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Remarks on the montane flora and vegetation types of the Guianas

Abstract

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Three main types of relief above 500 meters are found in the Guianas, i.e. the sandstone tabletop mountains of the Guayana Highland, the lateritic and bauxitic plateaus on basic volcanic rocks, and the granitic outcrops and other rugged reliefs on a crystalline base. For each type a list of mountains with their altitude and geographic position is presented. The most prominent features of the flora and vegetation of these three areas are given.

Studies carried out by ORSTOM in French Guiana for more than 25 years as well as by other botanical expeditions organized in the interior reveal that the flora and vegetation begin to change above a 500 m altitudinal limit (Fig. 1; Granville 1980, 1986, 1988; Granville & Cremers 1985, 1989).

In the Guianas the following three main types of geological relief are found above 500 m: (1) the sandstone tabletop mountains of the Guayana Highland, (2) the lateritic and bauxitic plateaus on basic volcanic rocks and (3) the granitic outcrops and other rugged relief on a crystalline base.

The submontane floras and vegetation types of the Guianas are found in these three areas (Seurin 1979, Krook 1979, McConnel 1962, Bleackley & Phil 1964) (Fig. 2).

1. Sandstone table mountains of the Guayana Highland or "Roraima Formation" (Fig. 3, Tab. 1, 2)

This area includes the highest reliefs occurring in the Guianas (up to 2800 m) and found principally in western Guyana where they are known as the Pakaraima Mountains. The highest peaks include Mt. Roraima (2772 m), Mt. Ayanganna (1760 m), Kopinang (1630 m), Pwipwitipu (1220 m), Mt. Aymatoi (1122 m) and Mt. Agoldwan (1036 m). Many other mountains situated in the same area reach 500 to 1000 m. In the Pakaraima Mountains, the sandstones are intruded at various levels by sills of gabbro with lateritic cover forming large plateaus (see chapter two). There is only one sandstone table mountain in Surinam, i.e. Tafelberg (1026 m), and none in French Guiana.

1.1. Vegetation

The vegetation types are extremely diversified and depend on the elevation and the steepness of the slopes. Forests on sandy soils are predominant at lower and medium altitudes while low, scrubby and

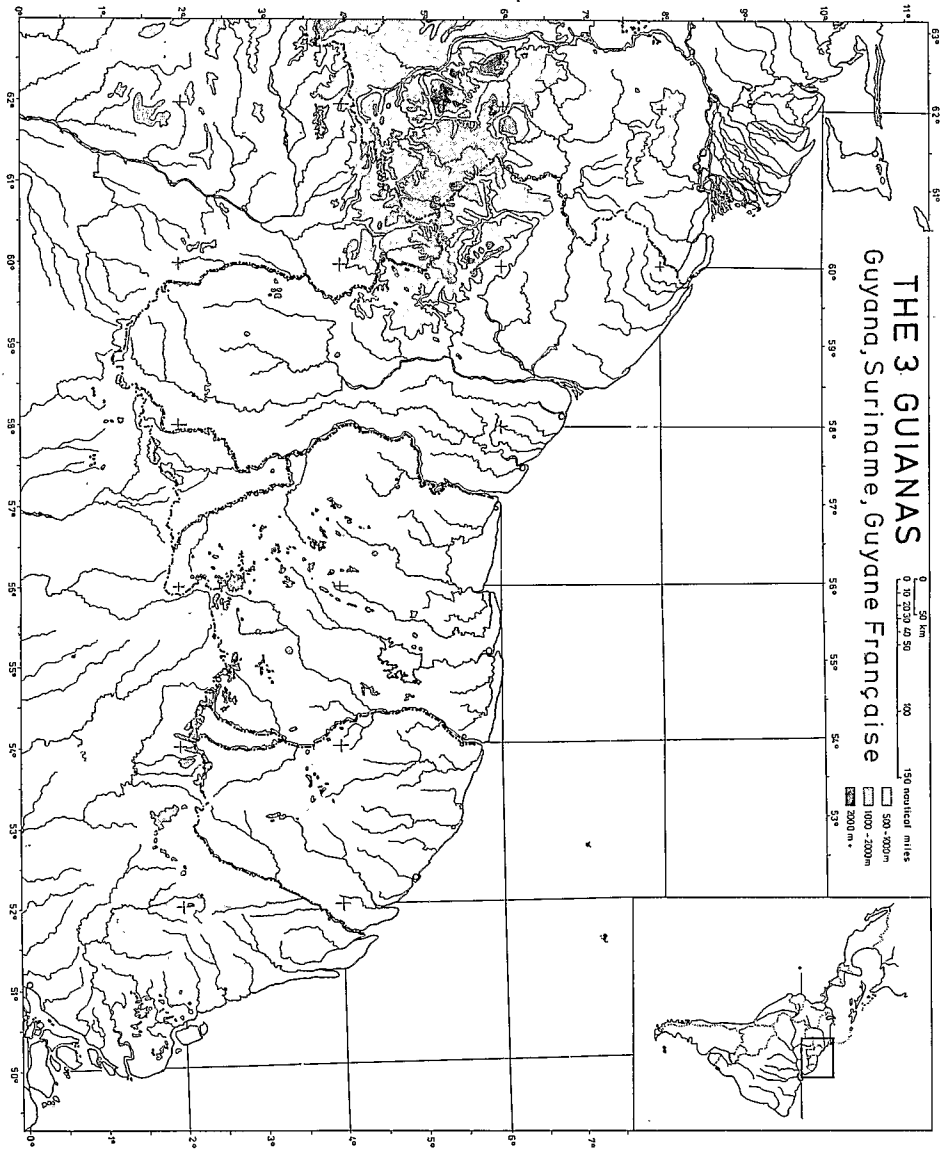

Fig. 1. The Guianas. Altitude in different shades.

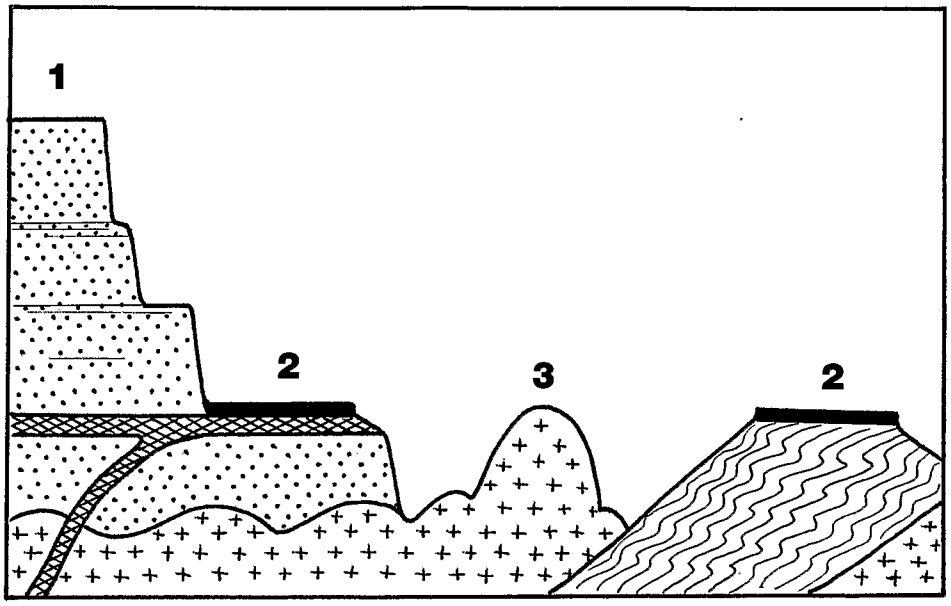

Fig. 2. The three main types of mountains overtopping 500 m in the Guianas (very schematic). 1. Guayana Highland, 2. Lateric and bauxitic plateaus on basic volcanic rocks, 3. Granitic outcrops and other rugged relief. – Dots: sandstones of the superposed Roraima sediments, crosshatches: gabros and dolerites, waves: other basic volcanic rocks, crosses: crystalline base.

open vegetation occurs on the highest mountains. Gradstein (1986) recognized the following four vegetation types on Mt. Roraima:

Riverine rain forest (up to 550 m) consisting of medium sized trees (20 to 30 m) with thin trunks and a well developed understory with the "ground densely covered with sclerophyllous leaves and generally devoid of plants";

Submontane rain forest (550 to 1200 m) on the lower slopes more or less similar to the preceding forest but richer in mosses and liverworts covering the trunks and the branches because of the persistant mist that increases with altitude;

Montane forest (1200 to 1600 m), a very "mossy" and rather low cloud forest growing on the steepest and highest slopes. Bryophytes form thick mats on tree trunks and occur as spectacular draperies and garlands hanging from the twigs of the understory. The soil is thin, very rocky, and more or less covered with scree, especially at the base of the cliffs;

Montane scrub and swamp (2000 to 2800 m), a low lying scrubby and herbaceous type of vegetation, very frequently wrapped in fog and clouds and exposed to rather strong winds. Montane scrub and swamp occur on the highest ridges, hill tops and plateaus above cliffs. The broadest and flattest zones give way to swampy white sand savannas rich in flowering herbs. Bryophytes are much less abundant than at lower elevations but the branches are covered with a very characteristic slimy mass of algae.

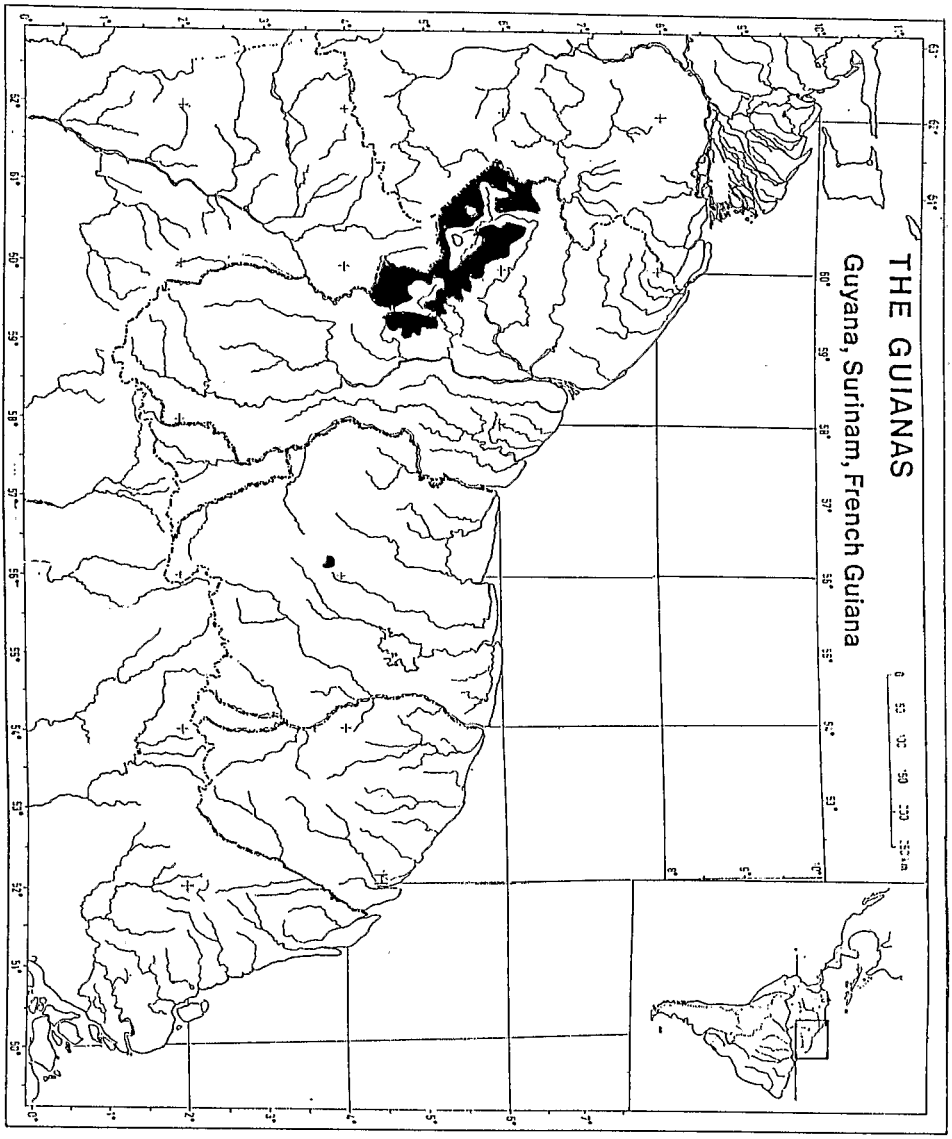

Fig. 3. The Guianas. Sandstone tabletop mountains of the Guayana Highland.

1.2. Flora

The flora of the Guayana Highland is remarkable because of its high endemicity at least on the summits of the sandstone tabletop mountains (called "tepuis" in Venezuela).

For the whole Guayana Highland region, endemicity at the specific level was estimated at 75 % (4000 species) by Maguire (1970). It could reach 90 % to 95 % on the summit of the tepuis (including those situated in Venezuela of which Cerro de la Neblina is the highest reaching 3000 m). According to Steyermark (1979, 1982), this proportion has been much overestimated and should be brought down to 5.3 to 63 % depending on the tepuis. It is about 54 % on the upper slopes and summit of Mt. Roraima.

At the generic level, endemicity is estimated by Steyermark at 8.5 % on the top of the tepuis. The 39 strictly summit endemic genera are: *Salpinctes (Apocynaceae), Crepinella (Araliaceae), Ayensua (Bromeliaceae), Achnopogon, Cardonaea, Chimantaea, Duidaea, Eurydochus, Glossarion, Guaicaia, Neblinaea, Quelchia, Tyleropappus (Asteraceae), Mycerinus, Tepuia (Ericaceae), Roraimanthus, Wurdackia (Eriocaulaceae), Celianella (Euphorbiaceae), Myriocladus (Poaceae), Pyrrorhiza (Haemodoraceae), Mallophyton, Neblinanthera, Tateanthus (Melastomataceae), Adenanthe, Adenarake, Tyleria (Ochnaceae), Phelpsiella (Rapateaceae), Aphanocarpus, Cephalodendron, Chondrococcus, Coryphothamnus, Duidania, Maguireocharis, Pagameopsis (Rubiaceae), Neblinaria, Neotatea, Neogleasonia (Theaceae), Achlyphila (Xyridaceae), Hymenophyllopsis (Hymenophyllopsidaceae).* The *Asteraceae, Cyperaceae, Rubiaceae* and *Rapateaceae* (of which one genus only is endemic to the summits but many other occur at lower altitudes) are especially well represented in low herbaceous vegetation. The *Rapateaceae* are considered to be one of the most typical families: "Perhaps no other family of flowering plants can be considered more characteristic of the phytogeographic province of Guayana than the *Rapateaceae*. Its members occupy a most prominent place on the "cumbres" of the tabular mountains and the open upland plains of the Gran Sabana of the Roraima sandstone regions" (Maguire 1958, 1965). Among the other endemic genera which are not restricted to the high altitudes, *Pakaraimaea (Dipterocarpaceae)* is the only genus of this family existing in the Western hemisphere. It is represented in the Pakaraima Mountains by *P. dipterocarpacea* (Maguire & Ashton 1977, 1980, Maguire & Steyermark 1981b).

Only two families seem to be endemic to this region (but absent in Guyana): the *Tepuianthaceae* (Maguire & Steyermark 1981a) and the *Saccifoliaceae* (Maguire & Murça Pires 1978).

At lower elevation (500 to 1500 m), in submontane and montane forests on slopes, many other taxa are endemic to the whole phytogeographic province of the Guayana Highland. The following are mentioned by Steyermark as an example of species endemic to the Pakaraima Mountains and Mt. Roraima area ("Venamo-Cuyuni Refuge"): *Matelea coriacea (Asclepiadaceae), Brocchinia micrantha, Cottendorfia gracillima, Guzmania steyermarkii, G. venamensis (Bromeliaceae), Cayaponia botryocarpa, Gurania simplicifolia (Cucurbitaceae), Sloanea crassifolia (Elaeocarpaceae), Senefelderopsis venamoensis (Euphorbiaceae), Chorisepalum acuminatum (Gentianaceae), Alloplectus savannarum, Rhoogeton leeuwenbergianus (Gesneriaceae), Caraipa psilocarpa (Clusiaceae), Endlicheria nilssonii (Lauraceae), Macrocentrum steyermarkii, Phainantha myrteoloides (Melastomataceae), Sauvagesia longipes (Ochnaceae), Dunstervillea mirabilis, Habenaria nilssonii (Orchidaceae), Epicryos guayanensis, Rapatea steyermarkii, Stegolepis steyermarkii (Rapateaceae), Calycophyllum venezuelense, Hillia psammophila, Ladenbergia venamoensis, Platycarpum rugosum, Psychotria hemicephaelis, Sipanea wilson-brownei (Rubiaceae), Cyphomandra bolivarensis, Solanum puberuloba, S. rufistellatum (Solanaceae), Cissus venezuelensis (Vitaceae).*

A preliminary review given by Maguire (1970) indicates that "... the historical relationships of the provincial flora of Guayana lie, in order, with those of: 1. the Brazilian Highland; 2. tropical Africa; 3. the Andes; 4. the Caribbean and 5. Malaysia". Considering only the endemic genera of the summit flora, 22.8 % are autochtonous; 17.7 % have originated from areas extraneous to the Guayana Highland at low altitudes (principally the Amazon Basin), 10.9 % are related to a predominantly Andean element and 48.6 % are related to distributions which express neither lowland nor highland predominance (Steyermark 1979, 1982).

2. The lateritic and bauxitic plateaus on basic volcanic rocks (Fig. 4, Tab. 1, 2)

These mountains are situated in the central part of Guyana, Surinam and French Guiana. The highest reliefs are: Eboropu Mt. (1295 m), a part of Pakaraima Mountains (up to 900 m) and Sororieng Mt. (579 m) in Guyana; Van Asch Van Wijck Gebergte (721 m), Lely Gebergte (694 m) and the Brownsberg (516 m) in Surinam; Montagnes Bellevue de l'Inini (851 m), Sommet Tabulaire (850 m), Monts Atachi Bacca (782 m), Montagne Massialine (775 m), Mont Belvédère (760 m), Monts Galbao (750 m), Montagnes de la Trinité (700 m), Montagne Bellevue de Maripasoula (647 m), Montagne Continent (640 m) and Monts Cottica (600 m) in French Guiana.

2. 1. Vegetation

The vegetation is rather uniform in comparison with that of the Guayana Highland and consists of submontane rain forest only.

The slopes, often regular and rarely steep but very slippery in rainy season, are covered with a high (30 to 45 m), rich and beautiful forest on deep clayey soils. The trunks are thick, the canopy is closed and the understory generally well structured and not very dense. As altitude increases, the mist promotes growth of vascular epiphytes in the canopy.

The summits sometimes consist of narrow ridges exposed to the wind but they are more often broad, flat plateaus with a thick lateritic crust covered by thin soils rich in small stones and gravels. High trees are infrequent and scattered, the forests are fairly low, scrubby, and are rich in lianas and epiphytes. At the highest elevations, we find a cloud forest with garlands and mats of mosses like that of the Guayana Highland forests. The most typical patches of cloud forest generally occur on the edges of the plateaus opposite to the wind (western side). On the broadest table mountains, one can notice temporary or more or less permanent ponds in the understory.

The deep and narrow valleys of the upper courses of the streams radiating from the summit plateaus constitute peculiar wet habitats and microclimates, screened from the wind, such as waterfalls, lateritic boulders, and clayey cliffs. The physiognomy of the vegetation is very often characterized by small palms, herbaceous ferns, and tree-ferns.

2. 2. Flora

The flora of each table mountain has its own characteristics (Granville 1988) but the following general features are common to all.

As Prance (1989) already pointed out, "... the tendency towards dominance accompanies the loss of species diversity in angiosperms." This is obvious on all the mountains we have explored in French Guiana, especially on the highest tops but even at middle elevation. Some species or groups of species scattered in forests at low alititudes, become abundant and form sometimes spectacular populations in the understory. For example, in French Guiana, the low lying forests on plateaus are dominated by *Myrtaceae* and *Myrsinaceae*. The *Rubiaceae*, particularly the genera *Psychotria* and *Faramea* are abundantly represented in the undergrowth by species more or less scattered elsewhere: *Faramea guianensis, F. multiflora, F. lourteigiana, Psychotria pungens,* and *Ps. uliginosa*. Some *Melastomataceae* like *Leandra agrestis* and *L. divaricata*, sparsely growing at low altitudes, often constitute monospecific strata in submontane forests. *Cordia nodosa* is restricted to small natural clearings. *Borreria alata* forms on some mountains dense patches on the ground. *Vriesia splendens*, not common under 500 meters, becomes very abundant in summit forests, not only on the branches and on the trunks among mosses and liverworts, but also on the ground

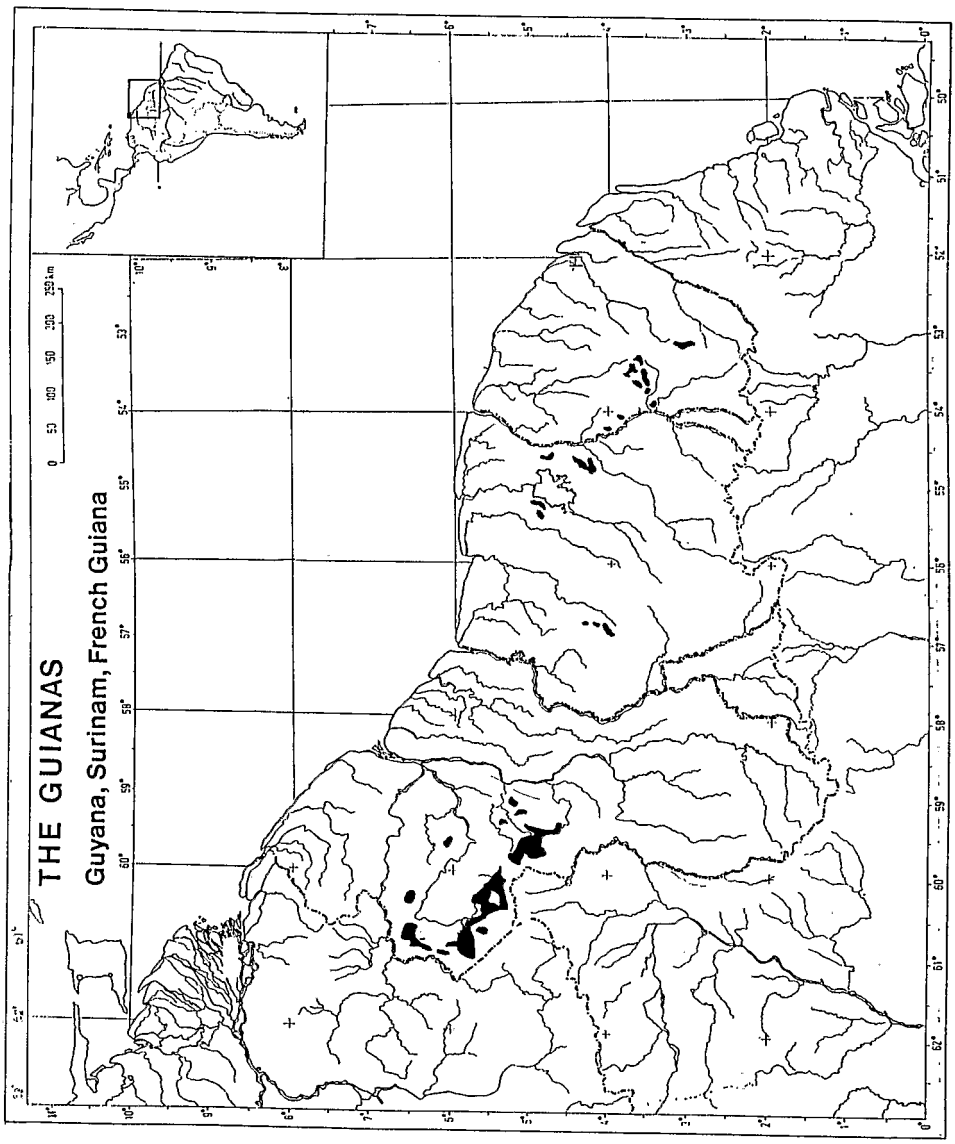

Fig. 4. The Guianas. Lateric and bauxitic plateaus on basic volcanic rocks.

Tab. 1. Distribution of the three main types of mountains overtopping 500 meters in the Guianas

	Sandstone table mountains of the Guayana Highland	Dissected plateaus capped by lateritic or bauxitic crust	Granitic rugged reliefs and rocky outcrops
Maximal altitude	2800 m (Guyana)	1295 m (Surinam)	1230 m (Surinam)
Guyana	Agoldwan Mt. (1036 m) Aymatoi Mt. (1122 m) Pwipwitipu (1220 m) Kopinang Mt. (1630 m) Ayanganna Mt. (1760 m) Roraima Mt. (2772 m)	Sororieng Mt. (579 m) Pakaraima Mts. (900 m) Eboropu Mt. (1295 m)	Wokrama Mts. (710 m) Makarapan Mt. (762 m) Kanuku Mountains (960 m)
Surinam	Tafelberg (1026 m)	Brownsberg (516 m) Lely Gebergte (694 m) Van Asch Van Wijck Gebergte (721 m)	Bemau Top (501 m) Rosevelt Piek (514 m) Kasikasima Top (718 m) Oranje Gebergte (728 m) Kayser Gebergte (861 m) Eilerts de Haan Gebergte (900 m) Acarai Gebergte (906 m) Bakhuis Gebergte (1027 m) Wilhelmina Gebergte (1230 m)
French Guiana		Mt. Cottica (600 m) Mgne Continent (640 m) Mgne Bellevue (647 m) Mgnes de la Trinité (700 m) Mt. Galbao (750 m) Mt. Belvédère (760 m) Mgne Massialine (775 m) Mts. Atachi Bacca (782 m) Sommet Tabulaire (850 m) Mgnes de l' Inini (851 m)	Massif des Emerillons (570 m) Mt. Saint-Marcel (635 m) Mts. Bakra, Pic Coudreau (700 m) Tumuc-Humac, Mitaraka (700 m)

Tab. 2. Prominent features of the three types of mountains overtopping 500 meters in the Guianas

	Sandstone table mountains of the Guayana highland	Dissected plateaus capped by lateritic or bauxitic crust	Granitic rugged reliefs and rocky outcrops
Soil & climatic	Summit: sandy, swampy soil; clouds, wind, relatively low temperature	Summit: thin soils with lateritic gravels on lateritic crust; clouds, wind	Very rugged relief; steep granitic bare slopes exposed to the sun, sandy-clayey soils

factors	Cliffs: bare sandstone Slopes: sandy soils	Slopes: deep clayey soils	thin or absent
Vegetation	Summit: montane scrub and herbaceous swamp Cliffs: epipetric plants Slopes: montane and sub-montane forests	Summit: low submontane liana forest Slopes: high submontane forest	Summit and base of the steep slopes: low, dry forest Steep slopes: epipetric, xeric, shrubby and herbaceous vegetation Other: medium sized forest
Flora	Rather high endemicity; many autochtonous elements	Low endemicity; related to Andean underfeatures flora and Amazon Basin forests	Medium endemicity; related to coastal and inland savannas flora (and sometimes to the Guayana Highland flora)

where it constitutes remarkable layers. The epiphytic taxa are particularly well represented in cloud forest: mosses and ferns, *Bromeliaceae, Orchidaceae, Araceae, Gesneriaceae, Begoniaceae, Ericaceae, Piperaceae* are abundant everywhere.

Lastly, some species are strictly endemic to submontane cloud forests, at least in the Guianas. The most remarkable are in French Guiana: *Geonoma triglochin* and *G. euspatha (Arecaceae), Dicranopygium pygmaeum (Cyclanthaceae), Vantanea* sp. nov. aff. *paraensis (Humiriaceae), Clidemia granvillei (Melastomataceae), Psychotria galbaoensis, Ps. lateralis, Ps. microbracteata, Ps. saulensis, Ps. urceolata, Ps. viridibracteata (Rubiaceae)* and many ferns: *Asplenium radicans* var. *cirhatum, A. repandulum, Ctenopteris mollissima, Ct. staheliana, Cyathea lasiosora, C. marginalis, Danaea moritziana, Diplazium gracilescens, D. grandifolium, D. radicans, Elaphoglossum longifolium, E. scandens, E. schomburgkii, Lonchitis hirsuta, Polybotria osmundacea, Polypodium caceresii, Thelypteris holodictya, Trichomanes membranaceum, Tr. polypodioides, Xiphopteris taenifolia.*

The study of floristic affinities of endemic species and distribution patterns of other submontane plants shows that the flora is related to that of the Andes on the one hand (Venezuela, Colombia, Ecuador, Peru, Bolivia) and that of the West Indies on the other hand (especially for epiphytic ferns), more than to the Amazon Basin flora (Granville 1988, 1990). Of course, the lateritic plateaus included in the Guayana Highland also have many species in common with the adjacent submontane rain forest on sandstones.

3. Granitic outcrops and other rugged reliefs on a crystalline base (Fig. 5, Tab. 1, 2)

These are especially well represented in Surinam by Wilhelmina Gebergte with Juliana Top (1230 m), the southern part of Bakhuis Gebergte (1027 m), Acarai Gebergte (906 m), Eilerts de Haan Gebergte (900 m), Kayser Gebergte (861 m), Oranje Gebergte (728 m), Kasikasima Top (718 m), Rosevelt Piek (514 m) and Bemau Top (501 m). In Guyana the Kanuku Mountains (960 m), situated in the inland Rupununi Savannas zone, Makarapan Mt. (762 m) and the Wokrama Mts. (710 m) belong to this category. In southern French Guiana some isolated outcrops overtop 500 m: the Tumuc-Humac area (a continuation of the Oranje Gebergte in Surinam) of which Mitaraka (700 m) is the highest point, Monts Bakra with Pic Coudreau (700 m), Mont Saint-Marcel (635 m) and the Massif des Emerillons (570 m).

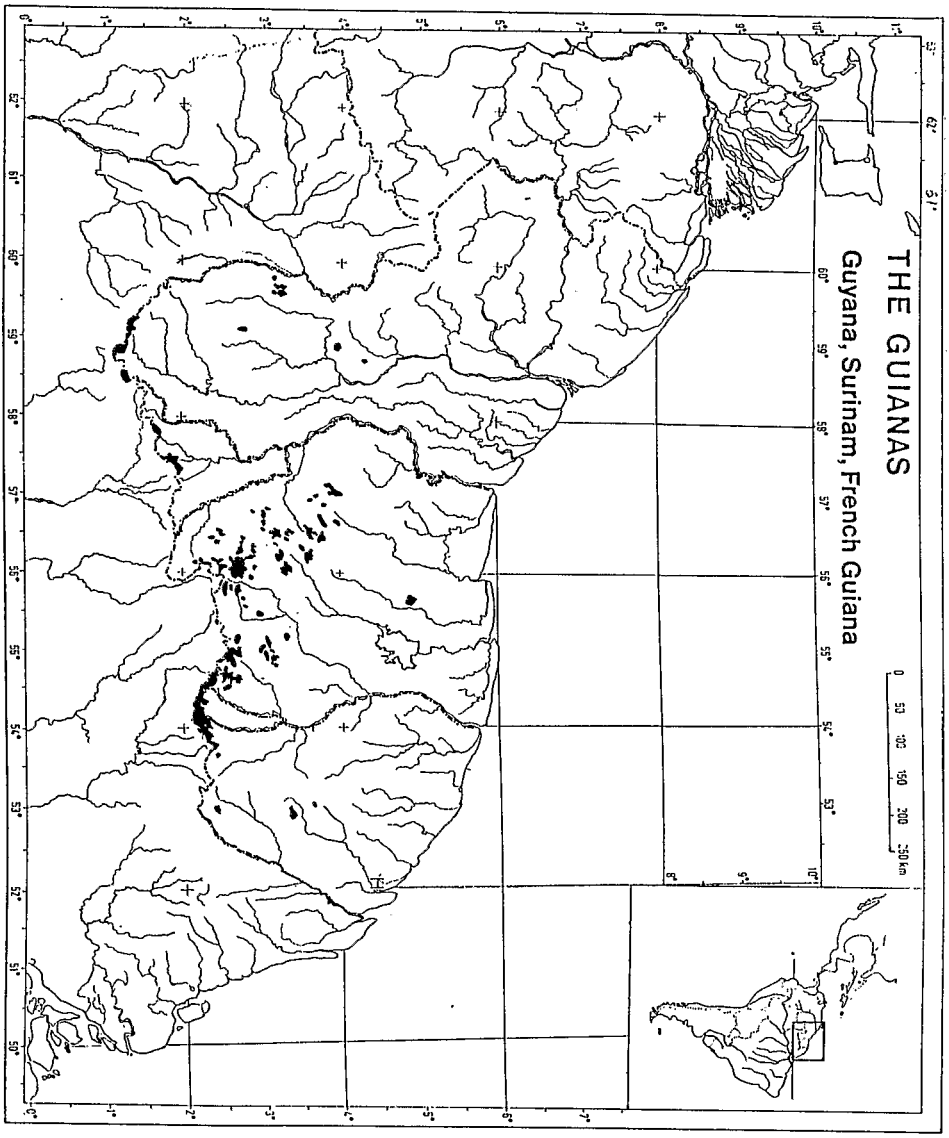

Fig. 5. The Guianas. Granitic outcrops and other rugged relief.

3.1. Vegetation

The vegetation varies depending on the thickness of the soil and the steepness of the slopes. In the Tumuc-Humac area, I distinguish the following vegetation types (Granville 1978):

Rain forest on crystalline bedrock is the predominant vegetation type. It occurs in valleys as well as on slopes and ridges where it presents a dryer facies. It is quite similar to forests growing at lower altitudes on the same kind of bedrock. These reliefs are generally much less massive and much more rugged and isolated than lateritic and bauxitic plateaus. Cloud forest is infrequent and is found only at the highest altitudes (800 m in Kanuku Mountains, Jansen Jacobs, Gradstein & Welle 1985). Moreover, the sandy clayey soils are not so rich and deep than the ones occurring on basic rocks. Consequently, the forests are lower and dryer. Huge granitic boulders are often seen in the understory. They harbour a few epipetric plants growing in half shade (as opposed to those growing in full light on bare slopes mentioned below).

Low dry forests occur mainly on very thin soils on the top of outcrops, in transition zones, and in belts between the base of the bare slopes and the rain forest. Treelets and shrubs rarely overtop 10 meters, xerophytic epiphytes are common in the understory, and herbs are frequent on the ground.

Bare granitic slopes ("savanes-roches" in French Guiana) have a very discontinuous, epipetric, xeric vegetation (succulents, sclerophylls, annual herbs) well adapted to the very inhospitable dark granite exposed directly to the sun. Dense patches of herbs and shrubs, often deciduous, are scattered on the slopes at places where dead leaves and organic matter can accumulate (hollows and cracks) without being washed away during the rainy season.

3.2. Flora

The most characteristic flora is growing on outcrops.

The low, dry forests are mainly dominated by *Myrtaceae (Calyptranthes* sp. pl., *Eugenia* sp. pl.) and secondarily by treelets and shrubs like *Inga virgultosa (Mimosaceae), Tapirira guianensis (Anacardiaceae), Guarea affinis (Meliaceae)* etc. Among the epiphytes, bryophytes can be abundant locally in small patches of cloud forest at relatively high altitudes. There are many orchids and bromeliads.

As I have already pointed out (Granville 1984), the increasing proportion of monocotyledons is related to ecological constraints. On the slopes, *Ischaemum guianense* and other *Poaceae* form dense patches in the moister places while *Pitcairnia geyskesii* is characteristic of the more arid zones where its creeping rhizomes, protected by mats of dead leaves, terminate in erect, spiny rosettes and red inflorescences. The most typical plants are: *Cyrtopodium andersonii, Encyclia ionosma (Orchidaceae), Anthurium solitarium (Araceae), Chamaecrista desvauxii* var. *saxatilis (Caesalpiniaceae), Melampodium camphoratum, Ichthyothere granvillei (Asteraceae), Stylosanthes hispida (Papilionaceae), Rhynchospora barbata (Cyperaceae), Ernestia blackii, E. confertiflora* and *E. rubra (Melastomataceae), Borreria* sp. pl. *(Rubiaceae), Utricularia* sp. pl. *(Lentibulariaceae).* As for the lateritic plateaus studied before, each mountain or group of mountains has its own characteristics. For example, *Epidendrum nocturnum* var. *tumuc-humaciense* is restricted to the Tumuc-Humac area while *Melocactus* sp. *(Cactaceae)* has been reported only from Voltzberg and the outcrops of the Sipaliwini area (Surinam).

According to my observations in the Tumuc-Humac Mountains (Granville 1978), based on the study of 148 species growing on bare, granitic slopes and in dry, shrubby, low forests, 42 % have a very wide distribution in South America, 27 % occur also in the Amazonian Basin in open places at lower altitudes (inland savannas, boulders along streams), and 22 % are endemic to the Guianas. Among the latter, 64 % are also found in coastal savannas or other low vegetation types whereas 36 % are typical montane plants growing most often above 500 meters like *Clusia kanukuana (Clusiaceae), Trilepis kanukuensis (Cyperaceae), Mandevilla surinamensis (Apocynaceae), Pitcairnia geyskesii* and *P. sastrei (Bromeliaceae), Epidendrum noctur-*

num var. *tumuc-humaciense, Croton stahelianus,* all growing on granitic mountains, but also *Clusia annularis (Clusiaceae), Sauvagesia tafelbergensis (Ochnaceae), Sipanea wilson-brownei (Rubiaceae), Asplenium zamiifolium (Aspleniaceae), Doryopteris sagittifolia (Pteridaceae)* growing also on Roraima sandstones.

It is interesting to notice that a few species have affinities with South-Eastern Brazil like *Doryopteris sagittifolia, Banisteriopsis gardneriana (Malpighiaceae)* and the genus *Trilepis.*

4. Conclusions

By way of conclusion, I suggest the following hypothesis. The Guayana Highland flora, at least at the highest altitudes, has its own features characterized by a high endemicity. The flora of the submontane and montane cloud forests on lateritic and bauxitic plateaus is more or less related to the wet forest flora of the Eastern slopes of the Andes, West and North of the Amazon Basin, while the more or less xeric vegetation types on granitic outcrops and other crystalline rugged reliefs are related to the dryest flora of Roraima sandstone formation and to the coastal and inland sandy savannas, even as far as South of the Amazon Basin.

This could be explained by the theory of the forest refugia developed by many authors: "During the last big glacial episode of the Würm occurring between 22000 and 13000 years before present (late Pleistocene), the drying up of the climate gave rise to an important retreat of the forest which was situated at this time in a certain number of refuges where the local climatic conditions favoured its maintainance" (Granville 1982). Most of the highest reliefs North and West of the Amazon Basin, now occupied by a very wet montane forest, could have acted as such refugia. Later, during the warmest interglacial episode of the Holocene, 6000 years ago (Flandrian transgression), at the recoalescence of the forest, the sea level was supposed to be about 10 meters higher than it is today, so that the Amazon formed a broad arm of the ocean which constituted an important ecological barrier with regard to floristic exchanges between North and South. Consequently, it is not surprising that the wet forest flora of the Guianan reliefs is more related to the one of other mountains situated to the North and to the West of the Guianas, as far as the Andes.

On the contrary, the granitic outcrops and other related reliefs with a more or less dry and low vegetation act as present day refugia of the xeric savanna flora which was much more spread throughout South America during the glacial episodes, especially the Würm and also other shorter dry periods of the Holocene (Granville 1982). At the time, the Amazon was narrower and scattered with many more islands which formed relays for floristic exchanges between North and South, accounting easily for the affinities with Central Amazon savannas and Southern Brazil.

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