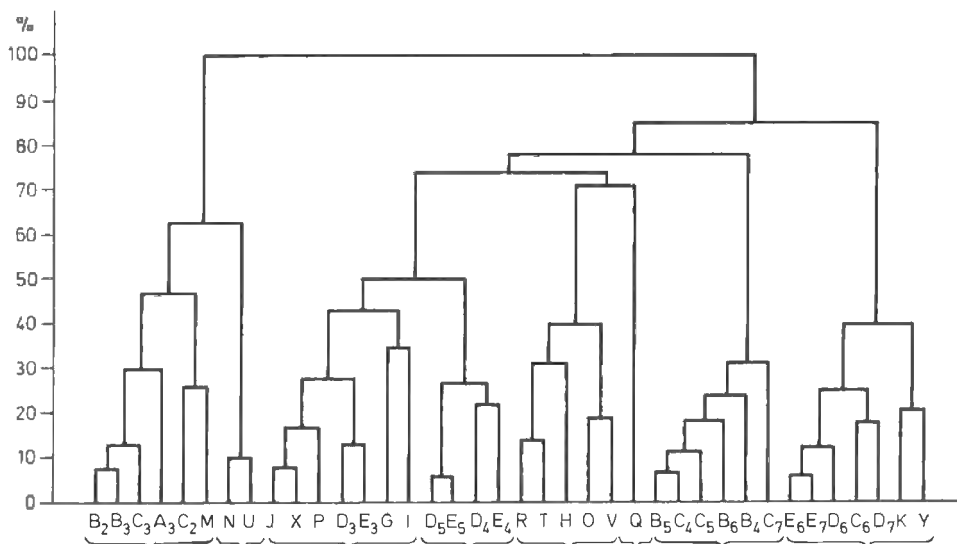


Fig. 79 The affinity of life-forms to the different *Lignosa* communities in Cuba. For abbreviations see Table 24

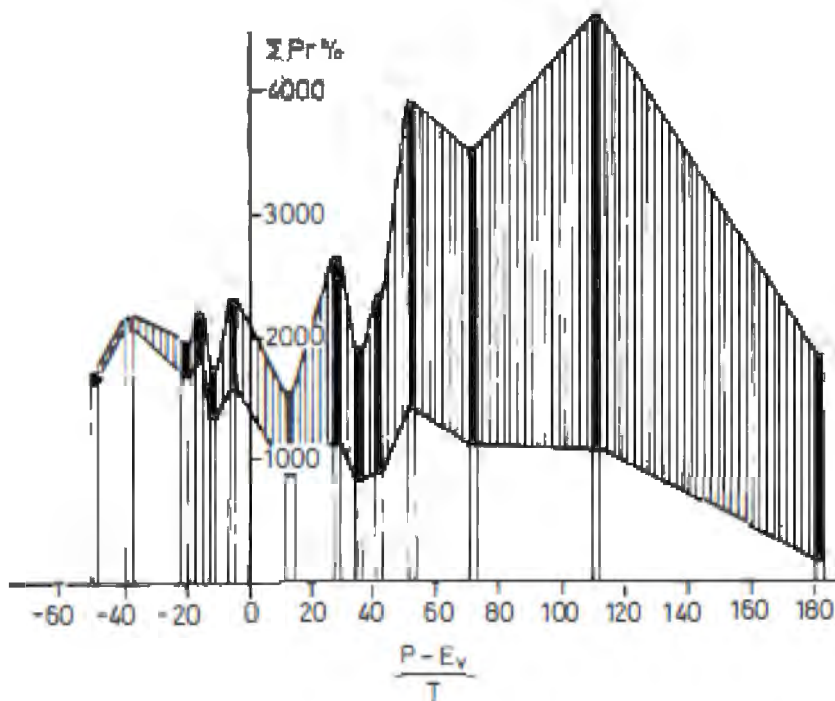


Fig. 80 The total frequency of lianes and epiphytes in the different Cuban climax plant communities, white columns: lianes, black columns: epiphytes

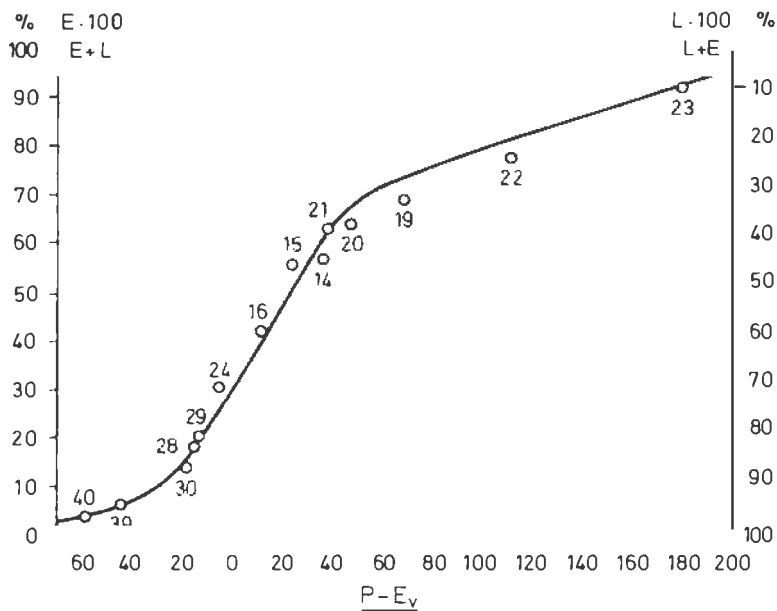


Fig. 81 Relative frequency of the lianes and epiphytes in zonal communities conditioned by humid and arid climates in Cuba. The numbers indicate the plant communities listed in Table 25

favourable for lianes and moisture is in favour of hygrophilous epiphytes may also be observed. The relationship is not best shown in this way, however. If the percentages of the two life-form classes,

$$\frac{\text{Fr.}_{\text{lianes}} \times 100}{\text{Fr.}_{\text{lianes}} + \text{Fr.}_{\text{epiph.}}} \quad \text{and} \quad \frac{\text{Fr.}_{\text{epiph.}} \times 100}{\text{Fr.}_{\text{lianes}} + \text{Fr.}_{\text{epiph.}}}$$

are taken as variables on the vertical axis, the resulting scattergram (Fig. 81.) will be easier to interpret. The shape of the curves suggests that Qg_h may be used for an adequate description of the relationships examined. The two life-forms appear to be balanced around the contact point between the seasonal-evergreen forests and semi-arid rainforests.

17.3.2 The relative distribution of xerophilous and hygrophilous epiphytes

The relationship between xerophilous and hygrophilous epiphytes was examined in a similar manner. The result (Fig. 82) resembles the one in Fig. 81 although the curve is shifted to the left. The reason for this difference is that the relative frequency of lianes, if compared to the hygrophilous epiphytes, is higher than that of the xerophilous epiphytes in almost all vegetation types studied. Exceptions are

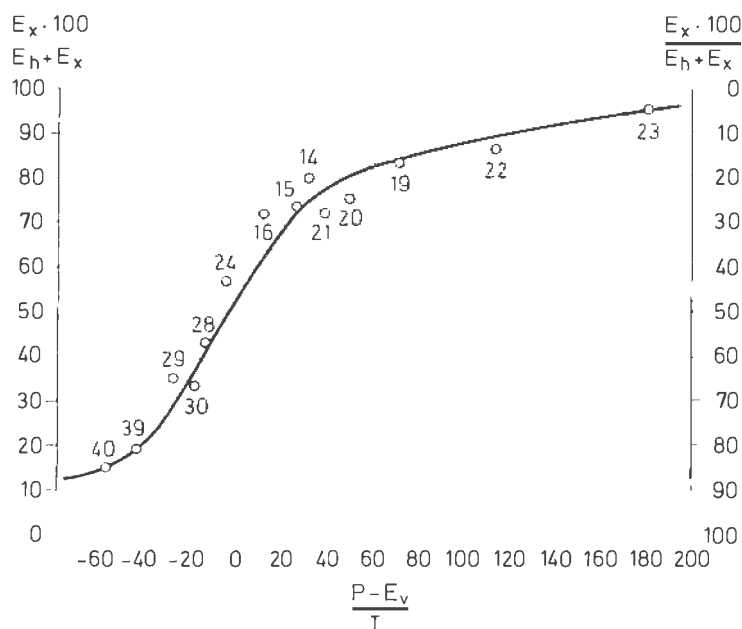


Fig. 82 The relative frequency of xerophytic (E_x) and hygrophilous epiphytes (E_h) in the different climax communities of Cuba. Numbers indicate the plant communities listed in Table 18

the karstic forests in which xerophilous epiphytes are much more frequent than lianes. Since karstic forests are predominantly edaphic communities of which the value of Q_{gh} is not characteristic, these are excluded from the comparison.

17.3.3 The vertical distribution of hemicryptophytes and chamaephytes

The influence of altitude upon the proportion of hemicryptophytes and chamaephytes in the herb layer was also examined. Raunkiaer (1908, 1934) has shown that the so-called "hemicryptophyte climate" is replaced by the "chamaephyte climate" between 2000 and 3000 m altitude in the temperate zone. The same trend may be observed in the tropical mountains, for example, in the paramos of the Andes, with a transition zone occurring between 4000 and 5000 m. It is to be noted, however, that similar trends are found in the forest belts of mountainous regions in the tropics. This is confirmed in Fig. 83 showing the percentage of chamaephytes in the forest communities of Sierra Maestra and Sierra de Moa at various altitudes. Both curves indicate a steep upward trend. It may be concluded that the percentage of chamaephytes much more rapidly increases on serpentine than on other bedrocks. This fact supports the author's view that given vegetation zones and the montane and subalpine elements occur at a much lower altitude on serpentine than on other geological formations.

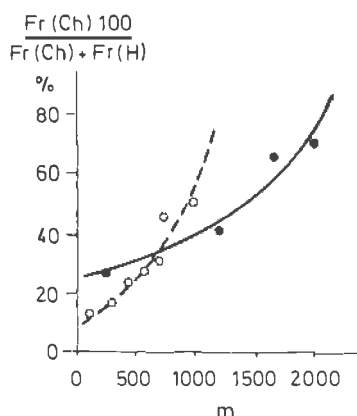


Fig. 83 The relative frequency of chamaeophytes (Ch) and hemicryptophytes (H) in the zonal plant communities conditioned by a vertical temperature pattern on limestone — and on serpentine - - -

17.4 Growth types and climatic gradients

The relationship between growth types and each climatic gradient was also studied in a manner already described. Clear-cut results were obtained with respect to the relationship between temperature and humidity gradients and the relative frequency of spinose elements and ecological leaf-size classes (see 18.6.1.).

17.4.1 Leaf-size index as an ecological indicator

The average leaf-size index, I_f , was calculated for the formations and community types listed in Table 26. It was found that the value of I_f with some fluctuations is characteristic of the actual vegetation type and also of its ecological conditions, especially moisture (Table 26). 15 climax vegetation types, 9 on limestone and 6 on serpentine, were selected and the I_f values were contrasted with some simple climatic gradients.

17.4.2 Leaf-size index and humidity

Upon examining the relationships between annual precipitation and I_f (Fig. 84), the following statements can be made:

- There is a linear relationship between annual precipitation and I_f for the climax types of both bedrocks.
- Climax noda tend to become more xeromorph on serpentine than on limestone.

Supposing that the annual precipitation in a limestone and a serpentine habitat is the same, the latter will appear more arid as if the annual precipitation were

Table 26 Leaf-size index values of the main Cuban lignosa-communities

Communitites	Leaf-size category					Frequencies			1—8	Leaf index
	1 mg	2 ma	3 me	4 no	5 mi	6 na	7 lp	8 ap		
1. <i>Paepalantho-Pinetum</i>			8	27	51	8			94	4.63
2. <i>Pinetum tropicalis-caribaeae</i>		3	20	22	47	12			104	4.43
3. <i>Quercu sagraeanae-Pinetum</i>		3	55	83	102	22			265	4.32
4. <i>Neomazaeo-Pinetum</i>		3	31	82	89	38		3	246	4.57
5. <i>Agavo cajalbanensi-Pinetum</i>		3	23	50	88	79	40	13	296	5.31
6. <i>Anemio-Pinetum cubensis</i>	3		12	47	121	24	4		211	4.76
7. <i>Rhynchosporo-Pinetum panictosun</i>	4	4	12	17	80	18	8		143	4.76
8. <i>Rhynchosporo-Pinetum typicum</i>				24	61	15			100	4.91
9. <i>Agavo shaferi-Pinetum</i>			10	20	165	43	10	10	258	5.21
10. <i>Rhynchosporo-Pinetum euphorbietosun</i>			4	22	104	30			160	5.00
11. <i>Euphorbio helenae-Pinetum</i>	3		33	42	248	111	5	3	445	5.02
12. <i>Shafero-Pinetum cubensis</i>	9		34	75	239	48			405	4.68
13. <i>Dracaeno-Pinetum cubensis</i>			22	64	306	64	14		470	4.97
14. <i>Cyrilloni-pensi-Pinetum</i>	20	10	94	103	132	60	6		425	4.23
15. <i>Podocarpus-Bonnetietum</i>	13	20	78	208	243	55	12		629	4.37
16. <i>Ilici-Laplaceionmoaensis</i>	16		32	136	346	94	26		650	4.82
17. <i>Ariadno-Phyllanthion</i>			26	80	296	140	30		572	5.12
18. <i>Spathelio-Bourrierietum</i>			32	46	428	142	28		676	5.13
19. <i>Calophyllo-Carapetum</i>	38	48	196	124	94	8			508	3.42
20. <i>Magnolio-Laplaceetum</i>	64	11	77	173	234	22			581	3.98
21. <i>Magnolio-Cyrilletum</i>	55	16	114	134	90	10			419	3.52
22. <i>Myrsino-Nectandretum</i>	64		18	118	254	46			500	4.27
23. <i>Ilici-Myricion cacuminis</i>	4		4	44	196	54	10	10	322	5.11
24. <i>Oxandro-Dipholietum jubillae</i>	4	24	164	188	208	6			594	3.99
25. <i>Coccothrinaci-Tabebuietum</i>		6	10	140	364	52	24	24	650	4.68
26. <i>Ceratopyxideto-Gaussietum</i>			74	82	230	44	4	26	460	4.77
27. <i>Tabebuio-Garryetum</i>		4	66	176	254	64	4	16	584	4.66
28. <i>Bombacopsi-Catallpetum</i>		10	102	254	442	64	16	4	892	4.57
29. <i>Coccolobeto-Burseretum</i>		10	106	284	452	60	14		926	4.53
30. <i>Zanthoxylo-Burseretum</i>	4	10	86	286	370	40	8	4	808	4.46
31. <i>Coccothrinaci-Tabebuion lepidotae</i>			20	36	242	138	66	12	514	5.45
32. <i>Rondeletio-Guettardetum</i>			36	54	220	172	76	16	574	5.43
33. <i>Copernicio shaferi-Tabebuietum</i>			30	48	204	198	80	4	564	5.46
34. <i>Zanthoxylo-Jacarandion cowellii</i>			22	54	244	204	106	8	638	5.54
35. <i>Quercion sagraeanae</i>	6	8	116	168	262	34		4	598	4.33
36. <i>Chrysobalano-Annonion palustris</i>			34	96	98	12	4		244	4.41
37. <i>Bursero-Lysilometum bahamensis</i>		6	48	176	308	66	16	10	630	4.74
38. <i>Swietenio-Metopietum brownei</i>			78	168	454	110	48	24	882	4.95
39. <i>Pseudocarpidio-Cordion</i>			12	96	399	207	109	18	841	5.46
40. <i>Consoleo-Ritterocereion</i>			8	80	387	283	126	68	952	5.68

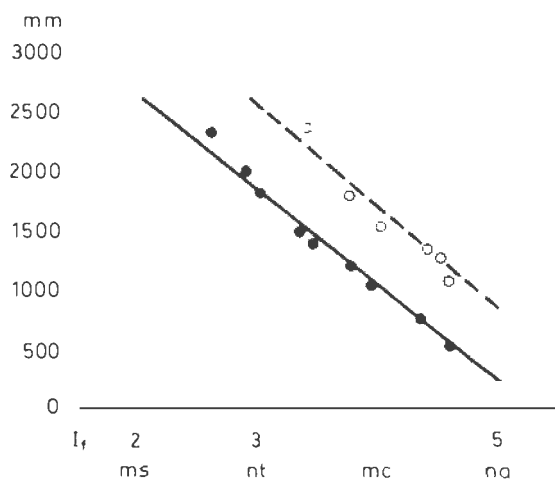


Fig. 84 The general leaf-size index (I_f) of different zonal plant communities in relation to the mean annual precipitation on limestone and on serpentine — — — — (Abbr. Table 23)

500—600 mm less than in the first. This is in part due to the unsatisfactory water balance of soils derived from serpentine: poor water permeability of upper strata, significant draining on the surface and strong desiccation through the capillaries. In addition, many physiological problems in plants are caused by abnormalities in the chemical composition of the soils, such as P shortage and too high magnesium and heavy metal concentrations. Thus, considering its structure, xeromorph appearance and the distribution of leaf-size classes, a given vegetation type on serpentine corresponds to a community of limestone habitats with 500—600 mm less annual precipitation.

With respect to the linear relationship mentioned it should be pointed out that the flora of Cuba has become highly specialized in xeromorph and sclerophyllous elements. The plants have become adapted to the dry climate using similar strategies in almost all vegetation types throughout the island.

- It may be assumed that the above relationship is not applicable to floras in which other adaptive mechanisms, e.g. abscission of leaves, are predominant.

17.4.3 Leaf-size index and temperature

Figure 85 shows the relationship between I_f for montane vegetation zones and the change of temperature and altitude. A serpentine mountain (Moa and Nipe) and an area with other bedrock types (Sierra Maestra) are contrasted. It can be seen that:

- a) Temperature and precipitation have similar effects on the average leaf-size index. Microphylls become dominant as average temperature or total precipitation decreases. In other words, during the development of microphyllous vegetation types the alteration climatic factors will lead to a similar modification of leaf-size.

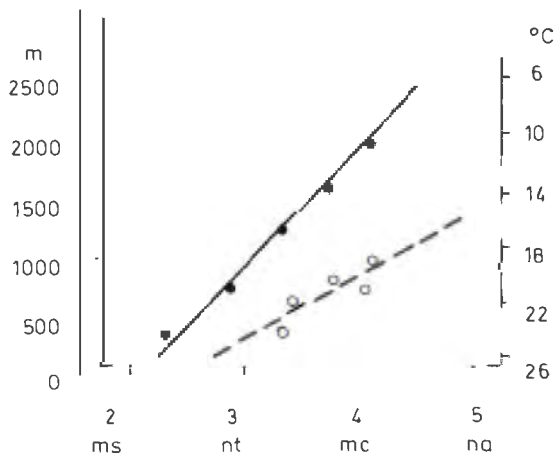


Fig. 85 The general leaf-size index (I_l) of different zonal forest communities in relation to the vertical temperature gradient on granodiorite and on serpentine — — — — (Abbr. Table 23)

b) The I_l values for the climax noda on both serpentine and other bedrocks linearly decreases as altitude increases or the annual mean temperature decreases, indicating the increasing dominance of nanophylls.

c) There is a remarkable difference between serpentine and all other rocks in the average leaf-size index for climax communities. In serpentine mountains a given leaf-size index may be observed at half the altitude where the same value is regularly indicated on other parent rocks. It means that the rate at which microphyllous vegetation develops along the altitude gradient is twice as high on serpentine than elsewhere.

d) As a consequence of this difference, a given vegetation type or belt occurs on serpentine at about half the altitude where a similar, structurally and physiognomically analogous vegetation is found in other regions.

17.5 “Thorn-index” as an ecological indicator

The above method was also applied to examine the frequency of spinous taxa, expressed by the “thorn-index”, I_s , given below:

$$I_s = \frac{F_{\text{spin}} \times 100}{F}$$

where F_{spin} is the frequency of spinous taxa (each indicated by an ! in the phytosociological table), and F is the sum of all frequency values in the community.

17.5.1 The application of thorn-index to the analysis of lignosa communities

I_s was calculated for each of the 40 lignosa nodes of Table 24. The results suggest that the actual values of I_s are characteristic of the communities. I_s gives valuable information about the water balance and water utilization of communities occurring in regions with similar flora history (e.g. a mountain or an island) or within a climatic zone, and the values may serve as a basis for ranking (Table 26).

17.5.2 Thorn index and humidity/aridity

Figure 86 shows the change of I_s as a function of annual precipitation in 16 climax lignosa nodes (7 on serpentine and 9 on limestone). It is demonstrated that:

a) There is a non-linear, inverse ratio between I_s and precipitation in the vegetation of both rock types.

b) The increased xeromorph character of the vegetation on serpentine is reflected by the frequency of spinous plants: at similar amount and distribution of precipitation many more spinous elements occur on serpentine than on other parent material (i.e., I_s is higher in the first case). As aridity increases the difference between the I_s scores for limestone and serpentine also increases.

c) The two curves converge and both approach the Y-axis at an annual precipitation about 3000 mm. In lowlands and hilly regions only such a wet climate can prevent spinous plants from growing in the vegetation of both parent rock types. At lower annual precipitation the two curves continuously diverge. As precipitation decreases the "physiological aridity" of serpentine habitats more rapidly increases than that of the limestone habitats with similar annual precipitation. The difference arising from this "physiological aridity" is equivalent to a

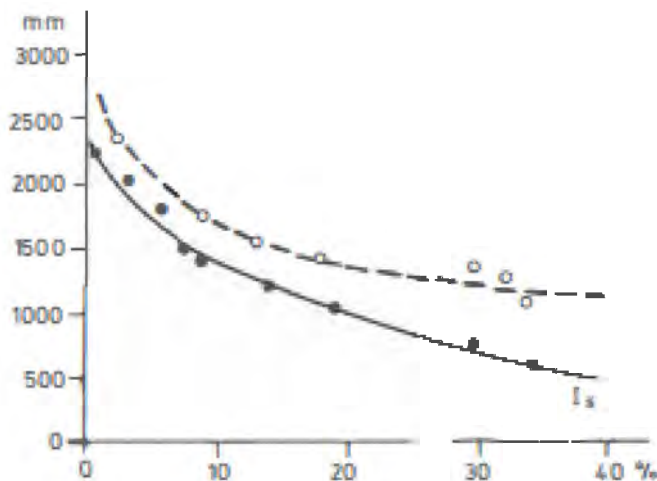


Fig. 86 The general "thorn index" (I_s) of the zonal plant communities in relation to the mean annual precipitation on limestone and on serpentine — — — —

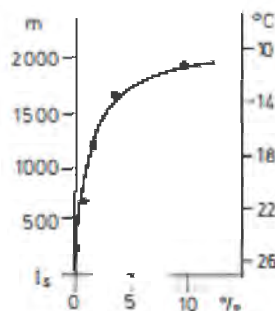


Fig. 87 The general spinosity index (I_s) of zonal plant communities of Cuba in relation to the vertical temperature gradient in an andesite mountain

shortage of 300 mm precipitation at 1500–2500 mm/year, and 400–500 mm if the annual precipitation is less than 1500 mm. This statement is in good agreement with those concluded from a comparative evaluation of the structure of vegetation types (17.2)

17.5.3 Thorn-index and temperature

The change of I_s as a function of temperature is shown in Fig. 87. Satisfactory data were obtained only in case of Sierra Maestra. A logarithmic relationship is indicated between I_s and altitude, whereas an inverse proportion between I_s and the annual mean temperature. The curve demonstrates that the relative frequency of spinous elements slowly and evenly changes up to the mossy forest belt and then, over the condensation level, more rapidly increases. The cooler temperature and stronger winds, as a result of the increased altitude, induce a reduction of assimilating surface, rather than the development of thorny structures. Whereas I_t was almost equally influenced by the decrease of precipitation and temperature (Figs 84–85), the distribution of I_s is much more affected by precipitation than by vertical temperature gradients.

18 Phytogeographical characterization of the flora of Cuba

18.1 A short historical review

Questions related to the origin of the flora and its phytogeographic characterization have been raised in several papers (Carabia 1945, Alain 1953, de Ponce-León 1955) published before completing 'The Flora of Cuba'. These papers, however,

contain many unreliable statements and lack precision. The only thorough relevant study is attributable to Alain (1958). Knowing the five volumes of 'The Flora of Cuba', Alain proposed the first phytogeographic categorization of species. Based on these findings many suggestions were made regarding the origin and the history of the flora of Cuba.

18.1.1 Alain's phytogeographic system

Alain (1958) proposed the use of seven distribution categories:

- Endemic species (no further refinement within this category)
- Antillean species: a. Greater Antillean, b. Antillean
- North American species, including three ecological groups: coastal, freshwater and savanna plants
- Central American and Mexican species
- South American species
- American species
- Cosmopolitan species.

18.1.2 Klotz's phytogeographic elements

Howard (1975) distinguishes among eleven geographic distribution types in the flora of Lesser Antilles. An improved version of Howard's chorographical system is outlined by Klotz (1978) who also considers both geographical and ecological aspects. However, these two aspects are confused by Klotz, and the system is too complex as the number of classes is unnecessarily large. Some details of this system are still undeveloped. For these reasons, Klotz's distribution categories will not be used in the present study. Instead, a similar but simpler phytogeographic classification developed by the author in 1973 is applied to the flora of Cuba. This system is introduced in the subsequent paragraphs.

18.1.3 A new distribution system

32 distribution types, partitioned into six groups, are distinguished. The entire known flora, including 6375 flowering plant taxa and 500 pteridophytes, is considered in the analysis. The distribution of phytogeographical types according to life-forms is also evaluated to reveal the role of each type in the vegetation. (Tables 27 and 28)

18.1.4 Native vs recent flora

The adventive species were excluded from Alain's quantitative studies, his conclusions refer only to the native (original) flora of the island. In order to compare his results with the findings of the present survey, the phytogeographical

Table 27 The phytogeographic analysis of the flora

Flora elements	Life-forms	Mg— MsP	Mc— MsP	McP	N— McP	NP	Ms P _{ms}	Mc P _{ms}	EP	LP
<i>Group of endemic species</i>										
Pinar del Río endemics		177	16	58	5	103	10	3	5	7
Isla de Pinos endemics		1	2	4	—	9	—	1	—	2
Endemics to both Pinar del Río and Isla de Pinos		3	1	13	13	11	1	1	—	—
Species endemic to western Cuba		5	19	26	11	39	8	3	—	1
Habana endemics		1	—	7	1	11	—	1	—	—
Mataanzas endemics		—	1	5	1	5	1	3	2	—
Las Villas endemics		5	9	30	—	40	4	6	1	2
Camagüey endemics		1	—	4	3	13	—	4	—	—
Species endemic to eastern Cuba		8	5	38	9	64	9	10	2	5
Oriente endemics		91	103	346	62	611	30	28	9	46
Pan-Cuban endemics		27	29	62	14	78	6	5	5	17
Total endemics		149	175	593	109	984	69	65	24	80
<i>Group of Caribbean species</i>										
Greater Antillean species		50	45	65	13	64	2	2	15	24
Antillean species		16	21	13	7	16	1	1	3	3
Antillean—Bahamean species		2	5	7	11	7	1	1	2	7
Bahamean species		5	11	7	—	18	—	—	1	1
Species of the Antilles, Florida and SE USA		5	8	2	1	2	1	—	—	2
Species of Cuba the Bahamas and SE USA		—	12	10	3	6	—	1	1	—
Species of Cuba, Florida and SE USA		2	—	2	1	4	—	—	—	1
Northern Caribbean species		10	4	7	6	14	1	3	—	5
Southern Caribbean species		10	5	6	3	9	—	—	1	3
Pan-Caribbean species		23	34	29	8	25	—	2	—	12
Total Caribbean species		123	145	148	53	165	6	10	23	58
<i>Tropical species with wider distribution</i>										
Species of Cuba, the Antille and South America		4	3	4	2	6	—	—	—	8
Species of Cuba, and South America		—	2	2	2	6	—	—	—	5
Neotropical species		33	36	29	14	46	3	—	6	38
Pan-tropical species		2	9	6	5	17	—	—	—	4
Total of widely distributed tropical species		39	50	41	23	75	3	—	6	55
Total of all tropical species		311	370	781	185	1224	78	75	53	193
<i>Group of extratropical species</i>										
North and Central American species		1	—	—	—	—	—	—	—	—
American species		—	—	—	—	1	—	—	—	—
Amphiatlantic and circumpolar species		—	—	—	—	—	—	—	—	—
Cosmopolitan species		—	—	—	—	—	—	—	—	—
<i>Group of adventive species</i>										
Neotropical adventives		19	3	10	6	7	1	—	—	4
Palaeotropical adventives		31	8	7	—	17	2	—	—	10
Extratropical adventives		—	—	—	3	—	—	—	—	2
Total adventives		50	11	17	9	24	3	—	—	16
Total Cuban flora		362	381	798	194	1249	81	75	53	209

of Cuba I. (based on the number of species)

SP	P _{Gr}	ΣP	Ch	H	G	HH	Th	TH—H	L _{an}	E _H	E _{Ch}	S _{CT}	ΣH	Total
7	—	221	20	59	4	12	12	3	24	3	2	—	137	358
—	—	19	4	28	2	1	2	—	2	1	—	—	40	59
—	—	33	12	36	2	6	6	1	2	—	—	—	65	98
3	—	105	5	39	7	8	2	2	14	1	—	—	78	183
2	—	23	2	2	—	—	1	1	3	—	—	—	9	32
1	—	19	1	6	1	—	—	—	—	1	—	—	9	28
3	—	100	7	25	6	—	7	1	2	—	1	—	49	149
1	—	26	5	—	—	—	3	1	—	—	—	—	9	35
4	—	154	6	27	—	—	1	—	3	—	—	—	37	191
13	—	1339	61	130	22	1	11	3	48	56	5	1	327	1666
4	—	247	9	50	10	7	11	2	32	11	—	—	132	379
38		2286	132	389	54	35	56	14	130	73	8	1	892	3178
7	1	288	21	85	16	5	16	3	28	33	11	—	218	506
2	1	84	2	31	6	3	6	1	9	11	—	—	69	153
1	—	44	2	10	2	3	4	—	6	4	—	—	31	75
1	—	44	1	10	1	1	2	—	6	4	—	1	26	70
—	—	21	2	39	8	7	3	3	3	2	—	—	67	88
—	—	33	2	17	8	4	8	1	9	—	—	—	49	82
1	1	12	2	60	3	17	7	2	2	2	—	—	95	107
2	—	52	9	34	2	6	13	3	6	1	3	1	78	130
2	—	39	3	18	5	2	5	—	11	16	7	—	67	106
3	1	137	12	67	11	1	22	5	11	23	14	1	167	304
19	4	754	56	371	62	49	86	18	91	96	35	3	867	1621
—	2	29	4	26	8	8	3	—	3	4	—	—	56	85
—	—	17	4	21	5	5	4	—	4	3	2	—	48	65
2	6	213	21	233	14	50	78	10	46	30	13	—	495	708
—	1	44	3	71	9	12	46	4	31	1	—	—	177	221
2	9	303	32	351	36	75	131	14	84	38	15	—	776	1079
59	13	3343	220	1111	152	159	273	46	305	207	58	4	2535	5878
—	—	1	—	19	—	14	6	1	—	—	—	—	40	41
—	—	1	1	23	2	10	7	2	—	—	—	—	45	46
—	—	—	—	5	—	—	—	—	—	—	—	—	5	5
—	—	—	2	8	—	11	6	2	—	—	—	—	29	29
8	1	59	2	17	6	2	15	2	9	—	1	—	54	113
1	8	84	2	45	5	2	26	2	15	1	—	—	98	182
—	—	5	3	23	3	1	37	9	—	—	—	—	76	81
9	9	148	7	85	14	5	78	13	24	1	1	—	228	376
68	22	3493	230	1251	168	199	370	64	329	208	59	4	2882	6375

Table 28 The phytogeographic analysis of

Flora elements	Life-forms	Mg— MsP	Mc— MsP	McP	N— McP	NP	Ms P _{ms}	Mc P _{ms}	EP	LP
<i>Group of endemic species</i>										
Pinar del Río endemics		2.1	4.2	7.2	2.6	8.2	12.6	5.1	9.6	2.9
Isla de Pinos endemics		0.3	0.5	0.5	—	0.5	—	1.7	—	1.0
Endemics to both Pinar del Río and Isla de Pinos		0.9	0.3	1.7	1.5	1.0	1.2	1.7	—	—
Species endemic to western Cuba		1.5	2.4	3.3	5.6	3.4	10.0	3.4	—	0.5
Habana endemics		0.3	—	0.9	0.5	1.0	—	1.7	—	—
Matanzas endemics		—	0.3	0.4	0.5	0.4	1.2	3.4	3.8	—
Las Villas endemics		1.5	2.4	3.6	1.0	3.2	5.0	8.5	1.9	1.0
Camagüey endemics		0.3	—	0.5	1.0	1.0	—	5.1	—	—
Species endemic to eastern Cuba		2.3	1.3	2.4	4.6	3.8	7.5	6.7	3.8	2.4
Oriente endemics		21.0	27.0	43.9	31.8	47.0	40.0	39.0	15.5	21.7
Pan-Cuban endemics		6.8	7.6	7.8	7.2	6.9	7.5	6.7	9.6	8.2
Total endemics:		37.0	46.0	72.2	56.3	76.4	85.0	83.0	44.2	37.7
<i>Group of Caribbean species</i>										
Greater Antillean species		14.9	11.8	8.7	6.8	5.7	2.5	3.4	28.9	11.6
Antillean species		4.7	5.5	1.9	3.6	1.4	1.2	1.7	5.8	1.4
Antillean—Bahamean species		0.6	1.3	1.1	5.6	0.6	1.2	1.7	3.8	3.4
Bahamean species		1.5	2.9	0.9	—	1.6	—	—	1.9	0.5
Species of the Antilles, Florida and SE USA		1.5	2.1	0.3	0.5	0.2	0.3	—	—	1.0
Species of Cuba, the Bahamas and SE USA		—	3.1	1.3	1.5	0.5	—	1.7	1.9	—
Species of Cuba, Florida and SE USA		0.6	—	0.3	0.5	0.4	—	—	—	0.5
Northern Caribbean species		2.9	1.0	1.1	3.1	1.2	1.3	5.1	—	2.4
Southern Caribbean species		2.9	1.3	0.8	1.5	0.8	—	—	1.9	1.4
Pan-Caribbean species		6.8	8.9	3.8	4.1	2.2	—	3.4	—	5.8
Total Caribbean species:		36.4	37.9	20.2	27.2	14.6	7.5	17.0	44.2	28.0
<i>Tropical species with wider distribution</i>										
Species of Cuba, the Antilles and South America		1.2	0.8	0.5	1.0	0.5	—	—	—	3.9
Species of Cuba, and South America		—	0.5	0.3	1.0	0.5	—	—	—	2.4
Neotropical species		9.8	9.4	3.8	7.3	4.1	3.8	—	11.6	18.4
Pan-tropical species		0.6	2.4	0.8	2.6	1.6	—	—	—	1.9
Total of widely distributed tropical species		11.6	13.1	5.4	11.9	6.7	3.8	—	11.6	26.6
Total of all tropical species		85.0	97.0	97.8	95.4	97.7	96.3	100	100	92.3
<i>Group of extratropical species</i>										
North and Central American species		0.3	—	—	—	—	—	—	—	—
American species		—	—	—	—	0.1	—	—	—	—
Cosmopolitan species		—	—	—	—	—	—	—	—	—
Amphiatlantic and circumpolar species		—	—	—	—	—	—	—	—	—
Total extratropical species:		0.3	—	—	—	0.1	—	—	—	—
<i>Group of adventive species</i>										
Neotropical adventives		5.6	0.8	1.3	3.1	0.6	1.2	—	—	1.9
Palaeotropical adventives		9.1	2.2	0.9	—	1.6	2.5	—	—	4.8
Extratropical adventives		—	—	—	1.5	—	—	—	—	1.0
Total adventives:		14.7	3.0	2.2	4.6	2.1	3.7	—	—	7.7
Total Cuban flora (%)		100	100	100	100	100	100	100	100	100

the flora of Cuba II. (percentages)

SP	P _{Gr}	ΣP	Ch	H	G	HH	Th	TH-H	L _H	E _H	E _{Ch}	S _{Ch}	ΣH	Total
7.6	—	6.3	9.2	4.5	2.4	6.0	3.2	4.7	7.3	1.4	3.5	—	4.8	5.7
—	—	0.5	1.8	2.3	1.2	0.5	0.5	—	0.6	0.5	—	—	1.4	0.9
—	—	1.0	5.3	2.9	1.2	3.0	1.6	1.6	0.6	—	—	—	2.3	1.6
4.5	—	3.1	2.2	3.1	4.2	4.1	0.5	3.1	4.3	0.5	—	—	2.7	2.9
3.0	—	0.7	0.9	0.2	—	—	0.3	1.6	0.9	—	—	—	0.3	0.5
1.5	—	0.5	0.4	0.6	0.6	—	—	—	—	0.5	—	—	0.3	0.4
4.5	—	2.9	2.2	1.9	3.5	—	1.9	1.6	0.6	—	1.7	—	1.6	2.3
1.5	—	0.7	2.2	—	—	—	0.8	1.6	—	—	—	—	0.3	0.5
6.1	—	3.2	2.2	1.4	—	—	0.3	—	0.9	—	—	—	0.9	3.0
19.8	—	37.0	26.7	9.7	13.0	0.5	3.0	4.7	14.6	26.9	6.9	25.0	11.4	26.2
6.1	—	7.2	3.9	4.0	6.0	3.5	3.0	3.1	9.7	5.3	—	—	4.6	5.9
54.6	—	63.0	57.0	30.5	32.1	17.6	15.1	22.0	39.5	35.1	12.1	25.0	30.6	49.9
10.8	4.5	8.8	9.2	6.9	9.5	2.5	4.3	4.7	8.5	15.9	19.0	—	7.7	7.9
3.0	4.5	2.6	0.9	2.5	3.6	1.5	1.6	1.5	2.7	5.3	—	—	2.4	2.4
1.5	—	1.3	0.9	0.8	1.2	1.5	1.1	—	1.8	1.9	—	—	11	1.2
1.5	—	1.3	0.4	0.8	0.6	0.5	0.5	—	1.8	1.9	—	25.0	0.9	1.1
—	—	0.6	0.9	3.1	4.8	3.5	0.8	4.7	0.9	0.9	—	—	2.3	1.4
—	—	1.0	0.9	1.4	4.8	2.0	2.2	1.5	2.7	—	—	—	1.7	1.3
1.5	4.5	0.4	0.9	4.8	1.8	8.6	1.9	3.1	0.6	0.9	—	—	3.3	1.7
3.0	—	1.6	3.9	2.7	1.2	3.0	3.5	4.7	1.8	0.5	5.2	25.0	2.7	2.0
3.0	—	1.2	1.3	1.5	3.0	1.0	1.4	—	3.4	7.7	12.0	—	2.3	1.7
4.5	4.5	4.2	5.3	5.4	6.6	0.5	5.9	7.8	3.4	11.1	24.1	25.0	5.8	4.8
28.8	18.0	23.0	24.6	29.9	37.0	24.6	23.2	28.0	27.6	46.1	60.3	75.0	30.2	25.5
—	9.1	0.9	1.8	2.1	4.8	4.1	0.8	—	0.9	1.9	—	—	2.0	1.3
—	—	0.5	1.8	1.7	3.0	2.5	1.1	—	1.2	1.5	3.5	—	1.7	1.0
3.0	27.5	6.5	9.1	18.8	8.3	25.1	21.2	15.6	14.0	14.4	22.4	—	17.2	11.2
—	4.5	1.3	1.3	5.7	5.3	6.0	12.4	6.3	9.5	0.5	—	—	6.2	3.4
3.0	41.1	9.2	14.0	28.3	21.4	37.7	35.5	21.9	25.6	18.3	25.9	—	27.1	16.9
86.4	99.1	95.3	95.6	88.7	90.5	79.9	73.8	71.9	92.7	99.5	98.3	100	87.9	92.3
—	—	0.03	—	1.5	—	7.1	1.6	1.6	—	—	—	—	1.4	0.7
—	—	0.03	0.4	1.9	1.2	5.0	1.9	3.1	—	—	—	—	1.6	0.7
—	—	—	0.9	0.6	—	5.5	1.6	3.1	—	—	—	—	1.0	0.3
—	—	—	—	0.4	—	—	—	—	—	—	—	—	0.2	0.15
—	—	0.1	1.3	4.4	1.2	17.6	5.1	7.8	—	—	—	—	4.2	1.8
12.1	4.5	1.8	0.9	1.4	3.5	1.0	4.1	3.1	2.7	—	1.7	—	1.9	1.8
1.5	36.4	2.6	0.9	3.6	3.0	1.0	7.0	3.1	4.6	0.5	—	—	3.4	2.8
—	—	0.2	1.3	1.9	1.8	0.5	10.0	14.1	—	—	—	—	2.6	1.3
13.6	40.9	4.6	3.1	6.9	8.3	2.5	21.1	20.3	7.3	0.5	1.7	—	7.9	5.9
100	100	100	100	100	100	100	100	100	100	100	100	100	100.0	100.0

analysis was done in two different ways, one analysis is based on the native flora (NF, 5998 taxa) while the other uses the complete actual flora (AF, 6375 taxa) (Tables 27 and 28)

18.2 Phytogeographical types and their distribution

18.2.1 Endemics

The number of endemic taxa is 3178, 49.9 % and 53 % of the actual and native flora, respectively. This proportion is expected to increase as 90 % of the newly discovered species in Cuba are endemic (Borhidi and Muñiz 1971b, 1972a,b, 1973a,b, 1977a,b,c,d, 1978, Borhidi and Kereszty 1979, Muñiz and Borhidi 1981, Lippold 1970, 1975, 1978a, Hadač 1970, Bisse 1974, 1975, 1980 Fernandez and Borhidi 1983, 1985). As much as 71.9 % of endemics are phanerophytes, the others being herbs. Most endemics are shrubs (984 species, 30.9 %). The microphanerophytes (593 species, 18.4 %) and hemicryptophytes (389 species, 12.3 %) are the second and third largest life-form classes within this chorological category. These figures indicate that communities with rich shrub layers, such as serpentine shrubwoods, scrubs, mogotes, semi-arid and humid montane shrublands were the most important evolutionary centres yielding new species.

18.2.2 The subdivision of endemics

For a better understanding of endemic elements they need to be subdivided so much the more because only a small percentage of them occur in the entire island. The majority of endemics are restricted to a given flora district or a flora sector (local and regional endemics). The system to be discussed below contains some artificial categories since the available distribution data of many species refer to administrative boundaries. Therefore, I had no choice but to make a distinction among the endemics of provinces, and those of western and eastern Cuba and the whole island. (It is noted that the taxa listed in the cenological tables are local endemics grouped (Fig. 88) into 14 districts and 4 regional endemics (Fig. 89) for sectors with natural phytogeographic boundaries. This classification maintains the three major groups mentioned above, because they are natural.)

18.2.3 The distribution patterns of endemics

The endemics are partitioned as follows:

a) **Pinar del Río endemics.** 358 taxa (AF: 5.7%, NF: 5.9%). The majority are shrubs (103 species, 28.7%), hemicryptophytes (59, 16.3%) and microphanerophytes (58, 15.8%). The percentages of herb lianes dominant in karstic forests (24,

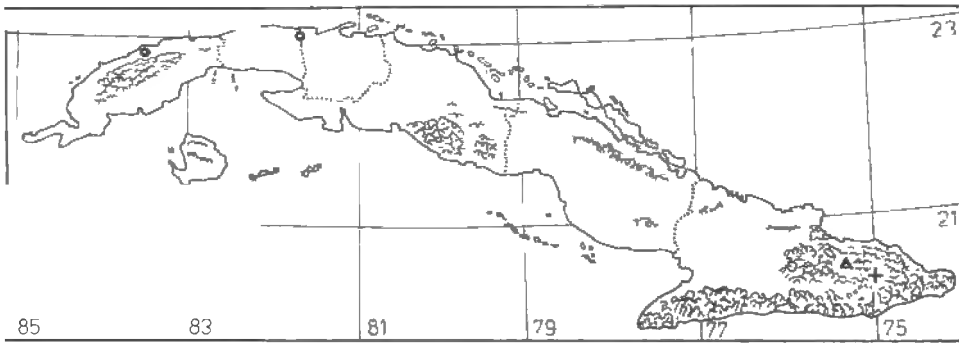


Fig. 88 Distribution of some local endemics in Cuba; left dot: *Phyllacanthus grisebachianus* Hook.f.; right dot: *Coccothrinax borhidiana* Muñiz; triangle: *Eosanthus cubensis* Urb.; cross *Clusia alainii* Borhidi

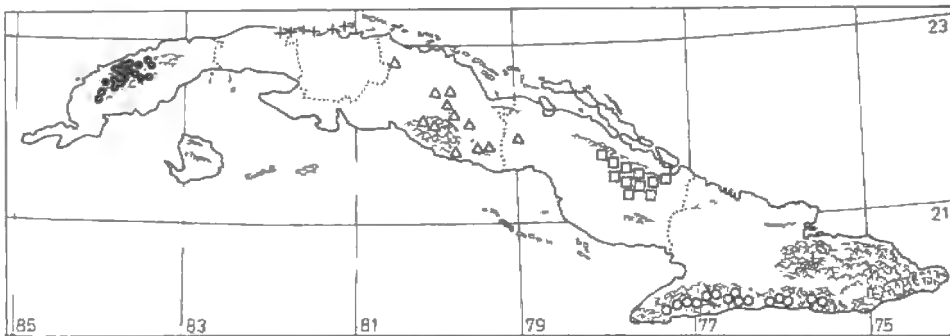


Fig. 89 Distribution of some regional endemics of Cuba; dot: *Gaussia princeps* Wendl. for Pinar del Río; cross: *Guettarda undulata* Griseb. for Matanzas; triangles: *Machaonia subinermis* Urb. for Las Villas; squares: *Copernicia cowellii* Britt. et. Wils. for Camagüey and circles: *Pinus maestrensis* Bisse for the Maestra range of Oriente (after Klotz 1978, Fernandez and Borhidi 1979)

7%) and of chamaephytes characteristic of coniferous forests (20, 6.1%) are also significant. The ratio of trees and herbs is 60:40. A variety of geographic and cenological distribution types are found, they are discussed in detail in chapter 19. Most famous representatives are: *Microcycas calocoma*, a 'living fossil' presumably with a Cretaceous origin, *Quercus oleoides* ssp. *sagraeana*, *Pachyanthus poiretii*, *P. tetramerus*, *Neomazaea phialanthoides* and *Spathelia brittonii* (Fig. 89), 9 *Erioculon*, 10 *Pilea*, 10 *Calyptanthus*, 17 *Eugenia* and 8 *Ipomoea* sp.

b) **Isla de Pinos endemics.** 59 taxa (AF: 0.9%), NF: 1.0%). Apart from the only endemic genus *Lepturidium*, these are mostly neoendemics. That is, they are morphologically similar vicariants of the corresponding Pinar del Río endemics. This fact demonstrates that Isla de Pinos and western Cuba became geographically isolated only at the end of the Quaternary. Since then only a relatively small differentiation of the flora was allowed. 71.4% are herbs, 50% are hemicryptophytes. The shrubs account for 11%, whereas small trees and dwarf shrubs give a total of 7.7%. Most species grow in open pine woodlands on sandy soils with poor

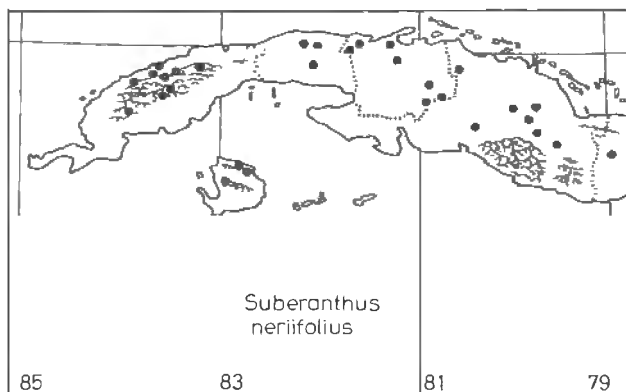


Fig. 91 Distribution of a typical West Cuban endemic *Suberanthus neriifolius* (A. Rich.) Borhidi and Fernandez

e) **Habana endemics.** 32 taxa, not more than 0.5–0.6% of the flora. 72% are phanerophytes, mainly shrubs (34.4%), small trees (25%), herb lianes (9.4%) and trunk-succulents (6.3%). These species are mainly found in the thorn scrubs of limestone karsts on the northern coast, in the mogotes of Jaruco and Somorrostro, etc. Also, in the serpentine shrublands around Campo Florido, e.g., *Leptocereus leoni* and *L. wrightii*, *Psidium havanense*, *P. munizianum*, *Pectis havanensis*, *Borreria cubana* and four *Eugenia* spp. etc.

f) **Matanzas endemics.** 28 taxa, 0.4% of the flora. 62.5% are phanerophytes, particularly shrubs (16.6%), small trees (16.7%) and also small palms and woody epiphytes (8.3% each). The commonest herb life-form is the hemicryptophyte, in which 25% of the species are included. These plants occur especially in the karsts of the northern coast (Seboruco plato) e.g. *Guettarda undulata* (Fig. 89) and *Coccothrinax borhidiana* (Fig. 88), and in the arid serpentine vegetation of Canasi e.g. *Borreria matanzasia*, *Melocactus matanzanus*, *Buxus gonoclada* and *Moacrotan revolutus*, etc.

g) **Las Villas endemics.** 149 taxa, 2.4% of the flora. 67% are phanerophytes including 26% shrubs, 20.7% small trees, 10% tall trees and 6% palms. The largest herbaceous life-form class is the hemicryptophyte (17%). Especially the montane rainforests and seasonal forests of Sierra Escambray are rich in endemics e.g. *Neobraccia howardii*, *Psychotria martii* and four *Dorstenia*, five *Pilea* and four *Calyptanthus* spp. The serpentine hills of Santa Clara and Motembo also have many endemics e.g. *Karwinskia oblongifolia*, *Eugenia subdisticha*, *E. clarensis*, *Guettarda roigiana*, *G. clarensis*, *Xylosma acunae*, *Paspalum motemboënsis* and *Scleria motemboënsis* etc. A number of endemic species are found in the arid evergreen forests on the southern rocky coast (four *Cheilophyllum* species) and in the savannas of eastern and western Las Villas (three *Copernicia* species).

h) **Camagüey endemics.** 35 taxa, 0.5% of the flora. 75% are phanerophytes, mainly shrubs (35.5%), small trees (19.5%) and dwarf palms (9.7%). The percentage of subshrubs (16.1%) and annuals (9.7%) is also significant. The majority of these species are endemic to the serpentine region north of the town of

Camagüey, e.g. *Copernicia cowellii* (Figs 89, 92), *Coccothrinax camagüeyana*, *C. pseudorigida*, *Cameraria microphylla*, *Guettarda camagüeyensis*, *Randia acunae* and *Reynosia camagüeyensis*. Only a few species occur in the northern limestone mountains (*Guettarda munizii*) and on the northern coast and in the islands (*Guettarda lanuginosa*, *Nashia cayensis* and *Crescentia mirabilis*). The wide plains in the south are completely free from local endemics.

i) **Endemics of eastern Cuba.** 191 taxa (AF:3.0%, NF:3.2%). 80% are phanerophytes, mainly shrubs (33.2%), small trees (20.7%), tall trees (10%) and palms (7.7%). The proportion of hemipterophytes is 13.2%. This category can be partitioned into meaningful groups. One contains the plants of montane rainforests that are endemic to the mountainous regions of both Oriente and Las Villas, e.g. *Magnolia cubensis sensu lato*, *Ocotea ekmanii*, *Hedyosmum grisebachii*, *Meliosma oppositifolia*, *Ossaea ottoschmidtii*, *Clidemia capituliflora*, *Gesneria viridis sensu lato* and *G. clarensis* etc. The endemics of the plains in eastern Cuba have to be distinguished from the previous group. The largest section of flatland endemics includes those found in serpentine areas, e.g. *Coccoloba geniculata*, *Jacaranda cowellii*, *Zanthoxylum minutifolium*, *Daphnopsis oblongifolia*, *Machaonia microphylla* and *Myrtus anomala* etc. The palms of microphyllous evergreen forests and derived savannas represent a smaller group (*Copernicia gigas*, *C. vesper-*



Fig. 92 *Copernicia cowellii* Britt. et Wils. the smallest wax-palm, endemic to the serpentine savannas and scrubs of Camagüey (Photo: A. Borhidi)



Fig. 93 *Copernicia rigida* Britt. et Wils. a tall wax palm endemic to the eastern lowland of Cuba (Photo: A. Borhidi)

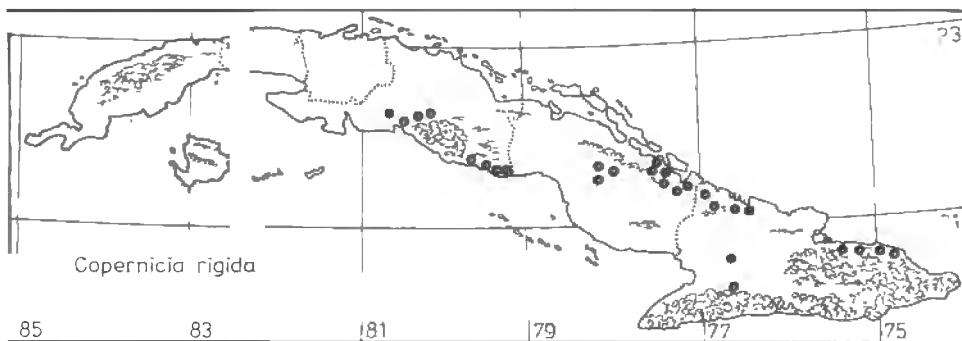


Fig. 94 Distribution of a typical east Cuban endemic *Copernicia rigida* Britt. et Wils. (Dahlgren and Glassman 1963, complemented)

tilionum, *C. rigida* (Figs 93–94), *C. baileyana* and *C. sueroana* etc.). Others are plants of moist floodplain forests (*Hildegardia cubensis* and *Hymenaea torrei* etc.) and xerophilous elements on the southern coast of Oriente and Las Villas (*Rhodocactus cubensis*, *Harrisia taylori*, *Pilosocereus brooksianus* and *Bourreria taylori* etc.). Consequently, this chorological type is more frequent in Oriente (123, 92%) and Las Villas (106, 81.5%) than in Camagüey (67, 49%).

j) **Endemics of the former Oriente Province.** 1666 species (AF:26.2%, NF:27.8%). Oriente has a key position regarding the development of the flora since 53.4% of the species endemic to Cuba are restricted to barely one-third of the area of this country. Also, Oriente endemics account for one-fourth of the total flora. The majority of them are phanerophytes (78.7%), including 611 shrub species (34.3%), 406 microphanerophytes (25.2%) and 194 mesophanerophytes (11.3%). Particular attention should be paid to the 39 endemic palm species that represent 40% of the palms in this island. Major life-form categories of herbs are the hemicryptophytes (130, 7.8%) and chamaephytes (61, 4%). A considerable part of lianes and epiphytes characteristic of tropical forests are Oriente endemics (94, 6.5% and 70, 4.4% respectively). Many geographic and cenological distribution types can be distinguished, their detailed discussion will be given later, under phytogeographic subprovince C. Genera with many Oriente endemics (numbers given in brackets) are: *Coccothrinax* 17, (see Fig. 109), *Lepanthes* (16), *Pleurothallis* (22), *Pilea* (37), *Coccoloba* (14), *Spathelia*, 10, (see Fig. 109), *Phyllanthus* (36), *Leucocroton* (16), *Buxus* (23), *Ilex* (17), *Calyptanthus*, (25), *Eugenia* (53), *Miconia* (24), *Ossaea* (40), *Lyonia* (21), *Cordia* (23), *Callicarpa* (19), *Tabebuia* (38), *Gesneria* (27), *Rondeletia* (40), *Psychotria* (28), *Senecio* (17), *Eupatorium* (28) and *Vernonia* (35). A random selection of noted species includes *Pinus cubensis*, *Podocarpus ekmanii*, *Dracaena cubensis*, *Illicium cubense*, *Persea anomala*, *Alvaradoa arborescens*, *Euphorbia helenae*, *Cyrtilla cubensis*, *Bonnetia cubensis*, *Clethra cubensis*, *Consolea macracantha*, *Spirotecoma spiralis*, *Jacaranda arborea* and *Tocoyena cubensis* etc.

k) **Pan-Cuban endemics.** 379 taxa (AF:6%, NF:6.4%). 64.4% are phanerophytes including shrubs (78, 20.8%), small trees (76, 19.7%) and forest-forming mesophanerophytes (56, 14.3%). Besides hemicryptophytes (50, 13.5%), the percentage of herb lianes (32, 8.6%) and woody epiphytes (17, 4.6%) is worth mentioning. This chorological category contains taxa occurring both in eastern and western Cuba. Some species are found in the entire island and Isla de Pinos, for example, plants of the coast, gallery forests, marshes and wet savannas, (as *Sabal parviflora* (Figs 95—96) *Pseudocarpidium ilicifolium* and *Sabal japa*), plants of the

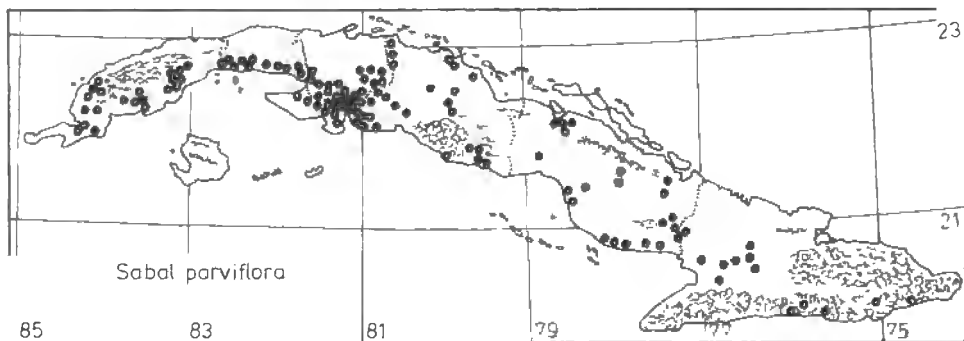


Fig. 95 Distribution of a Pan-Cuban endemic *Sabal parviflora* Becc. (Saakov 1970)



Fig. 96 Wet savanna of *Sabal parviflora* at the habitat of the original alluvial and swamp forests in the Zapata Peninsula (Photo: A. Borhidi)

serpentine belt *Neobraccia valenzuelana* Figs 53, 117, (*Phyllanthus orbicularis* (Fig. 127), *Annona bullata* and *Leucocroton moncadae*), ubiquitous forest lianes (*Platygyne hexandra* Fig. 115) *Securidaca elliptica* and *Banisteria pauciflora*), trees of semi-deciduous forests (*Ficus subscabrida*, *Erythroxylum havanense*, *Casasia calophylla* and *Guettarda calyptrata*), and spinous plants of xerophilous communities (*Gastrococos crista*, *Oplonia tetrasticha* Fig. 116) *sensu lato*, *Randia spinifex* and *Diospyros grisebachii*. Other species exhibit disjunct geographical distribution being restricted to three isolated spots in the mountains of Oriente, Las Villas and Pinar del Río (e.g. *Amyris lineata*, *Chione myrtifolia*, *Duranta fletcheriana* and *Peperomia hirta* etc.). There are species distributed in the mountains of Oriente and Las Villas and also in the coniferous region of western Cuba and Isla de Pinos. These are sometimes divisible into vicarious subspecies, e.g. *Hypericum styphelioides* (Lippold 1970). The number of species with a disjunct distribution confined to the ends of the island is also large. Most of these occur in the karstic forests, serpentine communities and mesophyllous forests (*Sloanea amygdalina* and *Mecranium haemanthum*) of Oriente and Pinar del Río. There is a species endemic to the arid zones of southern Oriente and northern Matanzas (*Croton litoralis sensu lato*) and others present in Oriente and Isla de Pinos (e.g. *Margaritara scandens*, *Tetramicra simplex* and *Erythroxylum longipes* etc.). Due to the disjunct geographi-

cal distribution of most species, this chorological type is overrepresented in Oriente (83%) and Pinar del Rio (72%) and underrepresented in Las Villas (57%), Habana (53%), Matanzas (36%), Camagüey (33.5%) and Isla de Pinos (30.5%).

18.2.4 Caribbean elements

This group is composed of species originating from within the Caribbean flora region that occur in the islands of Antilles and Bahamas, Central America or the northern part of South America. 1621 species belong to this chorological group (AF: 26.4%, NF: 28.2%). The origin of the flora of Cuba and its relationship to others are well-demonstrated by the fact that approximately three-fourth of the species (AF: 74.3%, NF: 79.2%) are endemic and Caribbean. 53.4% are herbs, the others being phanerophytes. Most species of wide geographical range are herbs whereas the narrowly distributed species are mostly phanerophytes.

The eventful geological past of the Caribbean region, the successive isolation of the archipelago and repeated transgressions of the sea explain that ten different chorological types may be recognized within the Caribbean species group. These are:

a) **Greater Antillean species.** They occur in at least two of four islands, Cuba, Jamaica, Hispaniola and Puerto Rico. 506 species in Cuba (AF: 8.2%, NF: 8.8%). Major life-form categories are: mesophanerophytes (95, 18%), microphanerophytes (77, 15.2%), shrubs (65, 12.9%) and hemicryptophytes (85, 16.8%). The proportion of epiphytes (58, 11.6%) and lianes (52, 10.2%) is relatively large because many rainforest species are of this chorological type. Most Greater Antillean elements of Cuba are also found in Hispaniola (391, 76%). Cuba and Jamaica have 212 (41.9%) species, Cuba and Puerto Rico have only 123 (24.3%) species in common. The Greater Antillean elements are not evenly distributed over the provinces. Oriente is the richest in this chorological type (401, 79%), Las Villas (224, 45%), Pinar del Río (202, 41%), Habana (150, 31%), Isla de Pinos (110, 22%) and Matanzas (109, 22%) are relatively poor. These percentages clearly indicate that Hispaniola resembles Cuba the most, especially Oriente, in floristic composition. The close relationship between the two floras is confirmed by the presence of 103 species (20.4%) not found outside Oriente and Hispaniola. At the same time, Oriente and Jamaica have as few as 31 (6%) species in common, half of those being epiphytic orchids easily propagated through aerial dispersion. Some important examples are: *Dilomilis montana*, *Oxandra lanceolata*, *Phoebe montana*, *Ocotea cuneata*, *Brya ebenus*, *Bernardia dichotoma*, *Diata myricoides*, *Hibiscus elatus*, *Garrrya fadyenii*, *Dipholis cubensis* and *Chrysophyllum argenteum*.

b) **Antillean species.** Species with geographical range including at least one island from the Greater Antilles and another from the Lesser Antilles. 153 taxa (AF: 2.5%, NP: 2.7%). 55% are phanerophytes, most of them are medium-sized mesophanerophytes (37, 12.4%), microphanerophytes (20, 13.2%) and shrubs (16, 10.5%). The number of hemicryptophytic taxa is 31 (20.3%). Many lianes (12, 7%) and epiphytes (14, 9.2%) occur since rainforests and mossy forests are rich in Antillean species. The number of Antillean elements decreases from east to the

west in Cuba. 83% of them are present in Oriente, 48% in Las Villas and 45% in Pinar del Rio. The fewest Antillean species are indicated from Matanzas and Isla de Pinos (31% in each). Noted species are: *Prestoea montana*, *Dichaea hystrix*, *Oxandra laurifolia*, *Cinnamomum elongatum*, *Ocotea leucoxylon*, *Lonchocarpus domingensis*, *Savia sessiliflora*, *Forestiera rhamnifolia*, *Calophyllum antillanum* and *Plumeria obtusa*.

c) **Antillean-Bahamean species.** This group includes taxa occurring both in the Antilles and in the Bahamas. Two subgroups are distinguished:

- Species of the Greater Antilles and the Bahamas absent from the Lesser Antilles, and

- Species present in both the Lesser and the Greater Antilles and also in the Bahamas.

This chorological type is represented by 75 species in Cuba (1.3% of the flora). 58, 6% are woody plants, mostly microphanerophytes (18, 25%) and woody and herbaceous lianes (13, 17.3%) because this chorological type includes many plants characteristic of coastal evergreen dry forests and other dry shrublands. The hemicyptophytes (10, 13.4%) and mesophanerophytes (8, 10.7%) are the next largest life-form categories. The richest province is Oriente (86%), the percentages are much lower elsewhere, e.g., 65% in Las Villas, 65% in Pinar del Rio and 56% in Camagüey. The relative frequency of Antillean-Bahamean species is the highest in Camagüey (3.11% of the flora). Some important species are: *Juniperus lucayana*, *Arthrostylidium capillifolium*, *Cattleyopsis lindenii*, *Ficus jacquinifolia*, *Lysiloma latisiliqua*, *Erythroxylon areolatum*, *E. confusum*, *Zanthoxylum cubense*, *Croton lucidus*, *Grimmeodendron eglandulosum*, *Buxus bahamensis*, *Maytenus buxifolia*, *Allophylus cominia*, *Evolvulus arbuscula* and *Oplonia spinosa sensu lato*.

d) **Bahamean elements.** As a matter of fact, this is a marginal case of the preceding category since the common species of Cuba and the Bahamas are included here. Only 70 species (1.1% of the flora). 62.8% are woody plants, mainly shrubs (18, 25.8%), mesophanerophytes (16, 22.8%) and microphanerophytes (7, 10%). Major herbaceous life-forms are the hemicyptophytes (10, 14.3%) and lianes (7, 10%). The number of Bahamean elements tends to decrease towards western Cuba, 75.7% of these species are present in Oriente, 65.7% in Camagüey, 48.5% in Las Villas and 42.8% in Matanzas. The relative frequency is the highest in Camagüey: 3.58% of the flora of this province. Mostly xerophilous species widely distributed in the island belong to this category. Small-leaved species of coastal dry evergreen forests and shrubwoods are: *Picrodendron macrocarpum*, *Pithecellobium hystrix*, *Caesalipinia bahamensis*, *Peltophorum adnatum*, *Croton rosmarinoides*, *Bucida spinosa*, *Lasiocroton bahamensis*, *Scolosanthus bahamensis* and *Jacaranda coerulea*. Others are characteristic of the serpentine shrubwoods, e.g. *Pseudocarpidium wrightii* and *Tabebuia lepidota*. Some species do not reach the main island, occurring only in the sandbanks parallel to the northern coast of Camagüey, e.g. *Pilosocereus millspaughii*, *Callicarpa hitchcockii* and *Cestrum bahamense*.

e) **Florida—Antillean species.** Their geographical range includes the Antilles and Florida. some of them may be absent from the Lesser Antilles (e.g. *Roystonea regia*) and others may be found as far as the southern plains of the United States, e.g. *Panicum condensum* and *P. scoparium*. 88 species in Cuba (1.4–1.5% of the

flora). 76% are herbs including 33 hemicryptophytes (44.2%), 8 geophytes (9.4%) and 7 helo-hydathophytes (8%). Of the woody plants the mesophanerophytes comprise the largest group (13, 14.8%). This chorological type is the most common in western Cuba, 65 species are present in Pinar del Rio (75.6 %). The highest relative frequency is indicated from Isla de Pinos (3.21% of the total flora). In addition to the species already given, the following are worth mentioning: *Nelumbo lutea*, *Swietenia mahagoni*, *Hypelate trifoliata*, *Canella winterana*, *Eugenia axillaris*, *E. maleolens* (*buxifolia*), and *Mastichodendron foetidissimum*.

f) **Florida—Antillean—Bahamean elements.** They differ from the preceding type in that the Bahamas are also within their geographical range. 82 taxa (AF:1.3%, OF:1.4%). 59.8% are herbs, especially hemicryptophytes (20.7%), lianes (9, 11%) and also geophytes and therophytes (9.8% each). The microphanerophytes (13, 15.9%) and mesophanerophytes (12, 14.6%) are the largest woody life-form classes. The plants of this chorological type are fairly evenly distributed over the country, 65% is the maximum (Habana) and 42% in the minimum (Matanzas). 55–56% of them occur in other four provinces. Many species common to the dry coastal evergreen forests and semi-deciduous forests are included, e.g. *Smilax havanensis*, *Ficus aurea*, *Schoepfia chrysophylloides*, *Zanthoxylum coriaceum*, *Picramnia pentandra*, *Alvaradoa amorphoides*, *Metopium toxiferum* and *Tetrazygia bicolor*.

g) **Species of Cuba, Florida and the south-western United States.** The origin of most taxa is not the tropical Caribbean region but the states of Georgia, South Carolina and Virginia in the temperate zone. It may be assumed that during the cool periods in the Quaternary these species migrated to the south through Florida without getting beyond Cuba. 107 species (AF:1.8%, NF:1.9%). 95 species (88.8%) are herbs: 56% are hemi-cryptophytes and 15.8% are helo-hydathophytes. The latter category probably includes species immigrated during the historic ages. They are most frequent in western Cuba, 58% of them are present in Pinar del Rio, 32% in Isla de Pinos. Their relative frequency is also the highest in these two provinces (approx. 2.5% of the flora). On the contrary, this chorological category represents only 4% of the flora in Oriente. The majority of species occur in pine forests and moist savannas, e.g. *Rhus copallina* ssp. *leucantha*, *Lyonia lucida*, *Erianthus giganteus*, *Xyris ambigua*, *Rhynchospora* spp. *Scleria* spp. and *Hypericum fasciculatum*. Others are aquatic or uliginal, e.g. *Fraxinus caroliniana* ssp. *cubensis* (Fig. 147), *Drosera brevifolia*, *Cabomba caroliniana*, *Tradescantia virginiana*. The range of some species is limited to Cuba and Florida. These tropical-subtropical plants are, for example, *Oncidium floridanum*, *Vallisneria neotropicalis* and *Bourreria cassinifolia* etc.

h) **North Caribbean species.** Their geographic range extends to Central America or Mexico (at least to the Yucatan peninsula) and also to the Bahamas and Florida. At the same time however, they are absent from the southern Caribbean region; Costa Rica, Panama, Colombia and Venezuela. 130 species in Cuba (AF:2.1%, NF:2.3%). 60% are herbs, mainly hemicryptophytes (34, 26.2%) and annuals (13, 10%). The proportion of mesophanerophytes (15, 11.6%), micro- and nanophanerophytes (14, 10.8% each) is also remarkable. The provinces of Habana (88, 67.7%) and Pinar del Rio (81, 62.3%) are the richest in species of this

chorological type. Some species, such as *Cassia ekmaniana*, *Diospyros anisandra*, *Neomacfadya podopogon* and *Cissus formosa*, are narrowly distributed being present only in Yucatan and the western end of Cuba. *Forchhammeria trifoliata*, a species more widespread in Central America, is to be also mentioned here. Another group with wider geographical range includes trees characteristic of coastal shrubwoods and forests, e.g. *Nectandra coriacea*, *Lysiloma bahamense*, *Caesalpinia vesicaria*, *Guajacum sanctum*, *Gyminda latifolia*, *Opuntia dillenii*, *Bumelia salicifolia*, *Jacquemontia jamaicensis*, *Citharexylum caudatum*, *Rachicallis americana*, *Strumpfia maritima*, *Picrodendron macrocarpum* (Fig. 97).

i) **South Caribbean species.** Species common to the Antilles and the northern part of South America, but missing from Central America, Mexico and Florida, that is, they occur exclusively in the southern Caribbean region. 106 species in Cuba (1.8% of the flora). The proportion of phanerophytes is 36.8%, these are largely mesophanerophytes (15, 14.6%). The largest group of herbs is the epiphytes (23 species, 21.7%), outnumbering the hemicyptophytes (18, 17%) and lianes (11, 10.4%). The greatest number of south Caribbean elements occur in Oriente (81, 78%). This number is reduced to 48 in Las Villas and to 44 in Pinar del Rio. Camagüey (20), Matanzas (20) and Isla de Pinos (21) have only quarter the number of species in Oriente. Some characteristic species are *Tillandsia caribaea*, *T. pulchella*, *Pleurothallis racemiflora*, *Amyris balsamifera*, *Zuelania guidonia*, *Ixora ferrea*, *Mikania hastata* and the *Peperomia* spp. etc.

j) **Pan-Caribbean species.** The geographical range of these species includes with some potential breaks the entire Caribbean region from Colombia and Venezuela to Mexico, Florida and the Antilles. The number of such species in Cuba is 304 (AF: 5%, NF: 5.3%). The ratio of phanerophytes and herbs is 45 : 55. The most

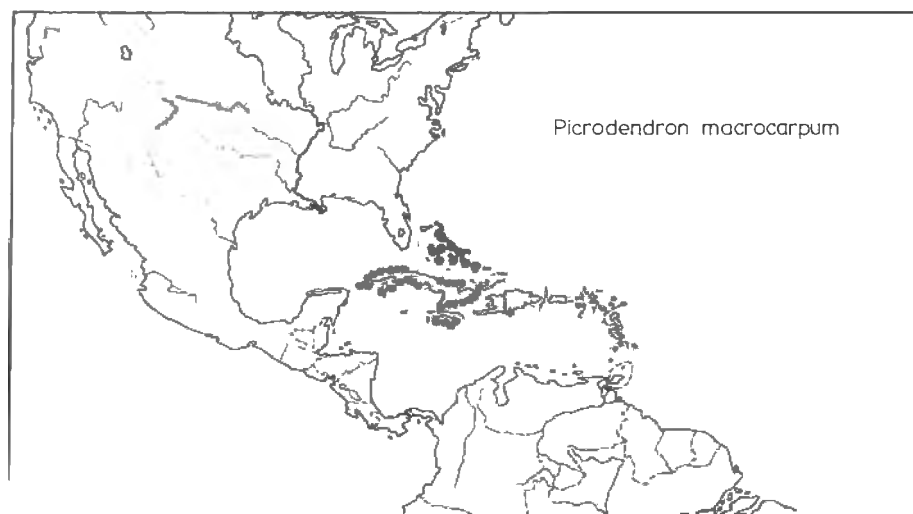


Fig. 97 Distribution of a North-Caribbean element, *Picrodendron macrocarpum* (A. Rich.) Britt. (after Klotz 1978)

frequent life-forms are hemicryptophytes (67, 22.1%), mesophanerophytes (57, 18.8%), epiphytes (37, 12.3%), and microphanerophytes (37, 12.3%). Almost half the species are distributed over the entire country, as the common elements of coastal evergreen forests, semi-deciduous forests and mesophilous forests. Others are found only at one or both ends of the island. As a consequence of this, the largest number of Caribbean species are detected in Oriente (236, 77.6%) and Pinar del Rio (213, 70%). Noted representatives are: *Tillandsia fasciculata*, *T. valenzuelana*, *Rhoeo discolor*, *Bletia purpurea*, *Celtis trinervia*, *Pseudolmedia spuria*, *Chrysobalanus icaco*, *Pithecellobium arboreum*, *Bursera simaruba* (Fig. 98), *Haematoxylon campechianum*, *Byrsonima crassifolia* (Fig. 72), *Ateramnus lucidus*, *Cyrilla racemiflora*, *Cupania glabra*, *Krugiodendron ferreum*, *Cordia gerascanthus*, *Antirhea lucida*, *Erithalis fruticosa*, *Swietenia mahagoni* (Fig. 99) and nine *Epidendrum* spp.

18.2.5 The group of neotropical elements

The third largest chorological group in the flora of Cuba is represented by 858 species (AF: 14%, NF: 14.9%). These species are derived from tropical South America and migrated to Cuba through many different ways. In Cuba they are among the most widely distributed and most abundant species, contrary to the majority of endemic species. Three types are recognized within this chorological group:

a) **South American—Antillean or eastern neotropical species.** Their geographic range extends from the tropical South America to the Antilles, as far north as Cuba. They may be absent from some islands in between and are completely missing from

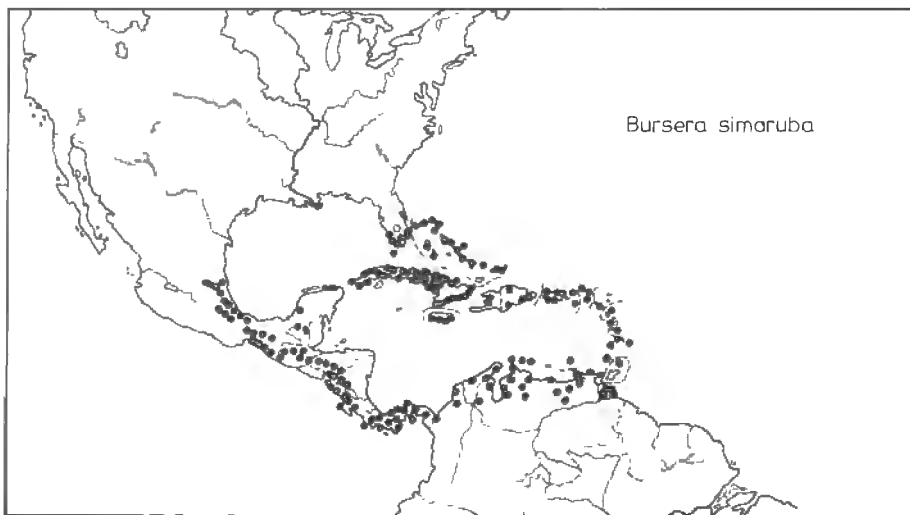


Fig. 98 Distribution of a Pan-Caribbean element, *Bursera simaruba* (L.) Sarg. (Klotz 1978, complemented)



Fig. 99 The most appreciated timber tree of the Cuban flora, the Cuban mahogany (*Swietenia mahagoni*) with fruits in the littoral semi-deciduous limestone forest of Isle of Pine at Punta del Este (Photo: A. Borhidi)

Central America. 85 species in Cuba (1.4–1.5% of the flora). 65.9% are herbs, mainly hemicryptophytes (30.7%), geophytes and helo-hydathophytes (9.4% each). Of the woody plants, the proportion of lianes (9.4%) and mesophanerophytes (8.2%) is the largest. 75% are present in Oriente, 56% in Las Villas and 52% in Pinar del Rio. Similarly to the Caribbean elements, most species occur either in western or eastern Cuba. One of the giant trees of the island, *Carapa guianensis*, belongs to this group. Other members are *Elleanthus linifolius*, *Spiranthes elata*, *Nymphaea amazonum*, *Hyperbaena domingensis*, *Crossopetalum rhacoma*, *Serjania diversifolia*, *Omphalea diandra*, *Prockia crucis* and *Miconia lanata*.

b) **South America—Cuba elements.** Species with disjunct geographical range excluding Central America and the other islands of the Antilles. Only 65 species (1.1% of the flora). 78.3% are herbs, mainly hemicryptophytes (21, 32.3%), woody and herbaceous lianes (9, 13.9%) and epiphytes. These species have very different, often isolated geographical range within Cuba. More than half the taxa (52.4%) occur in Pinar del Rio, less in the other provinces, and only 19% in Camagüey. In general, they are more frequent in western Cuba, where cyclonal activity is higher than in the east. As mentioned in section 5.3 the chorological characteristics of this group are most obviously explained by assuming cyclonal migration. Examples are:

The genus *Bonnetia* (Figs 100, 101), *Eragrostis salzmännii*, *Reimarochloa brasiliensis*, *Sorghastrum stipoides*, *Bulbostylis paradoxa*, *Burmannia bicolor*, *Epidendrum ionosmum*, *Gossypiospermum praecox*, *Drosera tenella* and *Byrsonima verbascifolia*.

c) **Neotropical elements.** Widely distributed species occurring in the tropical regions of Central and South America as well as in the West Indies. 708 species in Cuba (AF : 11.5%, NF : 12.3%), representing the second largest chorological type following the Oriente endemics. Their role in the vegetation is even more significant, because the majority of them are ubiquitous meadow and forest species, constant and even dominant in several plant formation. More than 45% occur in every province, the number of species in Oriente is 552 (79.5%). 70% are herbs, including hemicryptophytes (233 species, 32.9%) and therophytes (78 species, 11%). The groups of woody and herbaceous lianes (84 species, 11.9%), mesophanerophytes (72, 10.2%), epiphytes (49, 6.9%) and helo-hydrotophytes (50, 7.1%) are also large. Aquatic and uliginous species belonging to this group are *Typha domingensis*, *Gynerium sagittatum*, *Limnocharis flava*, *Thalassia testudinum* and *Nymphaea blanda*. Plants of the littoral zone are *Batis maritima*, *Coccoloba uvifera* and *Avicennia germinans*. Examples for ubiquitous forest species are *Pharus glaber*, *Olyra latifolia*, *Lasiacis divaricata*, *Bocconia frutescens*, *Cecropia peltata*, *Trichilia hirta*, *Urera baccifera*, *Chlorophora tinctoria*, *Clusia rosea*, *Tillandsia usenoides*. Some species of the coastal and rocky dry and evergreen forests: *Capparis flexuosa*, *C. cynophallophora*, *Guajacum officinale*, *Amyris elemifera* and

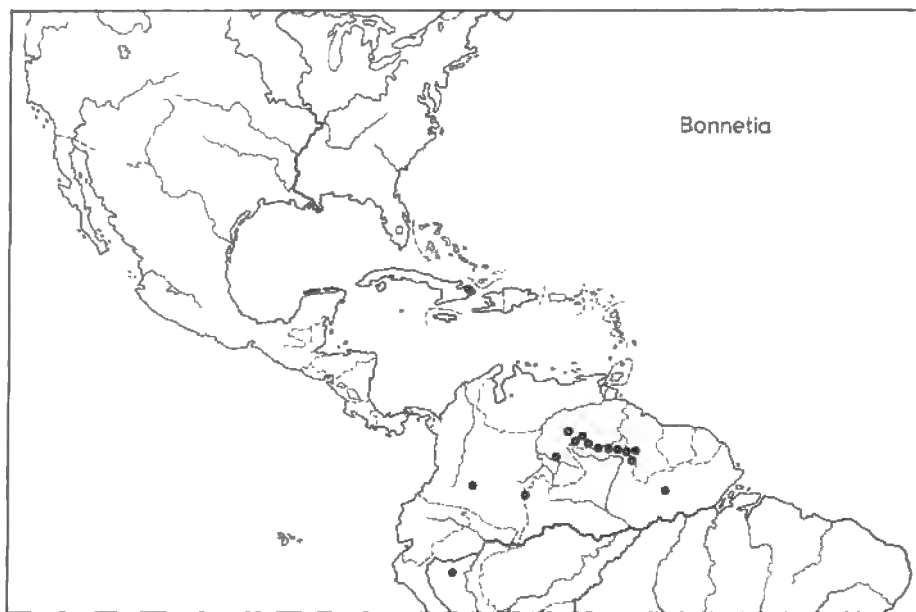


Fig. 100 Geographical distribution of a Cuban-South American genus, *Bonnetia* Mart. et Zucc. (Kobuski 1948)



Fig. 101 *Bonnetia cubensis* (Britt.) Howard an endemic tree of the sclerophyllous montane rain forests of the Moa range at Alto de la Iberia (Photo: A. Borhidi)

Andira inermis. Plants of semi-deciduous and mesophilous forests: *Cedrela mexicana*, *Guarea guidonia*, *Zanthoxylum martinicense*, *Hymenaea courbaril*, *Psidium guajava*, *Faramaea occidentalis*, *Amaioua corymbosa*, *Alibertia edulis* and *Chiococca alba* (Fig. 102). Rainforest elements: *Brunellia comocladifolia*, *Weinmannia pinnata* and *Didymopanax morototoni*. Savanna species are *Samanea saman* and *Curatella americana* etc.

18.2.6 Pan-tropical elements

In a wider sense this group includes species occurring in the tropical or subtropical regions of the world. Many subgroups can be distinguished, for example, African-Neotropical, Asiatic-Neotropical, Pacific-Neotropical etc. and the group of Palaeotropical species also present in the Antilles, e.g. *Phaius tankervilleae*. This classification is not detailed here, since these elements appear less significant in the study of the origin and development of the Cuban flora. The number of pan-tropical *sensu lato* species is 221 (AF: 3.6%, NF: 3.8%). 80% are herbs. Major life-form categories are the hemicryptophytes (71, 32.9%), therophytes (46, 20.8%) and lianes (35, 15.8%). Most of them are distributed all over the country, more than 55% of the pan-tropical species occur in every province. Oriente is the richest in pan-tropical species (187, 85.6%). Plants of the seashore and mangrove vegetation: *Philoxerus vermicularis*, *Sesuvium portulacastrum*, *Canavalia maritima*, *Ipomoea pes-caprae*, *Leucaena leucocephala*, *Rhizophora mangle* and *Conocarpus erecta*. Others, such as *Paspalum vaginatum*, *Fimbristylis*



Fig. 102 Geographical distribution of a neotropical element. *Chiococca alba* (L.) Hitchc. (Svenson 1946)

squarrosa, *F. annua*, *F. spathacea* and sixteen *Cyperus* spp. occur in swampy meadows. Some trees (*Ceiba pentandra*, *Acacia farnesiana*), lianes (*Caesalpinia crista* and *C. bonduc*, *Abrus precatorius* and sixteen *Ipomoea* sp. and weeds (*Mimosa pudica* and *M. pigra*) are also worth mentioning.

18.2.7 The group of extratropical species

Species assigned to this chorological group have a tropical geographic range significantly extended to the temperate zone, or vice-versa. Four types are recognized in Cuba including 121 species altogether (1.6% of the flora). The overwhelming majority of species are herbs (119, 98.4%). The types are as follows:

a) **North and Central American species.** 41 taxa (0.7% of the flora), herbs with one exception. 46.4% are hemicryptophytes and 32.2% are helo-hydatophytes. Their distribution in Cuba is sporadic, usually restricted to one province. Most species are found in western Cuba (52.7% in Pinar del Rio, 45.7% in Habana). Important representatives are *Panicum virgatum*, *Andropogon virginicus*, *Scirpus olneyi*, *S. validus*, *Proserpinaca palustris* and *Teucrium canadense*.

b) **American species.** Besides the neotropical region these are also found in the temperate zone of South and North America. 46 taxa (0.7% of the flora). 45 species are herbs (97.8%), mainly hemicryptophytes (23, 50%), helo-hydatophytes (10, 21.8%) and therophytes (7, 15.2%). These are concentrated to western Cuba, the greatest number of species occur in Habana (76.6%) and Pinar del Rio (68.1%), while Oriente (38.3%) and Camagüey (27.7%) have much less. *Brachiaria extensa*, *Fimbristylis spadicea*, *Pontederia lanceolata*, *Nymphaea odorata*, *Jussiaea peruviana* und *Teucrium cubense* are examples.

c) **Amphiatlantic and circumpolar species.** These otherwise well-separated types are combined to simplify the discussion. Only five herbs are present in Cuba (.08%), all hemicryptophytes. The circumpolar species (*Drosera rotundifolia*, *D. intermedia*) occur exclusively in the bogs of western Cuba. The amphiatlantic species (*Eleocharis parvula*, *Salicornia perennis* and *Suaeda fruticosa*) are more widely distributed seashore plants.

d) **Cosmopolitan species.** Their number is 29 (.5%). All herbs, including aquatic and uliginal plants and weeds, e.g. *Najas marina*, *Ruppia maritima*, *Lemna trisulca*, *Cynodon dactylon*, *Solanum nigrum*, *Datura stramonium* and *Ambrosia elatior*.

18.2.8 Adventive elements

The number of cultivated and introduced species naturalized in Cuba is relatively high (376, AF: 6.1%). 39.4% are phanerophytes, especially mesophanerophytes (61, 16.3%). The majority of herbs are hemicryptophytes (85, 16.3%) and therophytes (78, 20.6%). According to origin three groups are distinguished.

a) **Neotropical adventives.** 113 species (1.8% of the flora). 52.2% are woody plants, 2.5% are mesophanerophytes and 14.4% microphanerophytes. Most herbs are hemicryptophytes (15%), therophytes (13.2%), lianes (8%) and tree-sized forbs (7.1%). Examples are *Ananas comosus*, *Agave furcroydes*, *Castilleja elastica*, *Myroxylon balsamum*, *Annona muricata*, *Euphorbia pulcherrima*, *Theobroma cacao*, *Sterculia apetala*, *Ipomoea batatas*, *Anacardium edule* and *Thevetia peruviana*.

b) **Palaeotropical adventives.** 182 species (3% of the flora). 46% are woody plants, mainly mesophanerophytes (39, 21.5%). Dominant herbaceous life-forms

are the hemicryptophytes (24.9%), therophytes (14.3%) and lianes (8.2%). For simplicity, no distinction is made among adventives of African, Asiatic and Pacific origin. Moreover, species introduced from Australia, New Zealand and the tropical East Asia are also included here. Some examples: *Dichrostychnis cinerea* (a deleterious tree-weed epidemic in Cuba), *Tamarindus indica*, *Delonix regia*, *Indigofera tinctoria*, *Ricinus communis*, *Euphorbia lactea*, *Cryptostegia grandiflora*, *Catharanthus roseus*, *Lagerstroemia indica*, *Terminalia catappa*, *Syzygium jambos*, *Bambusa vulgaris*, *Cocos nucifera*, *Artocarpus incisa*, *Musa paradisiaca*, *Casuarina equisetifolia* and eight *Citrus* spp.

c) **Extratropical adventives.** Vegetable plants, ornamental garden plants and weeds originating from Eurasia or North America. 81 species (1.3% of the flora). 93.8% are herbs, mainly annuals and perennials (46, 56.8%) and hemicryptophytes (23, 28.4%). Particularly widespread in the province of Habana due to intensive anthropogenic effects and commercial transport. Some examples are *Lolium temulentum*, *Medicago lupulina*, *Hypericum perforatum*, *Daucus carota*, *Senecio vulgaris* and *Taraxacum officinale* etc.

18.3 A phytogeographical analysis of the pteridophytes of Cuba

Only twelve types are distinguished within this chorological group since Cuba, as well as the other countries of the Caribbean, are much less intensively surveyed for ferns than for flowering plants. Therefore, our present knowledge is not sufficient for subdividing even the endemics. Nevertheless, it is possible to make some general comments regarding the pteridophyte “flora” of Cuba. The proportion of endemics is much lower, whereas that of the widely distributed species is much higher than in case of the flowering plants. The reason is that pteridophytes are much older (time factor) and their migratory characteristics are more advantageous (Table 19).

18.3.1 Endemics

53 species (10.6% of the flora). Alain (1958) estimated the number of endemic species at 64 (12–13%). Proctor (1971/b and Walker (1954), however, showed that many taxa considered earlier as Cuban endemics are in fact present in Jamaica as well. Mainly terrestrial hemicryptophytic and geophytic ferns (19, 35.8% and 13, 24.5%), but the percentage of tree ferns (5, 9.5%), epiphytic ferns (7, 13.2%) and lianes (5, 9.5%) is also significant, indicating a relatively early isolation of montane rainforests. Examples are: *Isoetes cubana*, *Alsophila strigillosa*, *Anemia cajalbanica*, *A. coriacea*, *A. cuneata*, *Cyathea araneosa*, *C. cubensis*, *Dryopteris crypta*, *Polypodium flexuosum*, *Polystichum decoratum*, *Gymnogramma cubensis*, *Lindsaya cubensis* and *Lygodium cubense* etc.

18.3.2 Caribbean species

184 species altogether (36.8% of the flora). This chorological group may be subdivided into five types as follows:

a) **Greater Antillean elements.** 77 species (15.4% of the flora). Mainly hemicryptophytes (22, 28.5%) and geophytes (19, 24.7%), although the number of epiphytes (13, 16.9%), chamaephytes (11, 14.3%) and tree ferns (8, 10.4%) is also remarkable. More common species are *Selaginella stolonifera*, *Botrychium underwoodianum*, *Adiantopsis paupercula*, *Cheilanthes harrisii*, *Cyathea furfuracea* (Fig. 103), *C. pubescens*, *Diplazium unilobum*, *Elaphoglossum eggersii*, *Fadyenia hookeri* and *Maxonia apiifolia* etc.

b) **Antillean elements.** 38 species (7.6%). More than half the species are geophytes (12, 31.5%) and epiphytes (9, 23.6%). The hemicryptophytes (6, 15.8%), chamaephytes (5, 13.2%) and tree ferns (4, 10.6%) are less significant. Species belonging to this group are *Thelypteris pinnata*, *Stenochlaena sorbifolia*, *Pityrogramma sulphurea*, *Oleandra articulata*, *Odontosoria aculeata*, *O. uncinella*, *Hymenophyllum lanatum*, *Elaphoglossum martinicense*, *Dryopteris hastata*, *Cyathea arborea* (Figs 104, 105).

c) **Northern Caribbean elements.** 27 species (5.4% of the flora). Mostly hemicryptophytes (8, 33.4%), geophytes (8, 29.6%) and epiphytes (4, 14.8%). *Cyathea tenera*, *Adiantum deltoideum* and *Lycopodium montanum* are examples.

d) **Southern Caribbean elements.** Only five species, accounting for 1% of the flora. No tree-sized ferns and lianes occur in this group. Examples: *Adiantum cristatum*, *Dryopteris incisa* and *Hymenophyllum axillare*.



Fig. 103 Geographical distributions of a typical element of the Greater Antilles, *Cyathea furfuracea* Bak. (Tryon 1976)

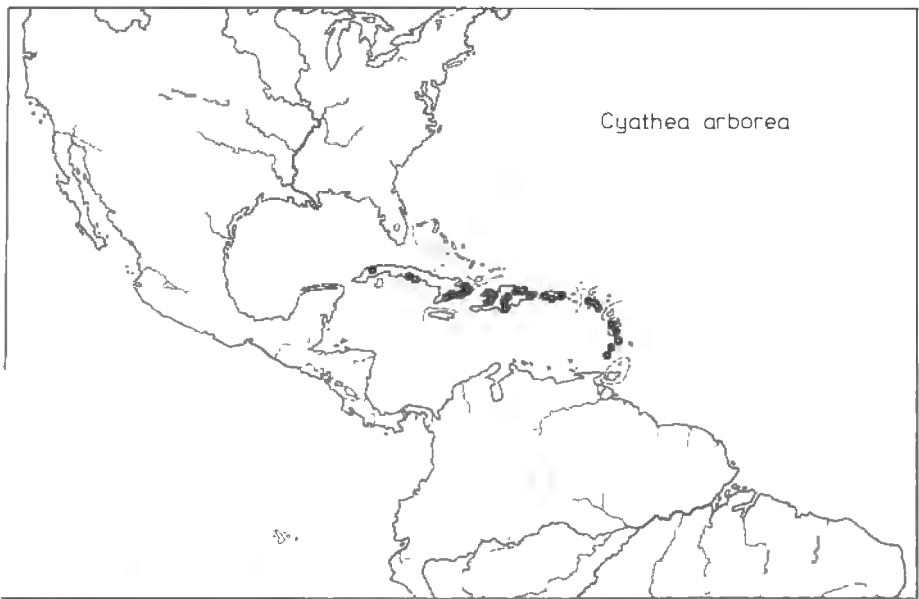


Fig. 104 Geographical distribution of an Antillean element, *Cyathea arborea* (L.) Sm. (Tryon 1976)



Fig. 105 Silhouettes of the leaf crown of the *Cyathea arborea* (L.) Sm. tree ferns on the Gran Piedra, Maestra range, at 1100 m a.s.l. (Photo: A. Borhidi)

e) **Pan-Caribbean elements.** 28 species (5.6% of the flora). Mainly hemicryptophytes (9, 32.1%) and geophytes (6, 21.4%), and also epiphytes (5, 17.9%), chamaephytes and tree ferns (3, 10.7% each). Noted species are *Alsophila aspera*, *Asplenium dentatum*, *Bolbitis nicotianifolia*, *Diplazium arboreum*, *Dryopteris sancta*, *Paltonium lanceolatum*, *Polypodium costatum*, *Hymenodium crinitum* etc.

f) **Central American elements, not found outside Cuba in the Antilles.** Nine species (1.8%). Six epiphytic rainforest ferns are of this chorological type. Examples: *Alsophila myosuroides*, *Anemia wrightii*, *Dryopteris asterothrix*, *Elaphoglossum revolutum* and *Hymenophyllum contortum*.

18.3.3 Neotropical elements

The largest chorological group of pteridophytes with 189 species (37.8%). Three life-forms, the hemicryptophytes (51, 27%), epiphytes (50, 26.4%) and geophytes (48, 25.4%) are fairly evenly represented. Other important life-forms are the tree ferns (14, 7.5%) and lianes (12, 6.3%). Some examples are *Lycopodium taxifolium*, *Equisetum giganteum*, *Marattia alata*, *Acrostychnum danaifolium*, *Alsophila aquilina*, *Anemia adiantifolia*, *Asplenium cristatum*, *Blechnum occidentale*, *Cyathea arborea*, *Dennstaedtia cicutaria*, *Dryopteris pedata*, *Elaphoglossum firmum*, *Hemionitis palmata*, *Hymenophyllum sericeum*, *Lindsaya stricta*, *Nephrolepis rivularis*, *Peltapteris peltata*, *Pityrogramma tartarea*, *Polypodium phyllitidis* and *Rhipidopteris peltata* etc.

18.3.4 American species

These elements also occur in the temperate zone of the continent. Two species, *Azolla caroliniana* and *Selaginella apus* accounting for 0.4% of the flora.

18.3.5 Pantropical elements

54 species (10.8% of the flora). Significant life-forms are the hemicryptophytes and geophytes (15, 27.8% each) and also the chamaephytes (12, 22.3%) and epiphytes (10, 18.5%). Examples are *Lycopodium cernuum*, *Psilotum nudum*, *Acrostychnum aureum*, *Asplenium cuneatum*, *Blechnum serrulatum*, *Dryopteris dentata*, *Elaphoglossum hirtum*, *Hymenophyllum polyanthos*, *Pityrogramma calomelanos*, *Polypodium duale* and *Trichomanes rigidum*.

18.3.6 Cosmopolitan elements

13 species (2.6% of the flora). Mainly geophytes (38.5%) and chamaephytes (30.7%) and also some aquatic ferns. *Lycopodium clavatum*, *Botrychium virginianum*, *Ophioglossum vulgatum*, *Adiantum capillus-veneris*, *Osmunda regalis*, *Pteris longifolia* and *Salvinia natans* are examples.

18.4 Some special distribution patterns

Further valuable information may be revealed regarding the origin and distribution of the flora if the importance of each chorological element in the provinces (floristic subsets) and in the whole country (floristic universal set) is examined and these importance values are compared. The results are summarized in Table 28 and Fig. 106. The latter illustrates the percentage distribution of chorological elements in the complete set of species, Fig. 106 shows the same for the flora of each province. In case of floristic subsets empty columns indicate chorological elements with a percentage lower than in the complete flora. Full columns refer to those having larger percentage and, consequently, an increased “role” in the corresponding subflora.

18.4.1 The importance of endemic and Neotropical elements

The most striking characteristic of the flora is the different role of endemics and Neotropical elements. Comprising two-third of total flora, these two chorological types are predominant in Cuba. More than half the species are endemics, many of them being restricted to one province (local endemics: El). Oriente is the only province where the percentage of local endemics exceeds the proportion of locals in the entire flora. The other extreme is represented by the Pan-Cuban elements (PCu) with local percentages always larger than their proportion in the total. The same holds true in respect of Neotropical (NTr), pan-tropical (PTr) and Antillean—South American (ASA) elements.

18.4.2 Greater Antillean elements and the species of Cuba, Florida and the south-eastern States

There is also a big contrast between the Greater Antillean species (GA) and those distributed in Cuba, Florida and the southeastern United States (CuFU). The first group is relatively more important only in Oriente and Las Villas. The other type however, has a percentage larger in western Cuba (Pinar del Río and Isla de Pinos) than in the whole country.

18.4.3 Extratropical and cosmopolitan elements

The fact that the percentage of North American extratropicals (NAm) and cosmopolitans (Csm) is larger only in Habana and Matanzas than their quota in the complete flora also deserves attention. This is a consequence of the intensive anthropogenic influence on the flora of these two provinces.

18.4.4 Conclusions

It may be concluded from the foregoing that

- The majority of endemics came into being under extreme environmental conditions and became highly specialized and isolated. They were unable to colonize larger areas having insufficient space or time, or migratory power and competitiveness.
- The widely distributed species originated from outside Cuba were more adaptive and competitive. These euryoecic species aggressively penetrated to Cuba and took a prominent part in the evolution of flora and vegetation.
- The island is not homogeneous in respect of flora evolution: there are at least two ancient and possibly some younger evolutionary centres. The largest and, probably, the oldest centre is Oriente, although the flora of western Cuba (Pinar del Rio and Isla de Pinos) is also of similar age and significance.

18.5 Chorological types of bryophytes

Crosby (1969) analyzed the geographic range of 230 selected moss species and came to conclusions concerning the distribution of mosses in the Antilles. Duarte (1979), at a conference held at the Botanical Institute of the Cuban Academy of Sciences, presented a new chorological analysis of the mosses of Cuba.

19 The phytogeographic characteristics of Cuba

19.1 Some outstanding phytogeographic features of Cuba

The floristic analysis and the study of chorological types suggest that the most important and most typical characteristics of the flora of Cuba are as follows: 1. Dominance of endemics, 2. Disjunction, 3. Vicariancy, 4. Inversion, 5. Microphyllia, 6. Micranthia, 7. Relics, and 8. Vulnerability.

19.2 The dominance of endemics

As shown earlier (Table 28), the endemics comprise a total of 51.4% native flora. This is outstandingly the largest percentage in the Antilles. Marie-Victorin and León (1942, 1944, 1956) attributed this to the high Mg and Fe concentrations of "limonite areas". According to Alain's (1958: 16) hypothesis, the reasons are the early isolation of the flora during the upper Miocene, the diverse edaphic conditions of the country and the arid climate of certain areas.

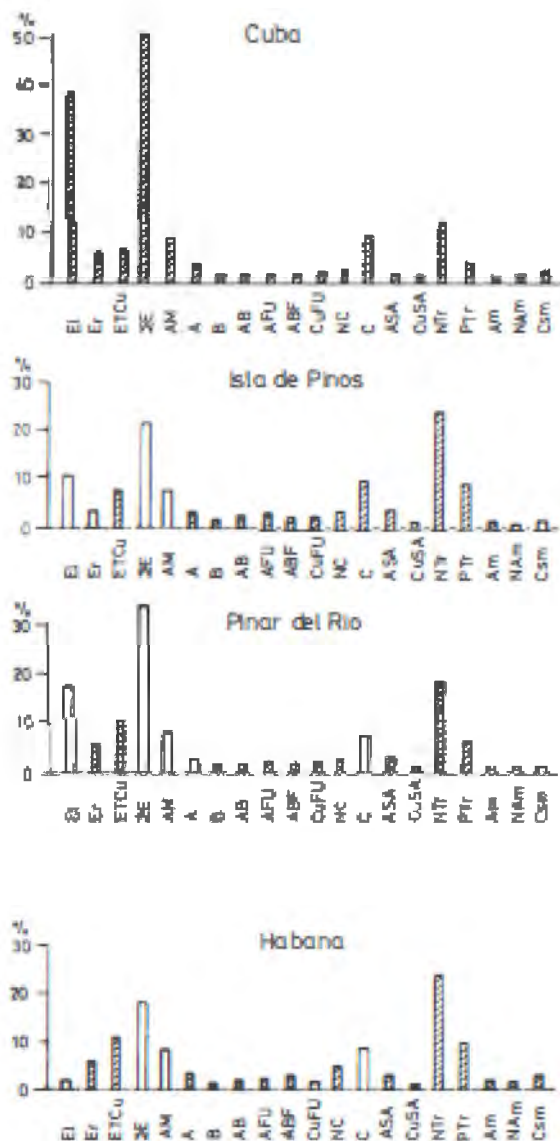
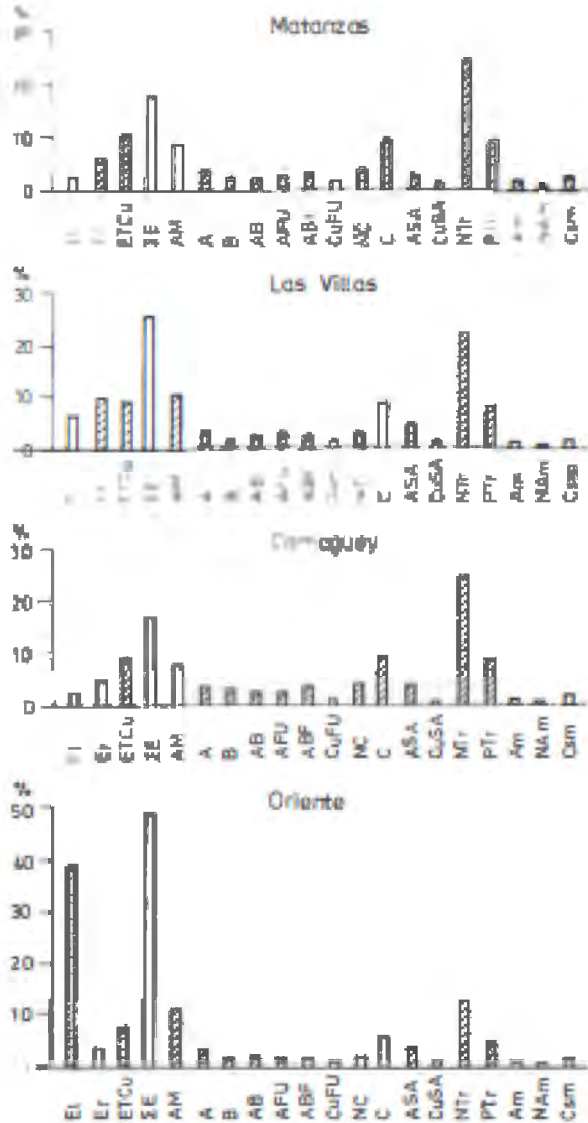


Fig. 106 Chorological analysis of the flora of Cuba and the partial florulas of the provinces. Abbreviations: El=endemic local; Er=endemic regional; ETCu=Pan-Cuban endemics; ΣE=all the endemics of Cuba; AM=species of the Greater Antilles; A=Antillean species; B=species of Cuba and the Bahamas; AB=species of the Antilles and the Bahamas; AFU=species of the Antilles, Florida and Southern United States; ABF=species of the Antilles, Bahamas and Florida; NC=North-Caribbean



species; SC=South-Caribbean species; C=Pan-Caribbean species; ASA=species of the Antilles and South America; CuSA=species of Cuba and South America; NTr= Neotropical elements; PTr=Pan-tropical elements; Am=American species; NAm=North American species; Csm=Cosmopolitan species

19.2.1 The ecology of endemic speciation

In examining the ecological background of the speciation of endemics Muñiz (1970) found that eight habitat types have a substantial influence on flora development. These habitats occur in 25 areas in Cuba. The habitat types with the number of areas in brackets are:

- Ferritic soils and tropical brown soils derived from serpentine (6)
- Ferrallitic soils derived from serpentine (5)
- Oligotrophic quartz-allitic yellow soils (2)
- White sandy habitats (2)
- Young, dry, coastal limestone areas (4)
- Young, montane, karstic limestone areas (2)
- Old, montane limestone karsts, “haystack mountains” (1)
- High montane areas

No doubt that the number of factors facilitating the speciation of endemics is large. The influence and importance of these factors differed with time and space. Factors potentially influencing speciation are listed below:

Insularity and isolation

Geographic factors

- external (insularity)
- internal (isolation)

Ecological factors

Orographic factors

- alternation of lowlands and mountains
- great relief-energy

Geological and edaphic factors

- serpentine and other ultrabasic rocks
- frequent occurrence of limestone karsts
- frequent occurrence of acid, slatey parent material
- frequent occurrence of acid, white sands

Sociological factors

- community mosaics
- communities as barriers of migration
- interactions between plants and animals

Climatic changes

Alternation of wet and dry periods

Alternation of cool wet and warm dry periods

Genetic factors

Mutagenic speciation

Hybridogenic speciation, introgression

Genetic drift

19.2.2 Horizontal distribution of endemics

The study of the horizontal and vertical distribution of endemics yields valuable information on the ecological effects influencing speciation and geographic range. Figure 107 shows the number of endemic species per area. The intertidal mangroves and coastal swamps are the poorest in endemics. The lowlands of Central Cuba and the southern part of Isla de Pinos are moderately poor, having 25–50 endemic species. Moderately rich areas (50–75) are the younger coastal limestone habitats (Guanahacabibes Peninsula, the southern coast of Las Villas and the northwestern coast of Oriente), the slatey outcrops and white sands in Isla de Pinos, the hilly regions of Central Cuba and the medium altitude zone of Sierra Maestra. The rich areas, containing 76–100 regional endemics, are the slatey outcrops of Pinar del Rio, the ancient serpentines of Cajalbana, the younger serpentine zone of Habana, Matanzas and Motembo, the rainforest region of Sierra Escambray, the southern coast at Sierra Maestra and its northern karstic zone (Guisa—Baire) in Oriente, and the limestones of the Sagua-Baracoa Massif. Most areas very rich in endemics (100–150) are on serpentine, three are younger (Santa Clara, Camagüey, Holguin) and three others are ancient latosol areas (Nipe, Cristal, Moa-Baracoa). In respect of endemic richness only the ancient conical karsts in the Sierra de los Organos, the montane zone of Sierra Maestra and the xerotherm semi-deserts of southern Baracoa are commensurable to the above localities. Outstandingly rich areas are found only in the montane zone of ancient serpentine mountains, such as the Nipe Mts., the surroundings of Pico del Cristal and the highlands of Moa (El Toldo, Iberia etc.), where more speciation-inducing factors (age, serpentine, isolation, montane character) are combined.

19.2.3 Vertical distribution of endemics

After reading the foregoing one would expect that the number of endemics increases as altitude increases, due to the montane effects. However, as our studies in Pico Turquino showed, the vertical distribution of endemics is a more complex matter. Figure 108a demonstrates that the number of endemics increases up to the lower limit of the cloud zone and then rapidly decreases. Its reason is that the vertical distribution of regional endemics of lowlands and mountains of medium height differs from that of the local montane endemics. The number of species from the first group increases up to 1000 m, hardly changes up to 1500 m and then falls suddenly. The number of montane endemics, however, abruptly increases between 1000 and 1500 m and does not change anymore. The disappearance of lowland regional endemics from the high altitude zone causes the decrease of endemic species (Fig. 108b). Contrary to the absolute figures, the relative proportion of endemics rapidly increases with altitude. That is, the few endemics occurring become predominant at higher elevations.

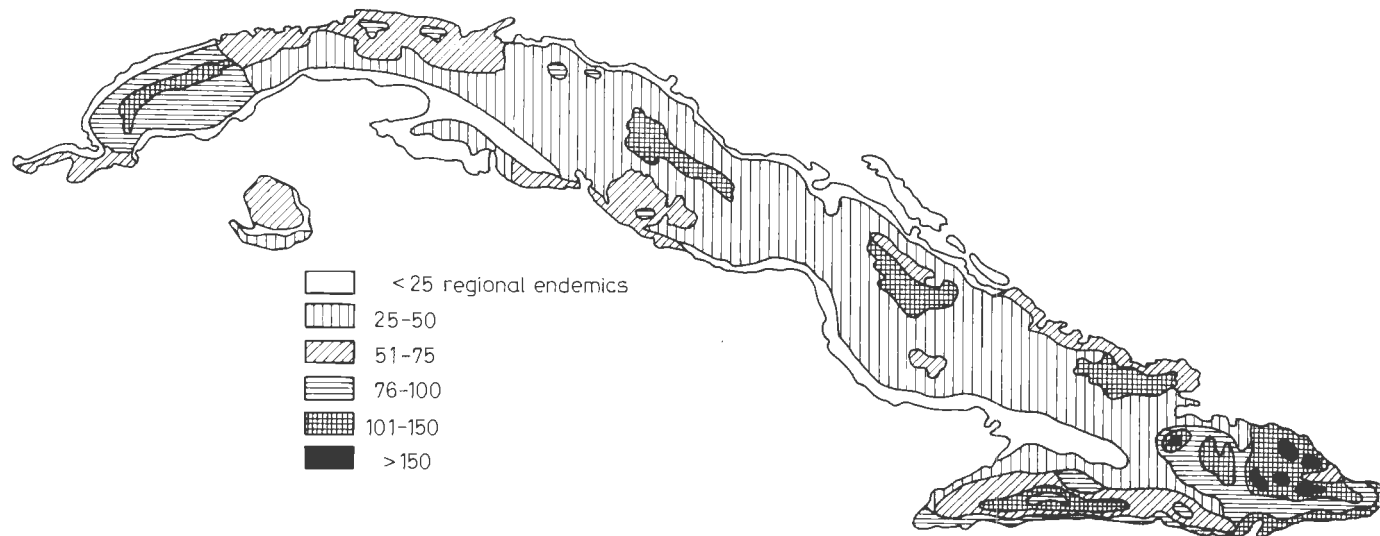


Fig. 107 The number of endemics in the different geographical regions of Cuba (Samek 1973, modified by Borhidi 1985)

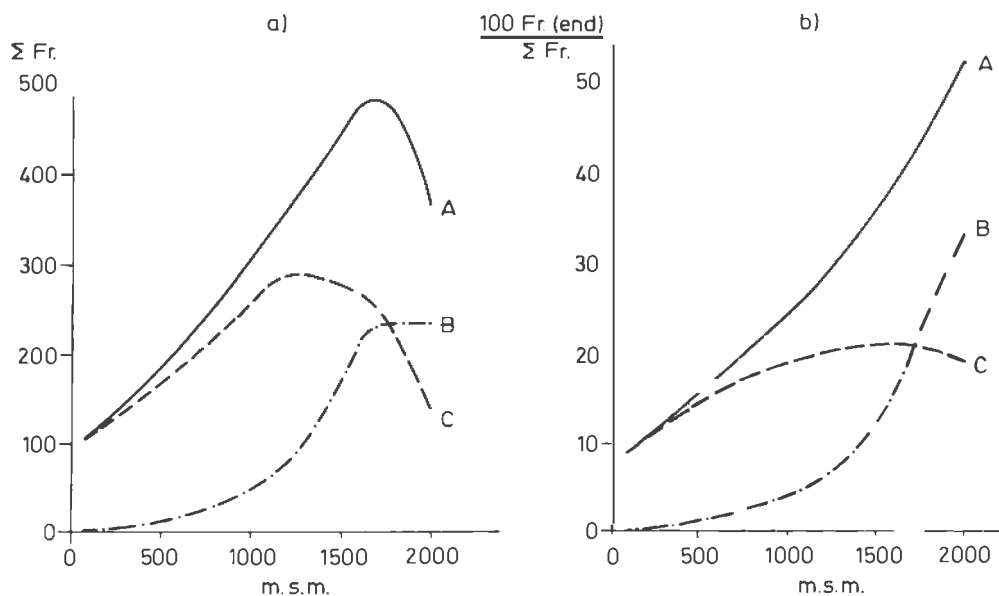


Fig. 108 Changes of the total a) and the relative frequency b) of the endemic species along a vertical gradient in Cuba. A: total of endemics; B: local endemics; C: regional endemics

19.2.4 Relationship between aridity and the number of endemics

Stebbins (1952) pointed out that ecological drought stimulates speciation. The ecological and chorological study of many Cuban endemics provides evidence for this phenomenon. The largest number and highest density of endemics may be observed in the arid zones (semi-desert, coast) and in the physiologically dry habitats (serpentine, limestone karsts, white sands). Also, the majority of endemics have xeromorphic leaves. Table 29 and Fig. 54 show the leaf-size distribution of 1115 tree and shrub species occurring in forty forest communities endemic to Cuba. Among macrophylls and mesophylls the widely distributed species dominate, but in the microphyll, nanophyll, leptophyll and aphyll categories the endemics outnumber the others and their proportion increases as leaf-size decreases.

19.3 Disjunction

Another chorological characteristic of the flora is disjunction, the separation of the geographic range of a given taxon into several isolated areas. Many different types of disjunction, such as bipolarity, bi-, tri- and multisectorial distribution may be observed in Cuba.

19.3.1 Bipolarity

The most striking type of disjunction is the bipolarity of geographical range of certain genera (Samek 1973c) that occur only in western Cuba and Isla de Pinos, and also in the mountainous regions of Oriente. This is the case with *Spathelia* (Fig. 109), *Purdiaea* (Figs 110), *Heptanthus* (Figs 111, 112), *Pinus*, *Podocarpus* and many other genera. The reason is that the eastern and western parts of Cuba have been isolated for a long period of time as from the beginning of the Tertiary. In most cases, the number of species in the disjunct genera is higher in Oriente than in western Cuba. The larger area and more diversified orography of Oriente cannot explain this observation, since the Sierra Maestra emerged only at the end of the Tertiary, and western Cuba has more diverse geology than Oriente. A more acceptable interpretation is that Oriente and the continent had been connected



Fig. 109 The geographical distribution of the genus *Spathelia* in Cuba (Samek 1973 and Borhidi 1985)

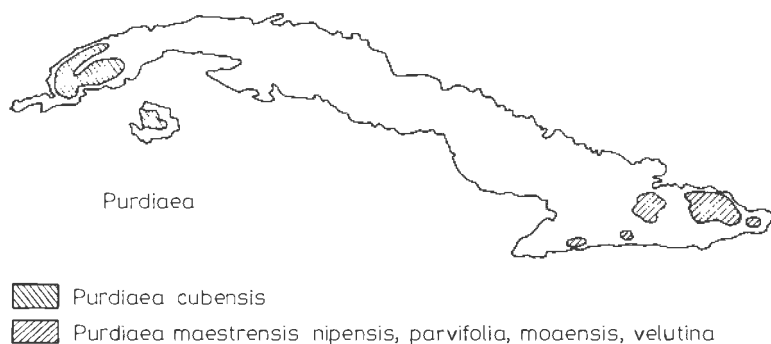
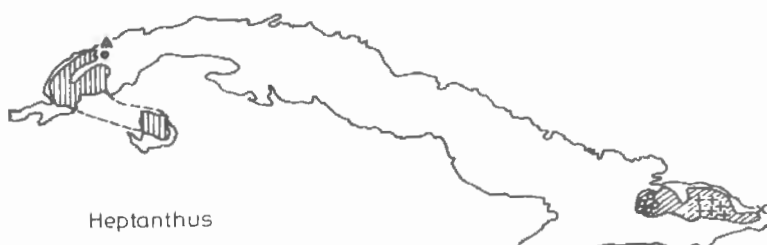



Fig. 110 The geographical distribution of the genus *Purdiaea* in Cuba (Thomas 1960, Samek 1973 and Borhidi 1985)



 *H. cochlearifolius*

• *H. ranunculaoides*

▲ *H. brevipes*

 *H. lobatus*

○ *H. cordifolius*

++ *H. Shaferi*

× *H. yumuriensis*

Fig. 111 The geographical distribution of the genus *Heptanthus* Griseb. (Borhidi 1972)



Fig. 112 A little endemic herbaceous plant of the riverside scrub vegetation: *Heptanthus lobatus* Britt. in the Nipe Mts. (Photo: A. Borhidi)

through Hispaniola for a relatively longer period of time, facilitating a steadier “gene supply” for this province, Geologists (Arlt 1917–1922, Schuchert 1935) pointed out that the separation of western and eastern Cuba preceded that of Oriente and Hispaniola, although botanists, following Urban (1923), disagreed. The present analysis of the flora, however, provides a botanical evidence for the geological results. It is noted that Silva (1979) arrived at the same conclusion in his studies on the Chiroptera fauna of Cuba.

At species level only a few examples of bipolar distribution exist. These species are found mainly on serpentines, e.g. *Amyris lineata*, *Vernonia angustissima* and *Croton bispinosus*, but also in limestone karsts, such as *Byttneria microphylla* and *Neoregnellia cubensis*.

19.3.2 Bisectorial geographic distributions

Another type of disjunction is represented by some rainforest species (*Magnolia cubensis*, *Hedyosmum grisebachii*, *Ocotea ekmanii*; see Figs 138, 245) occurring both in the mountains of Oriente and the Guamuha Massif. Up to the early Tertiary, these regions were connected as still indicated by the presence of the relict block-mountains of Sierra de Najasa. This connection, however, must have come to an end in a short time, since most common elements belong to ancient dicotyledonous families (Magnoliaceae, Lauraceae, Chloranthaceae, etc.). Two other types of bisectorial distribution have developed between the mountainous region of western Cuba and the Guamuha Massif: 1. the plants of karstic forests and other limestone areas (*Sapium leucogynum* and *Miconia cubensis*) and 2. species on serpentines in Pinar del Rio and the Escambray mountains (*Coccothrinax crinita* and *Linodendron venosum*).

19.3.3 Trisectorial distributions

The occurrence of several taxa at three isolated spots (western Cuba, Guamuha Massif, Oriente) indicates that these areas had been separated for a long period of time in the Tertiary as a result of shallow-sea transgression of the island. The genera of *Lyonia* and *Vaccinium* some montane forest species, such as *Tetrazygiopsis laxiflora* and *Sapium pallens*, and some acidophilous species e.g. *Hypericum styphelioides* exhibit such a trisectorial distribution. As a consequence of longer geographic and ecological isolation of the *Hypericum styphelioides* populations, this species is divided into three subspecies (Lippold 1970). Some taxa considered earlier to have bi- or tri-sectorial distribution, proved to be taxonomically heterogeneous, such as *Amyris lineata*, *Croton brittonianus*, *Ditta myricoides*, *Lyonia elliptica*, *Vaccinium cubense* etc.

19.3.4 Multisectorial areas

Several serpentine species have relatively large geographic ranges occurring in many isolated spots. In these cases the cause of disjunction is the scattered occurrence of acceptable habitats, rather than the prehistoric geographic effects. Examples are *Phyllanthus orbicularis* (Fig. 127), *Neobraccia valenzuelana* (Fig. 117), *Rondeletia camarioca* and *Jacaranda cowellii* (Fig. 131). This type of geographical range is characteristic of the common species of the numerous isolated serpentine areas, as well as the plants of the isolated coastal limestones (*Castela calcicola*, *Machaonia havanensis*, *Dendrocereus nudiflorus* and *Neobraccia angustifolia* etc.).

19.4 Vicariancy

The third characteristic feature of the flora of Cuba is the abundance of vicarious taxa. All types of vicariancy are widespread. This fact indicates prehistoric isolations and allows to surveyor to make inferences concerning the influence of ecological factors on evolution and the development of certain related taxa.

19.4.1 Geographic vicariancy

Many examples exist in Cuba. Figure 113 shows the range of two endemic vicarious genera of lianes, *Lescaillea* and *Harnackia*. Both occur in pinewoods and evergreen shrublands on latosols derived from serpentine. This serves as an evidence suggesting a relationship not only between the recent vegetation of the Cajalbana and Nipe Mountains, but also in the past flora development of these regions. Further examples are *Anemia coriacea* (Fig. 128) and *Moacroton* (Fig. 130) among many others. The ranges of the subgenera *Thrinax* and *Hemithrinax* also exemplify geographic vicariancy (Fig. 114). *Thrinax radiata* is a species of rocky and sandy beaches, whereas *Th. morrisi* and *Th. drudei* occur in the karsts of western

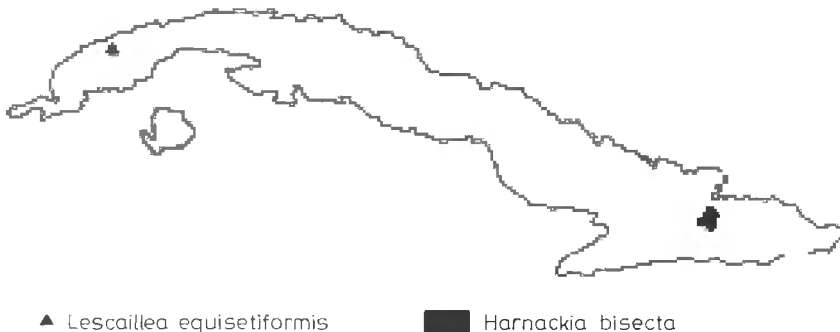


Fig. 113 The geographical distribution of the genera *Lescaillea* Wr. ex Sauv. and *Harnackia* Urb. (Borhidi 1985)

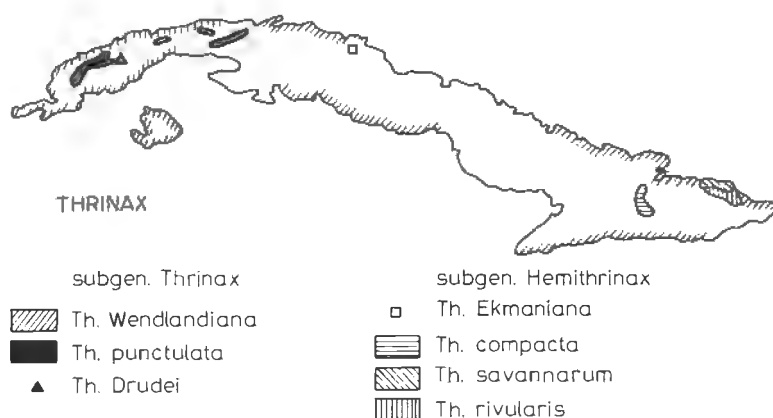


Fig. 114 The geographical distribution of the genus *Thrinax* in Cuba (Borhidi 1985)

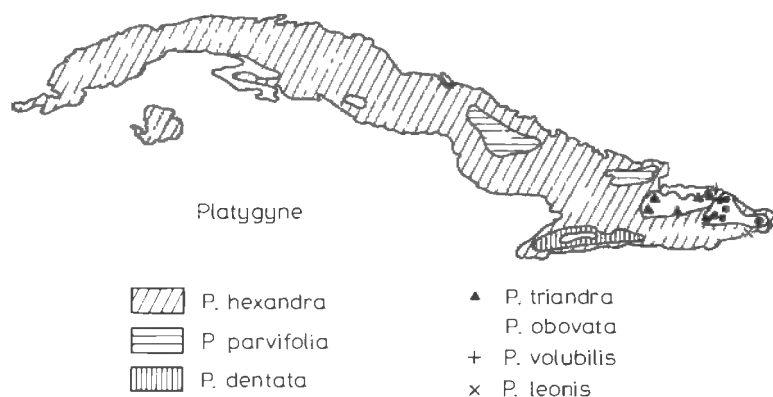


Fig. 115 The geographical distribution of the species of genus *Platygyne* Muell. Arg. (after Borhidi 1972)

Cuba replacing each other. In central and eastern Cuba *Thrinax* is substituted by the subgenus *Hemithrinax* (*T. ekmaniana* and *T. compacta*). Their ecological vicariads, namely *T. rivularis* and *T. savannarum*, occur on the serpentine of Moa. The latter two are cenological vicariads of each other, being forest and scrub species, respectively.

19.4.2 Combinations of geographic and ecological vicariancy

The genus *Platygyne* (Fig. 115) exhibits both types of vicariancy discussed so far. *Platygyne hexandra*, an ubiquitous species found all over the country, is replaced by *P. parvifolia* on serpentines in Camagüey and Holguín, by *P. dentata* in the montane zone of Sierra Maestra, and by four other species in the serpentine

mountains of northeastern Oriente. Furthermore, the latter four species are also vicarious in their geographic distribution within the province. This observation supports the view that speciation is more intensive on serpentines than on other bedrocks (Borhidi 1972a). For this process the Cuban species of the *Oplonia* genus serve also as a good example (Fig. 116). An interesting exception is genus *Neobraccia* (Fig. 117) with two species on serpentine, *N. ekmanii* endemic to Moa and the Pan-Cuban *N. valenzuelana*. Although the latter occurs on all serpentine outcrops in Cuba, the morphological variability of populations living under different climatic conditions remains within specific limits. Conversely, the ancestral form of the limestone species has been broken into four vicarious species along the coasts consisting of primitive and recent limestones. These species constitute morphologically well-separated small populations with considerably isolated geographic distributions.

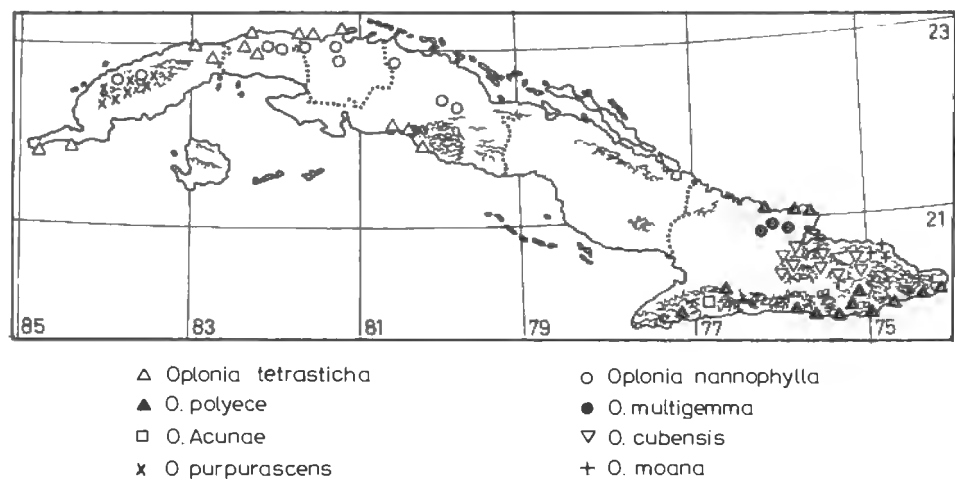


Fig. 116 The geographical distribution of the species of genus *Oplonia* Raf. in Cuba (Borhidi and Muñiz 1978)



Fig. 117 The geographical distribution of the species of genus *Neobraccia* Britt. in Cuba (Borhidi 1985)

19.4.3 Ecological vicariancy at the infraspecific level

The ecological factors affecting speciation may be best investigated and demonstrated through examples of infraspecific vicariancy. This term means that a young species of great migratory and penetrative power colonizes new habitats which in turn modify the populations. *Maytenus buxifolia* (Fig. 118), an Antillean species is a good example. It separates into five vicarious subspecies in Cuba: the widely spread ancestor, two subspecies on serpentines (ssp. *cajalbanica* in western Cuba and ssp. *serpentini* in the east), and an extremely drought-tolerant subspecies in the semi-desert belt (ssp. *cochlearifolia*). An endemic microphyllous drought-tolerant shrub, *Reynosia mucronata* (Fig. 119) exhibits similar vicariancy. The ancestor occurs in the shrublands of central Cuba with preference in favour of neither limestone nor serpentine. However, the populations on the latosols of Nipe Mts. (ssp. *nipensis*) and the stands occurring in the semi-desert zone of southern Baracoa (ssp. *azulensis*) are geographically isolated subspecies (Borhidi and Muñiz 1971).



Fig. 118 The geographical distribution of the subspecies of *Maytenus buxifolia* (A. Rich) Griseb. in Cuba (Borhidi 1985)

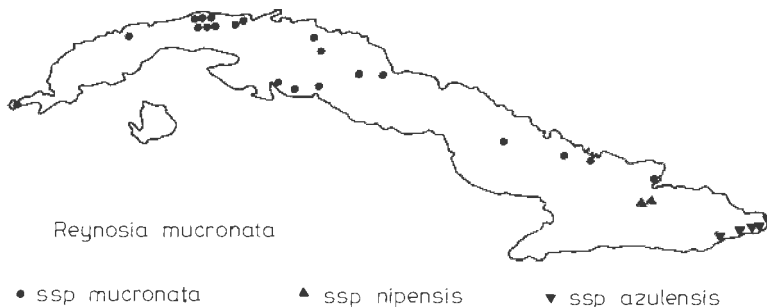


Fig. 119 The geographical distribution of the subspecies of *Reynosia mucronata* Griseb. in Cuba (Borhidi 1985)

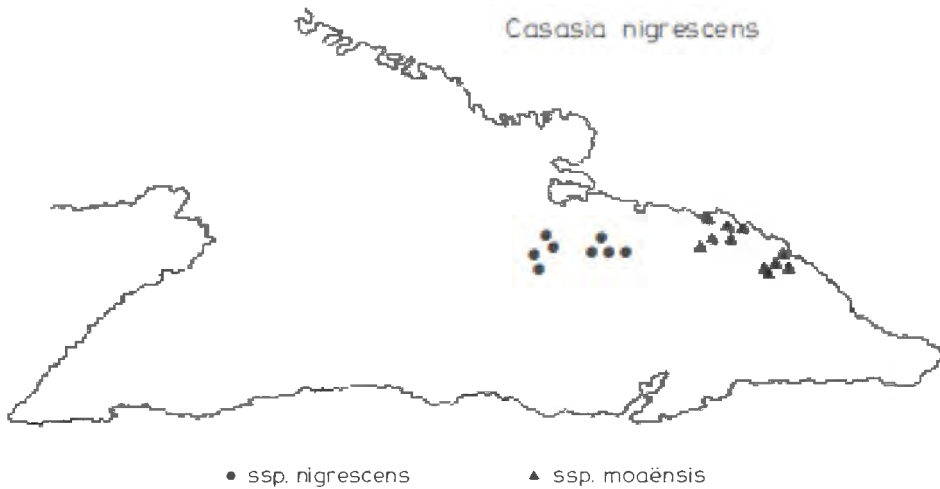


Fig. 120 The geographical distribution of the subspecies of *Casasia nigrescens* (Griseb.) Wr. ex Urb. in Cuba (Borhidi 1985)

19.4.4 Geographic vicariancy at the infraspecific level

The infraspecific geographic vicariancy indicates climatic changes in the recent geological past and casts light upon the role of potential cenological barriers. Examples are found in the serpentine mountains of northeastern Oriente. The climate of this region might have been that of tropical rainforests in the Holocene. Since then, a gradually drying climatic gradient has developed. As a result of this change some species, e.g. *Casasia nigrescens* (Fig. 120), *Amyris stromatophylla* (Borhidi and Muñiz 1973a) and *Anemia coriacea* (Fig. 128) divide into vicarious subspecies with large leaves in Moa and with small leaves in the Cristal and Nipe Mountains.

19.4.5 Phytosociological isolation and vicariancy

The geographic vicariancy of subspecies may often be facilitated by the existence of species-saturated communities or vegetation types in different habitats separating the drifted populations, e.g. those of mountains alternating with more or less wide valleys. This possibility has already been mentioned. Here, only the distribution of the subspecies of *Calycogonium rosmarinifolium* (Fig. 121) is shown, although the vicarious subspecies of *Phyllanthus erythrinus* (Webster 1958) could also have been selected as a good example.

19.5 Inversion of floristic elements

Another typical feature of the flora, observed mainly in western Cuba, is inversion (Samek 1973). Certain genera of the mountains or the temperate regions, which otherwise occur positively in high mountains at similar latitude, are found in

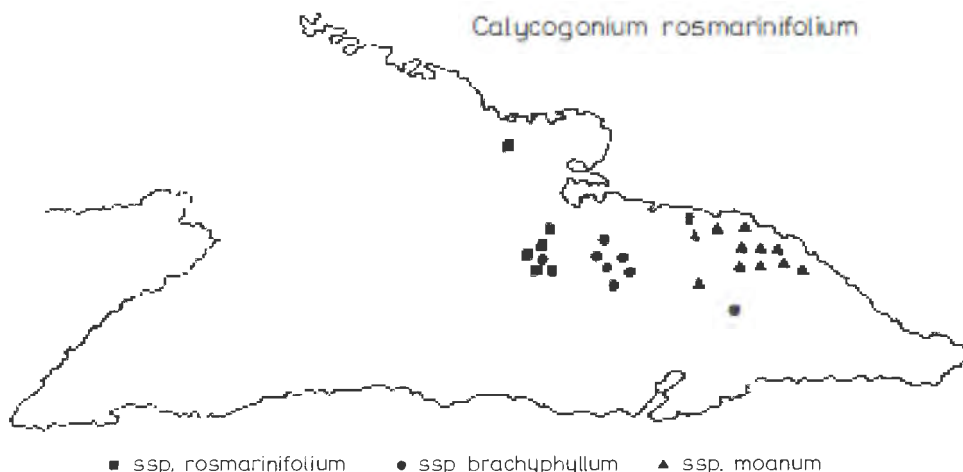


Fig. 121 The geographical distribution of the taxa of the *Calycogonium rosmarinifolium* Griseb. group (Borhidi 1985)

Cuba at low elevation. Examples are *Pinus*, *Podocarpus*, *Kalmiella*, *Vaccinium*, *Lyonia*, *Befaria cubensis* and *Quercus oleoides* ssp. *sagraeana* etc. Inversion is probably caused by two factors: 1. One of the cool periods during the Quaternary when these species or their ancestors reached Cuba and became established in the lowlands and hills 2. The abundance of serpentines and other rocks and soils (e.g. slate and quartz sand) of poor nutrient supply, which might have facilitated the adaptation of cool-resistant species to the increasing mean temperature (such inversions may develop under the same conditions even today). The vegetation inversion occurring on soils derived from serpentine is discussed in detail in Chapter 13. Of course, this is accompanied with the inversion of floristic elements constituting the corresponding vegetation type. In addition to the above-mentioned taxa, this phenomenon is exemplified by the species of *Myrica*, *Ilex*, *Lobelia*, *Laplacea* and *Baccharis* occurring on serpentines or white sands.

19.6 Microphyllia

This is an important feature characteristic not only of the flora of Cuba but also of the flora of the West Indies. As pointed out in 19.2.4 aridity must have had an important role in influencing speciation. Table 29 shows that of the 1115 species examined, 800 (72 %) proved to be microphyll, nanophyll, leptophyll and aphyll, most of those (563 species) being endemics. There are numerous genera represented in Cuba and the Antilles by highly specialized microphyll, sclerophyll or spinous sections or species, but the corresponding taxa in the continent are broad-leaved. Examples are *Plinia*, *Myrcia*, *Calyptranthes*, *Eugenia*, *Rondeletia*, *Machaonia*, *Psychotria*, *Phyllanthus*, *Croton*, *Acalypha*, *Jacaranda*, *Tabebuia*, *Byrsonima* and *Malpighia* etc. Typical West Indian genera are *Catesbaea*, *Scolosanthus*, *Ottoschmidtia*, *Acidocroton*, *Picrodendron*, *Krugiodendron* and *Sarcomphalus* etc. Their abundance and substantial cover in the vegetation may advance the

conclusion that during the main period of the flora development in the West Indies there was a direct relationship with the continental flora composed of drought-tolerant elements. Then, the flora must have further evolved in a warm, arid subtropical climate, probably in the second half of the Miocene.

Table 29 The leaf-size distribution of 1115 tree and shrub species occurring in 40 native forest communities of Cuba

Leaf-size category	Non endemics		Endemics		Total	
	No.	%	No.	%	No.	%
macrophyllous	6	100	0	0	6	100
mesophyllous	58	65	30	35	88	100
notophyllous	96	43	125	57	221	100
microphyllous	163	33	337	67	500	100
nanophyllous	45	22	155	80	200	100
leptophyllous	14	20	56	80	70	100
aphyllous	5	18	25	82	30	100

19.7 Micranthia

A striking feature of the flora of the Antilles, and particularly of Cuba, is its richness in small-flowered plants, whereas the floras of Palaeotropical and Neotropical regions in the continents abound in showy, big-flowered species. Among many thousands of plant species illustrated in Botanical Magazine and Gardenflora, Antillean species only occur occasionally. (None of the 3000 endemics in the exceptionally rich flora of Cuba has large enough flowers to deserve the honour of being the ‘national flower’, so *Hedychium coronarium*, an Asiatic species was given this title.) The small flowers are pollinated by endemic, highly specialized microscopic-sized insects that are usually not capable of long distance flying. To avoid strong winds blowing from the sea, these insects stay in the shelter of plants. Thus, gene flow between remote plant populations is occasional, if not impossible. This barrier must have contributed significantly to the isolation of populations subjected to genetic drift, and resulted in the formation of numerous vicarious endemics. The fact that most vicariads differ very little from one another indicates the influence of genetic drift. Therefore, some taxonomists consider these vicariads as simple varieties. However, this view is unacceptable since the morphology of these microspecies is stable, the segregation is complete and no intermediate forms and genetic relationships exist. Micranthia may be a partial explanation of the discrepancy that genera represented by only one or two widespread species in the continent may fall into a dozen of endemic species with geographic range restricted to a single mountainous region in the Antilles.

19.8 Relict character

The flora of tropical moist vegetation types, such as lowland and submontane rainforests and seasonal evergreen forests in the Antilles is relatively young and contains few endemics. It is likely that these types had become widespread only at the end of the Pliocene and during the pluvial periods synchronous with the Pleistocene inter-glacials. During the Pleistocene the flora rich in Tertiary xerophilous and sclerophyll elements retreated. This process still goes on. In my opinion the recent climate is far too moist for the sclerophyll vegetation types and the constituting species. The increase in the number of permanently established deciduous and semi-deciduous species deriving from other community types supports this view. This degradation process is significantly accelerated by human impact. The formerly widespread by evergreen formations (thickets, woodlands, forest and pinewoods) composed of Tertiary sclerophylls are now restricted to relict habitats, serpentines and the slopes and cliffs of conical karsts. The geographic range of endemic sclerophylls, which account for 40% of the flora, covers not exactly 20% of the area of the island. The relict character of the flora is clearly demonstrated by the presence of primitive, taxonomically isolated groups (*Microcycas*, *Dracaena*, *Cneorum*, *Spathelia* sect. *Brittonii* and sect. *Splendentes*, and *Harpalyce* sect. *Cubenses*, etc.), the abundance of disjunct geographical distribution types, and the large number of local endemics represented by small populations.

19.9 Vulnerability

In general, island floras are vulnerable for several reasons:

- a) the populations colonizing new biotopes are selected from a reduced gene pool.
- b) There has been no possibility of changing this gene pool for millions of years.
- c) As a consequence of isolation, the ecological tolerance and genetic flexibility of populations decreased, so that
- d) The competitiveness of species generally decreased or even disappeared in all but one respect.
- e) Therefore, they cannot react satisfactorily upon new ecological impacts, cannot take the advantage of succession, and cannot resist to or force back new competitors.

Island floras are usually composed of ecologically rigid populations not qualified to adapt to major environmental changes. The social recuperability is reduced, the populations and communities are vulnerable to external effects. The vulnerability of the flora of Cuba is more pronounced for the following reasons:

- The island flora itself is constituted of sets of ancient, isolated floras,
- Most endemics have adapted to the extreme ecological conditions of oligotrophic or bare areas. Thus, the level of metabolism became low in these organisms and their competitiveness diminished.
- The sociability of many endemics is low.

There are some rare taxa represented by few populations, and few individuals

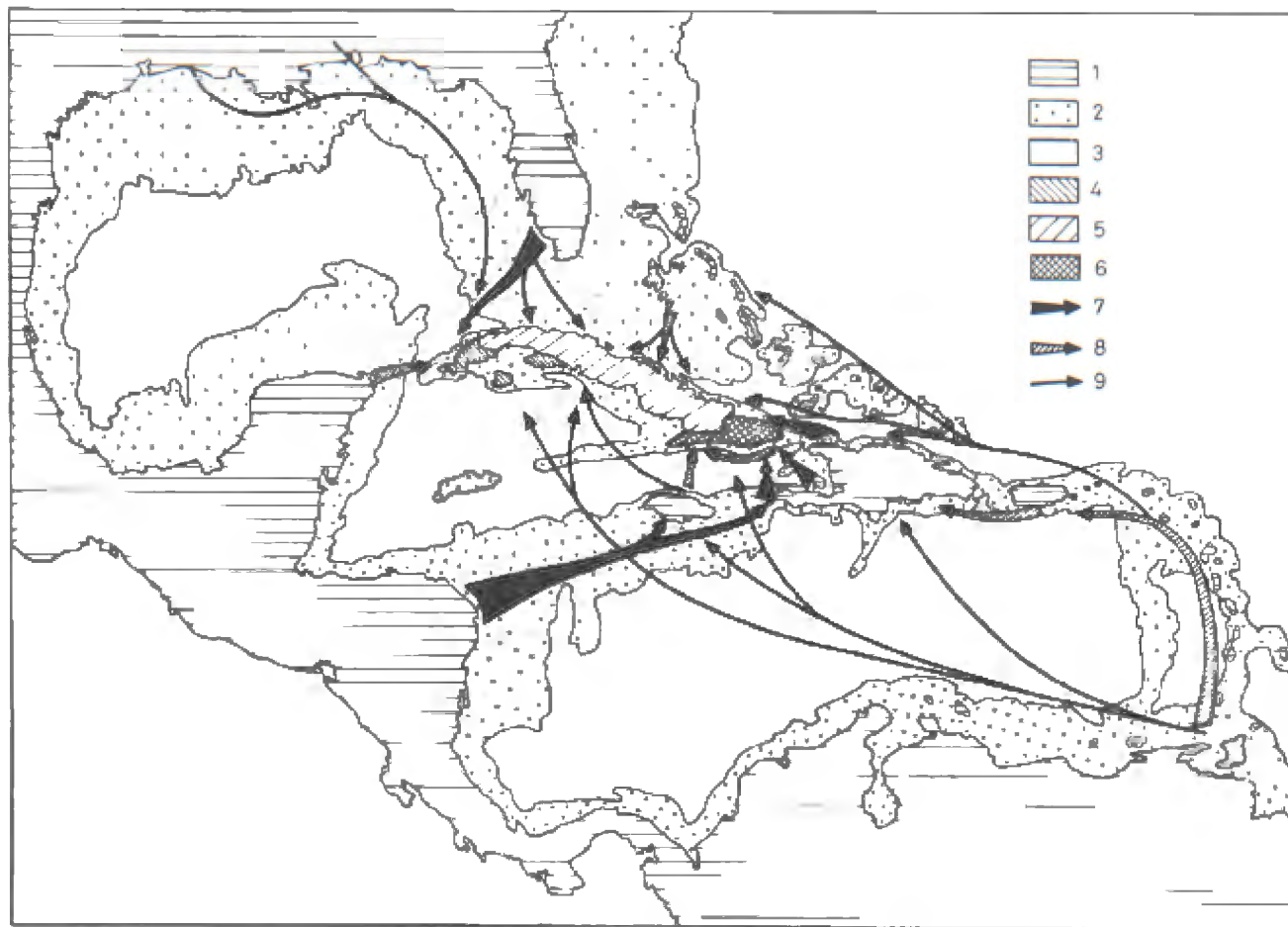


Fig. 123 Origins of the flora of Cuba. (Alain Liogier 1958, strongly modified). 1. Continents and islands, 2. Shallow seas (< 1000 m deep), 3. Deep seas (depth more than 1000 m), 4. West Cuban plant-geographical subprovince, 5. Middle Cuban plant-geographical subprovince, 6. East Cuban plant-geographical subprovince, 7. Main migration routes of the flora, strong floristic affinity, 8. Important migration routes of the flora, characteristic floristic relations, 9. Less important migration routes of the flora, clearly recognizable floristic effects

therein. Consequently, the flora of Cuba is one of the most endangered island floras of the world. The list of endangered species of Cuba contains about a thousand items which amount to 16.5% of the entire set of flowering species in the island. Approximately 30% of the endemics are endangered.

20 The origin and migration of the flora of Cuba

20.1 Palaeobotanical and geological evidence

Our knowledge on the origin and migration of the flora of Cuba is insufficient. As few as three noteworthy findings have been reported, one probably from the Eocene and another from the Pleistocene of Sierra de Chorrillo, and the third from the Miocene of Yumuri Valley in Matanzas (Graham 1974). The total number of taxa coming from these three periods is still below fifty. Moreover, no palynological data are available from the Quaternary of Cuba. Then, the only possibility to give a rough picture on past changes in the flora is offered by the simultaneous analysis of the recent flora, geographical distribution types and of the tectonic events revealed by structural geology.

20.1.1 Corral's version of Wegener's theory

The geological past of the Antilles has been described by Corral (1939, 1940) in accordance with Wegener's theory (Fig. 122). It is conceivable that portions of the Greater Antilles used to be connected to one another and to South America, as Corral claims. However, these lands must have started to become separated from the continent not later than the Upper Triassic. Due to chronological unreliabilities and consequential inconsistencies in Corral's theory, it was soon rejected (Alain 1958) and Schuchert's (1935) concepts were accepted.

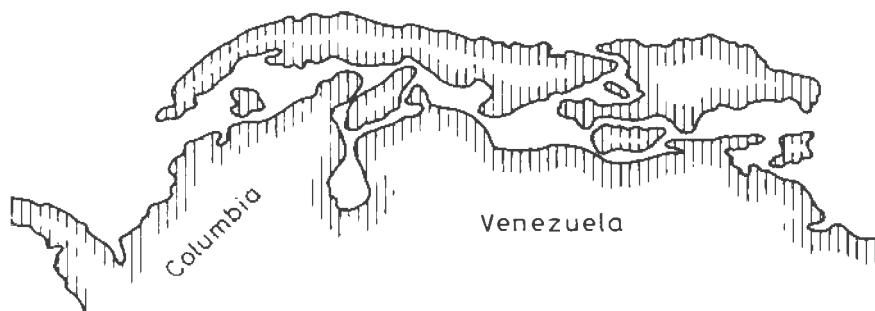


Fig. 122 The geographical position of the Greater Antilles in the late Miocene according to Wegener's theory in the interpretation of Corral (1939)

20.1.2 Schuchert's concepts on the Tertiary in the Antilles

According to Schuchert, the Greater Antilles had been connected to Central America via a land strip of Honduras from the Triassic to the Late Pliocene, apart from short intervals in the Upper Cretaceous and the Upper Oligocene. Eastern Cuba was connected to the continent via the Cayman Ridge and indirectly via the Nicaragua Ridge, Jamaica and Hispaniola. In addition, there was also a connection to the Bahamas and Florida during the Upper Cretaceous and the Eocene. In the Upper Oligocene Cuba became separated from Hispaniola and Yucatan, and its connection to the continent ceased to exist any longer. Although in the Middle Miocene Cuba and Hispaniola had been united again for a short time, no link was formed between the Antilles and Honduras. In the Upper Miocene Cuba finally became completely separated from all the other islands of the Antilles and the continent. According to Schuchert, the Honduras—Jamaica—Hispaniola land strip was finally broken only at the beginning of the Pleistocene. In my view, however, this break up must have been completed in the Miocene, as suggested by the very primitive mammal fauna of the Greater Antilles.

20.1.3 The influence of Schuchert's concepts on phytogeographical interpretations

The recent position of the West Indies, which is wedged in between two continents and surrounded by narrows and closed bays, gives the impression as if the West Indies were a sort of appendage of the continent that became separated not long before. Some botanists consider the flora of the West Indies as a descendant of the continental flora in which the widespread and highly variable continental species are represented by endemic subspecies 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). He suggests that the flora is mainly of Neotropical origin and the elements immigrated from five different directions (Fig. 123). This problem will be considered later in more detail.

20.1.4 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 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 palaeogeographic 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.

20.1.5 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 (1968) 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 vary. Schuchert (1935), Woodring (1954), Eardley (1954), Butterlin (1956), Tikhomirov (1967) and Judoley and Furrázola-Bermúdez (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), Dengo (1969), 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, Dengo 1969, Molnár and Sykes 1969, MacGillavry 1970, Malfait and Dinkelman 1972, Mattson 1973 and Iturralde-Vinent 1975, 1977) explain the development of the Caribbean Plate on the basis of the continental drift and, in general, of the expansion of the 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 to be found now). 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 km, 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 the general vertical movement started leading to the emergence of the Cayman and Nicaragua Ridge. Thus, the archipelago and Central America became connected. This process was completed in the Pliocene and then the islands started to separate. Finally, the recent shape of the islands was formed in the Pleistocene.

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

Although Caribbean plate tectonics poses many unresolved problems (Howard 1979: 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.

20.2.1 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.

20.2.1.1 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 and 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 on the southern hemisphere. The new studies by Pócs and Reyes revealed obvious relationships between the liverwort floras of the Guyana Plateau and of the serpentine plateaux in Cuba. It is well-known that the Guyana Plateau is one of the oldest block mountains in South America derived undoubtedly from Gondwanaland.

20.2.1.2 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.

20.2.1.3 Peri-Afro-American elements

The evolution of the specially distributed peri-Afro-American elements may also be dated back to the plate phase. Table 30 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.

Table 30 Examples of peri-Afro-American genera

Genus, Family	Total species	South America, West Indies	West and Central Africa	East 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		3
<i>Rheedia</i> (Clusiaceae)	50	37		13
<i>Ravenala</i> (Musaceae)	2	1		1
<i>Savia</i> (Euphorbiaceae)	25	15		9
<i>Stenandrium</i> (Acanthaceae)	25	22		3

Of the fifteen genera listed, eleven occur in Cuba, four genera (*Carpodiptera*, *Savia*, *Oplonia* Fig. 124) and *Stenandrium* have their evolutionary centres in the Antilles.

According to Stearn (1971) this distribution type may have 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. 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 (Fig. 125). 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; see Gradstein *et al.* 1983).

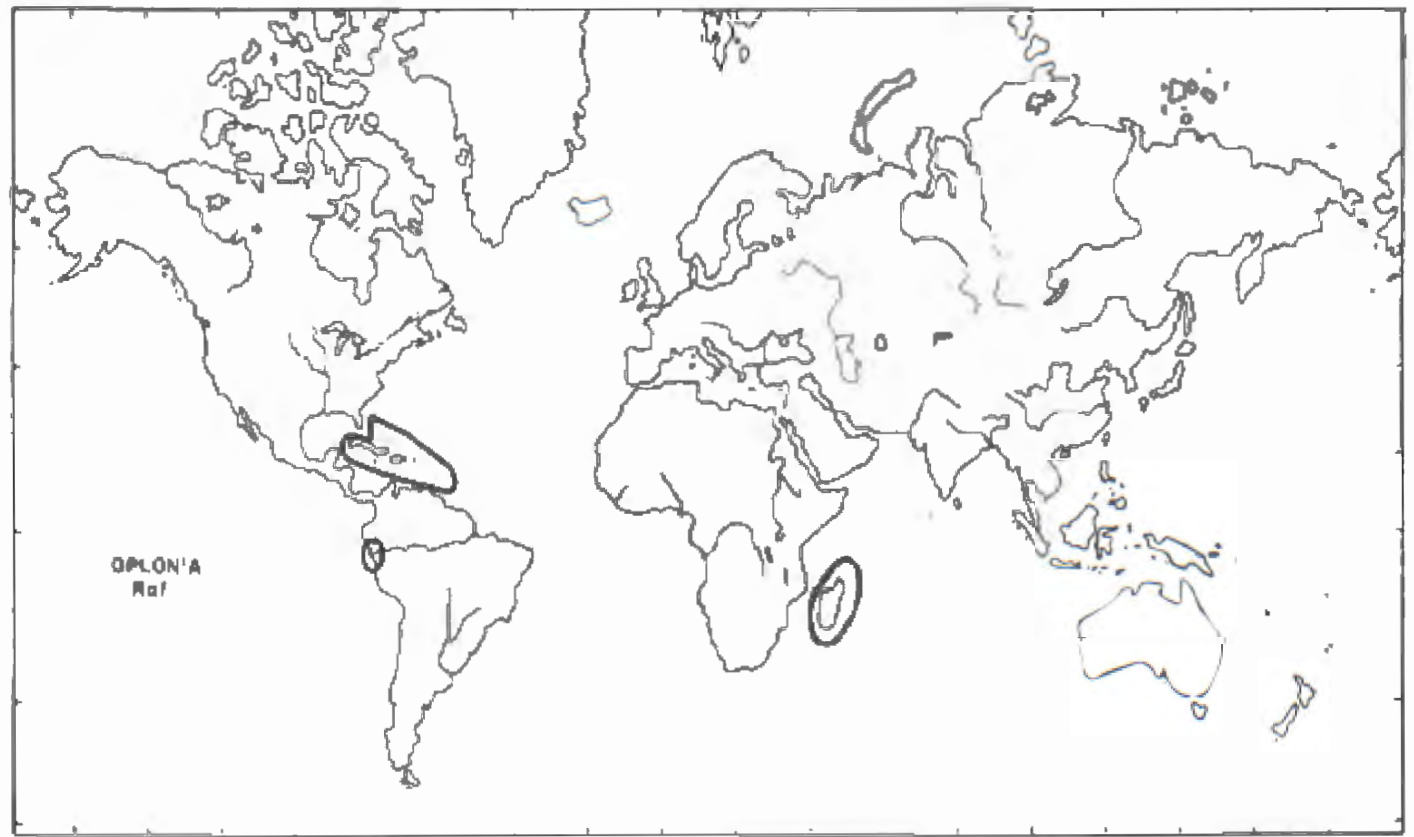


Fig. 124 The geographical distribution of a peri-Afro-American genus: *Oplonia* Raf. (Stearn 1971, Borhidi and Muñiz 1978)

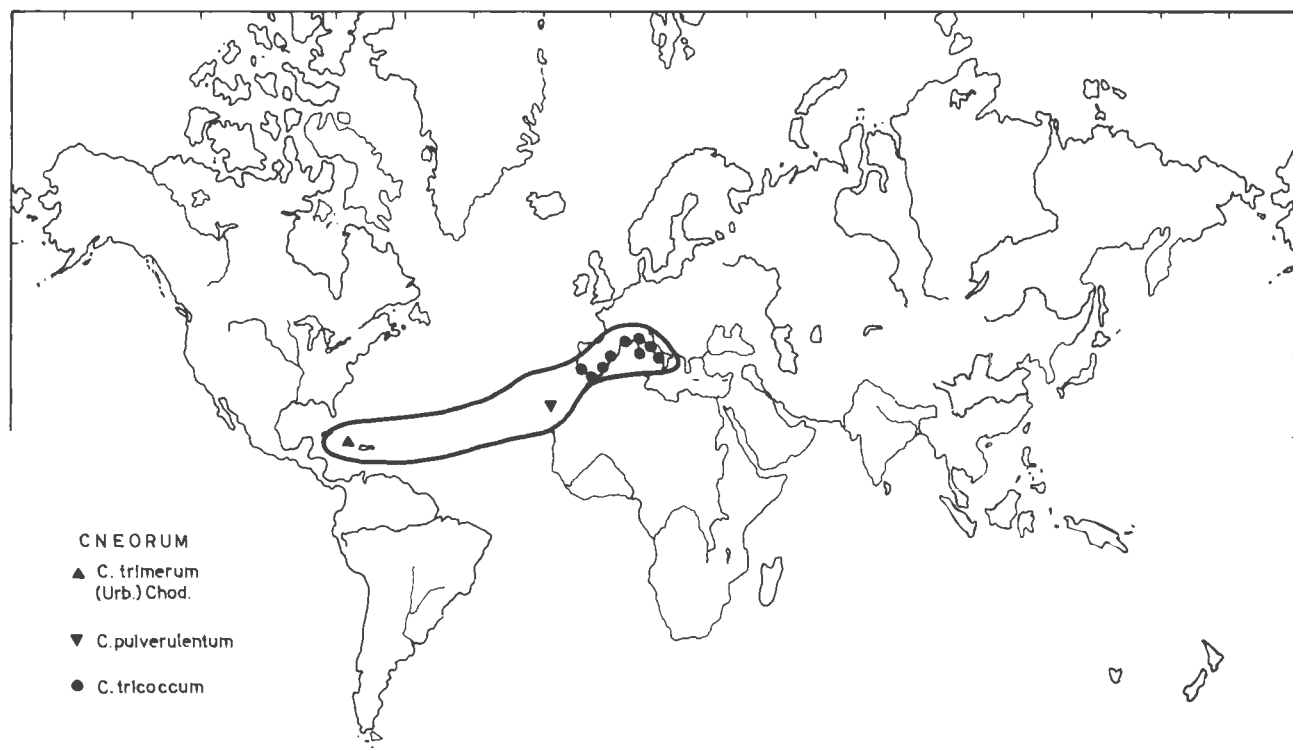


Fig. 125 The geographical distribution of a peri-Tethyan genus: *Cneorum* L. (after Chodat 1926, Borhidi 1982)

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*, *Myrica*, *Spathelia*, *Purdiaea*, *Calophyllum* and those listed in Table 30.

20.2.2 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 the Caribbean Plate started 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.

20.2.2.1 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 originated from the Honduras flora. According to my hypothesis, 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*, *Fagara*, *Pilea*, *Rondeletia*, *Psychotria*, *Guettarda*, *Miconia*, *Ossaea* and *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 *Schmidtottia*—*Isidorea*; the group *Phialanthus*—*Ceratopyxis*—*Shaferocharis*; the group *Antillia*—*Urbananthus*—*Spaniopappus*; the group *Scolosanthus*—*Eosanthus*; the group *Pinillosia*—*Tetraperone*—*Koehneola* and the group of *Espadaea*—*Goetzea*—*Henoonia* etc.

20.2.2.2 The sclerophyllous broad-leaved Madrean–Tethyan vegetation

Axelrod (1975) recognizes that the high similarity between the mediterranean vegetation of North America and Eurasia—North 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

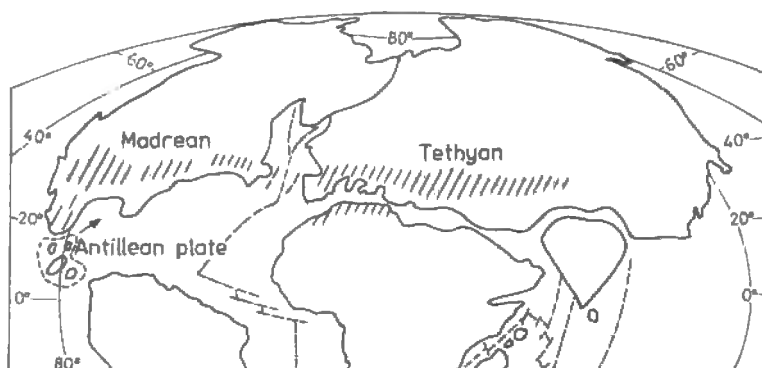


Fig. 126 Early Tertiary position of the continents and the Antillean plate; areas (hatched) potentially occupied by Madrean-Tethyan or Peri-Tethyan sclerophyllous vegetation (Axelrod 1975, with some reconstructions)

Oligocene and Miocene of southern Eurasia, with many species in common. This vegetation, quite uniform in appearance, was named the Madrean–Tethyan vegetation after its westernmost limit, Sierra Madre, and the Tethys Sea, along the northern coast of which this vegetation type was spread (Fig. 126). It was extensive too, in the Upper Miocene of Central Europe. For example, the Sarmatian flora described from Hungary (Andreánszky 1956, 1962a,b) is also designated by Axelrod as being part of the Madrean-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-gneis domes, lava, limestone dog-tooth areas etc.).

20.2.2.3 The southern link

Axelrod pointed out correctly that the laurel forests of the Canary Islands belong to the Madrean-Tethyan vegetation, representing its southernmost portion. However, he did not consider 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 Madrean-Tethyan vegetation, which should preferably be termed the Peri-Tethyan sclerophyllous vegetation, developed in the Greater Antilles. In addition to the Madrean-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 charrascals (dry evergreen shrublands), pine-oak woodlands, coniferous-laurel forests, and pine-*Dracaena* forests of Cuba are relicts left of the southern portion of the Madrean-Tethyan vegetation.

20.2.2.4 The Madrean-Tethyan flora in Cuba

The sclerophyllous broad-leaved Madrean-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 Madrean-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*.

20.2.2.5 Neotropical sclerophylls in the Madrean Tethyan vegetation of Cuba

The southern part of the Madrean–Tethyan vegetation has its own typical features. Numerous species of the earlier established tropical broad-leaved 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 group 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*, *Sarcomphalus*, *Doerpfeldia*, *Pachyanthus*, *Scolosanthus*, *Catesbaea*, *Notodon*, *Nashia*, *Sauvalella*, *Leucocroton*, *Phidiasia*, *Lescaillea*, *Harnackia*, *Phania*, *Shafera*, *Moacroton*, *Hemithrinax*, *Ceuthocarpus*, *Schmidtottia*, *Roigella*, *Suberanthus*, *Kodalyodendron*, *Henonia*, *Linodendron*, *Adenaea* and *Tetralix* etc.

20.2.2.6 Drought-resistant ecotypes

The numerous newly occurring sclerophyllous species and genera were only one indication of the adaptation to the dry climate of the Miocene. The thin-leaved trees of the Honduras flora also became 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 on the continent. Examples are *Ceiba pentandra*, *Trichilia glabra*, *T. hirta*, *Cupania macrophylla* and *Bursera simaruba* etc.

20.2.3 Archipelago phase

The third period is termed the archipelago phase. It came about at 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 that period are the ecological specialization of floras isolated from one another and, as a consequence of this, the internal migration of species. In that phase the flora and fauna of Cuba were subjected to severe climatic and geological changes. In the Pliocene and the Pleistocene the humid climate frequently alternated with dry periods. The effects of this climate are clearly indicated by the stratification of latosols in the Nipe 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 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.

20.2.3.1 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 originated in this way.

20.2.3.2 The broad-leaved semi-deciduous Yucatan flora

It is striking 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.

20.2.3.3 Elements from the temperate North America

The next most important region influencing the flora of Cuba, particularly western Cuba, is Florida and the south-eastern 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: 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. In my view, the flora of 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 Vuilleumier (1971). Consequently,

instead of assuming a land bridge it is more reasonable to trace back the Florida — western Cuba relationship to the Madrean–Tethyan flora. As already seen, this sclerophyllous evergreen flora originally contained several genera from the families of the temperate zone. In addition, there was adequate 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, also 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 post-glacial period, when the Central American subtropical flora retreated to the western coast of the gulf, forcing back the remnants of the Madrean–Tethyan flora to a north-western and north-eastern direction.

20.2.3.4 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 of, 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 135) 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 unfavourable ecological and cenological conditions, such as the saturation of the flora, may prevent otherwise feasible migration.

20.3 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 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.

20.3.1 Two principles of internal floristic changes in Cuba

1. Oriente is the earliest cradle of the Cuban flora, a starting point for the most important migrations.
2. The floras of mountains are older than those of the lowlands. The flora and vegetation of plains originated from the mountainous regions.

20.3.2 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). The centre of these movements, that were directed from the east to the west, was the mountains of Oriente. The low differentiation and specialization 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 in the late Tertiary and in the Quaternary (Pliocene and Pleistocene). 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 from 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 originated from different mountains, may have been caused by the repeated "shake up" of the flora of the 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 the pine 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.

20.4 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 *Phyllanthus*, Judd (1981) on *Lyonia*, Dahlgren and Glassman (1963) on *Copernicia* and Howard (1947) 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 type (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 data (León 1936, 1939, Marie-Victorin and León 1942, 1944, 1956, Webster 1956–58, Borhidi and Muñiz 1977, Klotz 1978, Borhidi and Fernandez 1984 and Borhidi 1973, 1981, 1985, 1986).

20.4.1 Evolutionary centres and migratory routes of the serpentine vegetation

The distribution of some typical elements of the serpentine vegetation is shown in Figs 127, 131. The evolutionary centres and principal migratory routes are illustrated in Fig. 132. The section *Orbicularia* of the genus *Phyllanthus* is a typical serpentinophilous group that includes many species occurring on the old latosols of northeastern Oriente. Of this section, *Ph. orbicularis* is the only species that is found on all the serpentine outcrops of the island (Fig. 127). Like *Neobraccia valenzuelana* (Fig. 117), 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. 113) and species (Figs

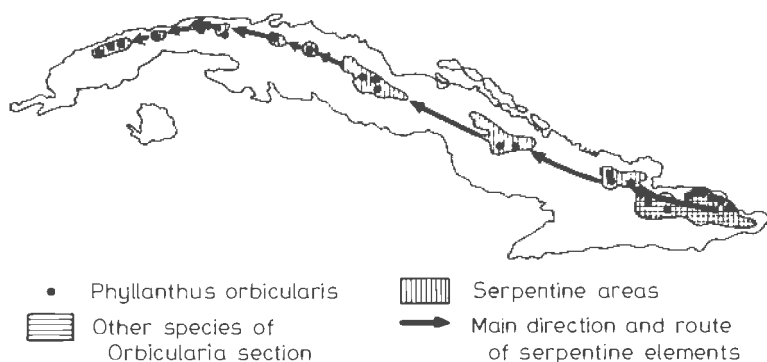


Fig. 127 Geographical distribution of the serpentine areas and the *Orbicularia* section of genus *Phyllanthus* in Cuba (Webster 1958)



Fig. 128 Geographical distribution of *Anemia coriacea* Griseb. s.l. (Borhidi 1985)

128—131) 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 (*Neobracea*) or by animals (*Phyllanthus*). They may have had wider distribution earlier, but due to the depletion of habitats (Kruckeberg 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* (Fig. 128), *Moacroton* (Fig. 130), *Lescaillea* (Fig. 113) and *Harnackia* etc., were distributed during the earlier stages. Later, some serpentinophilous species, e.g. *Jacaranda cowellii*, *Coccoloba geniculata*, *Zanthoxylum nannophyllum* (Fig. 131) and *Platygyne parviflora* (Fig. 115), migrated replacing the above mentioned taxa in the plains of eastern Cuba. In these stages the species with continuous distribution, such as *Neobracea 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.

132). The first and the oldest is Moa from which the serpentine flora of the entire island, and the flora of other latosol mountains in north-eastern Oriente, the Baracoa-Jauco zone and the Cristal and Nipe Mts 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



Fig. 129 *Moacroton trigonocarpus* (Wr. ex Griseb.) Croiz. an endemic characteristic element of the dry evergreen serpentine scrub "charrascal" of the Cajalbana range (Photo: A. Borhidi)

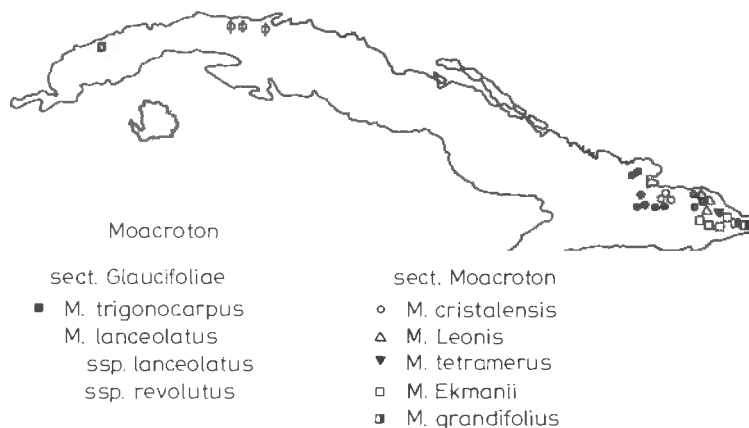


Fig. 130 Geographical distribution of the serpentinicolous, endemic Cuban genus: *Moacroton* Croiz. (Borhidi 1985)



Fig. 131 Geographical distribution of *Coccoloba geniculata* Lindau, *Jacaranda cowellii* Britt. and Wils and *Zanthoxylum nannophyllum* Urb.



Fig. 132 Centres of evolution and routes of migration of the serpentinicolous flora in Cuba (Borhidi 1985)

Cajalbana in western Cuba. A part of its flora retreated to the serpentine blocks which rose later in central Cuba, especially to Habana and Matanzas. Many latosol elements of this flora became adapted to the acidic slatey habitats of Pinar del Rio and Isla de Pinos. In Fig. 132 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.

20.4.2 Evolutionary centres and migratory routes of the flora of limestone cliffs

The flora of limestone karsts has two primary evolutionary centres (Fig. 133). 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 the island. 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 Hills, e.g. *Bombacopsis cubensis*, *Thrinax morrisii* (Fig. 114) and *Phania matricarioides*. 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, inland

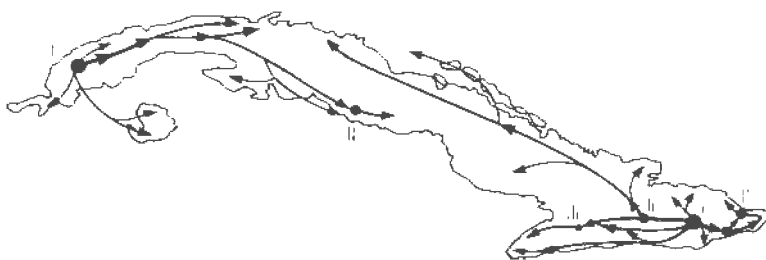


Fig. 133 Centres of evolution and possible routes of migration of the flora of the limestone tropical karsts (mogote formations) (Borhidi 1985)

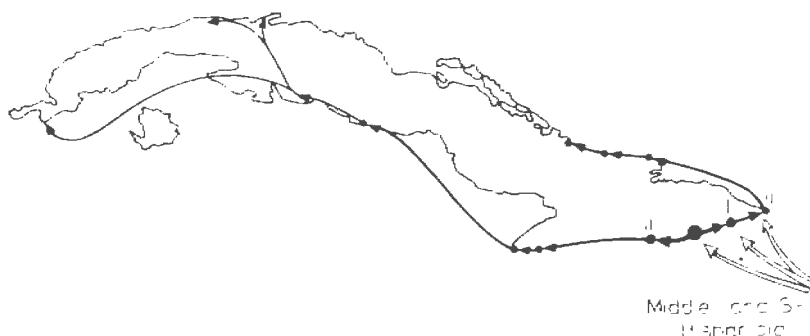


Fig. 134 Possible centres of evolution and routes of migration of the semi-desert, xero-megathermophilous elements in Cuba (Borhidi 1985)

mountains of Cuba itself were old coastal zones serving as refuges 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 originated from primary soils derived from serpentine (e.g. Nipe Mts, Monte Libano). Of the many isolated 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 it possible for the flora of Monte Libano to spread over the semi-desert coastal zone. As a result of

this migration, xero-megatherm species evolved (see 20.4.3). 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 north-western 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 Caguaguas (see the distribution of *Thrinax*; Fig. 114). 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 phytogeographical sectors of central Cuba (see Fig. 187)

20.4.3 Evolutionary centres and migratory routes of the xero-megatherm elements (Fig. 134)

Some semi-desert xero-megatherm elements originating from central and southern Hispaniola, 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 urbanii* (Fig. 135), *Victorinia* and *Isidorea* (Fig. 136)



Fig. 135 Geographical distribution of *Omphalea commutata* Muell. Arg. and *Petitia urbanii* Ekm. (Alain 1972 and Borhidi 1985)



Fig. 136 Geographical distribution of the genus *Isidorea* A. Rich. (Borhidi 1985)

etc., now restricted to the actual and previous coastlines. 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 north-western Oriente and northern Camagüey, in the southern foothills of Escambray Mts, and on the northern rocky coast between Habana and Matanzas decreases in that order.

20.4.4 Evolutionary centres and migratory routes of the montane rainforest elements (Fig. 137)

The evolutionary centres and migratory routes of the flora in the montane rainforests are shown in Fig. 137. The distribution of *Hedyosmum* serves as an example (Fig. 138). Again, the main centre is the lower and old mountains in the

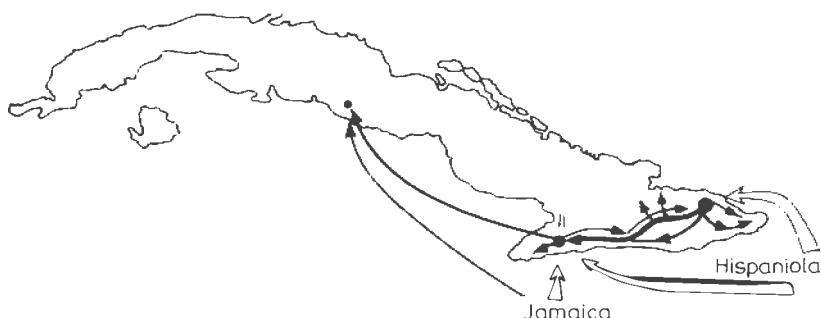


Fig. 137 Centres of evolution and possible routes of migration of the montane rainforest elements in Cuba (Borhidi 1985)

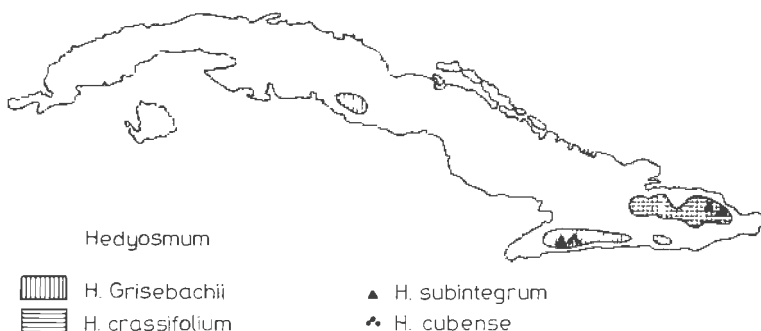


Fig. 138 Geographical distribution of the *Hedyosmum* species in Cuba (Borhidi 1985)

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, Nipe, Purial, Imías, 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 during the cooler periods of 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 extended to as 200–300 m altitude. This montane flora was mixed with Jamaican and southern Hispaniolan montane elements and, during the cool periods 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.

20.4.5 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 del 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 supports this fact (see Figs 331–336).