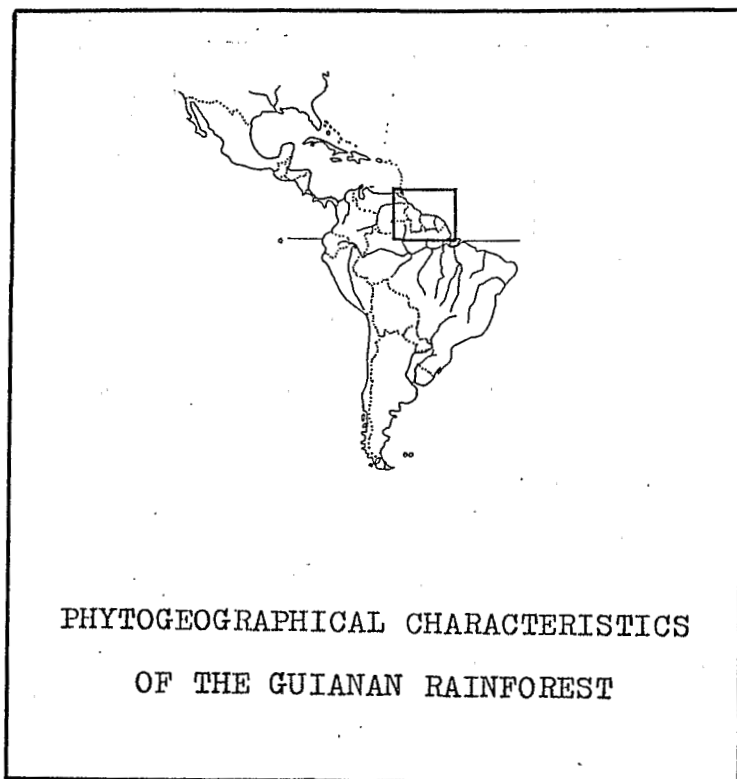




SYMPOSIUM TROPICAL BOTANY: PRACTICE AND PRINCIPLES

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Jean-Jacques de Granville

Institut Français de Recherche Scientifique
pour le Développement en Coopération
Centre ORSTOM de Cayenne

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Key words : Phytogeography, flora, vegetation, endemism, refugia, Guianas.

Summary : After a presentation of the Guianan area (situation, geomorphology and climate), the author gives a short description of each vegetation type occurring in the Guianas : upland or inland tropical evergreen moist forests, montane and lower montane forests, inundated forest types, transition forests, forests on white sand soils, herbaceous swamps, savannas, scrub vegetation of the bare rocks. In a second chapter, he analyses some distribution patterns of different taxa represented in the Guianan rain forest (Meliaceae, Caryocaraceae, Tabernaemontanoideae, Musaceae, Zingiberaceae, Arecaceae, Passifloraceae, Lindsaeaceae). The endemism of the Guayana Highland region is briefly discussed and the floristic affinities of the Guianas are given in relation with the theory of South American refugia.

Mots clefs : Phytogéographie, flore, végétation, endémisme, refuges, Guyanes.

Résumé : Après une présentation de la région des Guyanes (situation, géomorphologie et climat), l'auteur donne une brève description de chacun des types de végétation existant dans les Guyanes : forêt humide tropicale sempervirente de l'intérieur, forêt de montagne et de basse montagne, forêts inondées, forêts de transition, forêts sur sables blancs, marais herbeux, savanes et broussailles sur rochers nus. Dans un second chapitre, il analyse quelques modèles de répartition de différents taxons présents en forêt guyanaise (Meliaceae, Caryocaraceae, Tabernaemontanoideae, Musaceae, Zingiberaceae, Arecaceae, Passifloraceae, Lindsaeaceae). L'endémisme de la région des hauts plateaux gréseux guyanais fait l'objet d'une courte discussion et les affinités floristiques des Guyanes sont données en relation avec la théorie des refuges en Amérique du Sud.

Physiography

The geographical unity of the three Guianas is constituted by a Precambrian eroded base, sweeping from the Orenoque Delta in Venezuela, to the Amazon Delta, beyond the Amapa, in Brasil. It is commonly named the Guiana Shield. However, the political boundaries of the Guianas limit the region, from the East to the West, to French Guiana (which is a french department), Suriname (former Dutch Guiana) and Guyana (former British Guiana). These two latters are now independant countries. The Guianas are situated between $1^{\circ} 15'$ and 8° North, $57^{\circ} 10'$ and $66^{\circ} 28'$ West (fig.1).

In the coastal zone, the Precambrian base is overlaid by Quaternary marine silts forming the alluvial coastal plain or lowlands. This coastal plain, very narrow in French Guiana, is much wider in Guyana and Suriname. It has many various vegetation types (mangrove, swamps, savannas, forests) but, as we will see further, the flora is little original.

Everywhere esle, in the interior zone or uplands or inlands, it is the bedrocks of the Guiana Shield which give to the landscapes their physiognomy, depending on the nature of the rocks : more or less undulating terrain, multitude of hills isolated by the meshes of the hydrographic network. The soils are red, clayey, ferrallitic. In some places, the bedrock is overlaid by continental, detritic, leached white sands where dry forests and savannas are found.

On the basic rocks, fragments of residual lateritic crusts overcoming the Guiana Shield, form through and through tabular mountains which are remains of former peneplains. Their altitude vary from 300 to 1200 m.

Lastly, the highest reliefs are constituted by old sandstones, the Roraima Formation or Guayana Highland, superposed to the Guiana Shield, principally developed in Venezuela (tepui), reaching 2800 m in Guyana (M^t Roraima) and 3000 m in Venezuela (Cerro de la Neblina). Like the lateritic crusts, these mountains are relics of more extensive areas destroyed by erosion after the Oligocene-Miocene uplift.

The climate of the Guianas is equatorial, hot and wet with a short dry season in March and a longer one from September to November. The average annual rainfall vary, depending on the localities, from 1500 to more than 4000 mm. The trade winds are prevailing during all the year, from the South-East in dry season, from the North-East in rainy season. The average annual air temperatures are included between 25° and 30° C at low altitudes. They may be depressed at night to 5° C on the tepuis.

Distribution of the vegetation; situation of the forests in connection with the different vegetation types

In what follows, we use the recent classification of the American tropical forests by Prance (1979, 1987) but also those of Beard (1944), Fanshaw (1952), Richards (1952), Davis and Richards for the forests (1933, 1934), Lindeman (1953) for the coastal vegetation, Hooek (1971) for the savannas.

1. The forests of the Guianas

- 1.a. The upland (or inland) tropical evergreen moist forest grows directly on the hills of the Precambrian base and is opposed to the lowland tropical moist forests occurring

on the alluvia of the coastal plain. These "upland forests" have been named "lowland tropical moist forests" by Prance, "lowland rain forests" by Richards, "rain forest" by Fanshaw.

1.a.1. Forests on ferrallitic soils :

This type occurs from sea level up to 400--600 m. It is the high evergreen rain forest the most common in the Guianas. It is also the richest formation, found everywhere on undulating terrain, on well drained soils, with a climate rather uniform and annual rainfall of more than 2000 mm.

In Guyana, Davis and Richards characterized three different types and Fanshaw two associations, all based on the species dominance. The "mixed forest consociation" is considered like the climatic climax of the low Essequibo region. We think that a classification based on ecological features is more valuable for a wide area than those based on floristic data because the floristic composition vary from the East to the West of the Guianas, even in the same ecological conditions. For instance, in French Guiana, we remarked that the forests occurring on the basic laves and gabbros of the Paramaca series are higher and richer than those growing on conglomerates, quartzites or crystalline bedrock (table 1).

The general characteristics of these forests are a high and dense canopy of 20 to 45 m with a few emergent trees up to 50-60 m. The species diversity is enormous and there is a correlation between higher rainfall and increasing diversity. According to different authors, the tropical american forests have between 100 and 300 tree species per hectare. The forest inventories carried out by ORSTOM show a diversity of 746 trees over 15 cm in diameter for the whole French Guiana. The families are distributed as shown in table 2.

1.a.2. Forests on lateritic crusts :

Occurring mainly on the top of the hills on basic rocks, they are less species diverse, lower, with many lianas and a scrubby understory. Most of them are found at medium altitudes and are associated to the montane forests.

1.b. The montane and lower montane moist forests

1.b.1. The lower montane forests grow approximately from 400-600 m up to 1000-1300 m. Prance (1987) notices that "small changes in altitude can have extremely important changes in vegetation type, physiognomy, species composition and climate" and "there are many small patches of typically montane or cloud forests on small outcrops throughout the lowland region. Also the altitudinal limits of the different forest types vary considerably depending on local climate effects, soil, latitude etc...". These forests are scattered throughout the Guianas on the highest hills, often overlaid by a lateritic crust (see above) and reaching 860 m in French Guiana (Montagnes de l'Inini, Sommet Tabulaire), 1200 m in Suriname (Juliana Top). They are wrapped in fog during the rainy season and also in the morning during the dry season. Mosses and vascular epiphytes are abundant. Some species of trees seem to be dominant, especially trees with latex, depending on the localities : each tabular summit has its own characteristics. Prance points out that, in the montane formations, the tendency towards dominance accompanies the loss of species diversity.

1.b.2. The Guayana Highland is found in western Guyana. In Suriname, only the Tafelberg (1000 m) belongs to this

formation. At the tricorners of Guyana, Venezuela and Brasil, the Mount Roraima rises to 2800 m. It is a complex mixture of vegetation types : the lower mountains have a large quantity of forests, the tallest ones have more open and scrubby vegetation, except for the gallery forests along the streams. In many cases, there is a direct transition to open savanna and swamp formations on the summits of the mountains.

1.c. The inundated forest types

The various classifications proposed by the botanists show how difficult it is to divide these forests in well definite types. Although all these classifications are based on the duration of the flood, the limits between the permanent swamp forests and the periodically flooded forests seem not clear (table 3).

- 1.c.1. The permanent swamp forests of France correspond roughly to the swamp forest of Beard, Fanshaw and Lindeman. However, the permanent swamp forests are said to be dominated by palms when, according to the others, true permanent swamp forests have a few palms, the latter occurring principally in marsh forest. We consider that palms can be found in both types but only a few species tolerate permanently flooded soils : Euterpe oleracea and Mauritia flexuosa. Trees commonly found in these forest types are Triplaris surinamensis and, in Guyana, Mora excelsa, more or less intermixed with species of the neighbouring herbaceous swamps. The permanent swamp forests occur generally on recent coastal and subcoastal marine alluvia, in low ground, behind natural levees.

1.c.2. The periodically flooded forest (Prance) or marsh forest (Lindeman) :

The mangrove forest is daily flooded by the tide. It can be divided in two types :

- the coastal mangrove, very poor in species and consisting of Avicennia nitida, is a pioneer and unstable vegetation linked to the moving of the silt banks from the East to the West.

- the estuary mangrove where Rhizophora racemosa is dominant.

The other marsh forests are divided by Prance in tidal swamp forest near the coast and seasonal swamp forest along the muddy water rivers, when Lindeman distinguishes four types based on floristic composition. Virola surinamensis and Symphonia globulifera are, with the palms, the most characteristic species.

Lastly, Prance mention the flood plain forest, commonly found along the creeks and flooded by quickly draining flash floods. In spite of a lower diversity, it is rather similar to the rain forest on well drained soils.

1.c.3. The gallery forests are found along water courses in the Roraima-Rupununi savannas. Mauritia flexuosa is frequent in this type.

1.d. The transition forests

According to Prance, they are intermediate between the tall rain forest and the open areas. So, they may be compared to the seasonal forest of Beard and Fanshaw,

living on well drained soils but in areas with a more pronounced dry season, generally on subcoastal and coastal sandy alluvia. (table 4).

1.d.1. The evergreen seasonal forest :

From the beach to the interior and with an increasing species diversity and a canopy progressively higher, Lindeman distinguishes four types in the coastal plain of Suriname. The typical evergreen seasonal forest is the most common one.

Some upland areas have also transition forests like the low lying scrub forest of the granitic outcrops, the open forests at the margins of Gran Sabana, the liana forests found especially near the Roraima.

1.d.2. The semi-evergreen seasonal forest of Fanshaw corresponds to the dry forest of Prance with high deciduous trees and evergreen treelets in the understory. This type is found only in the western area of the Guianas with a more seasonal and much dryer climate.

1.e. The forests on white sand soils (Prance) or dry evergreen forest (Beard, Fanshaw) or savanna forest (Lindeman) are generally found on former sea beaches, along the coast. They occur also on leached continental sands and sandstones.

1.e.1. The wallaba forest is an important facies with dominance of Eperua falcata and Eperua rubiginosa, occurring on white leached sands, mostly in Guyana.

1.e.2. The xeromorphic rain forest, woodland and scrub are progressively more open and lower formations, the two latter included by Lindeman in the term of savanna forest. All are characterized by more or less tortuous trees with

coriaceous small leaves. Humiria balsamifera is often dominant, as also Humiria floribunda, Clusia nemorosa, Clusia fockeana.

2. The other vegetation types

2.a. The herbaceous swamps of the recent coastal plain are divided by Lindeman in several different types of increasing species diversity from the sea to the interior : the Eleocharis mutata community, the brakish Typha angustifolia - Cyperus articulatus swamps, the Leersia hexandra swamps, the fresh water swamps on pegasse with ferns and Cyperaceae, the Echinochloa polystachya swamps.

2.b. The savannas

2.b.1. The coastal savannas occurring principally on the former coastal plain are divided by Hooek in low savannas, on sandy impoverished soils and high savannas on more clayey soils. The latters are more species diverse and have a continuous herbaceous cover.

2.b.2. The inland savannas do not occur in French Guiana but cover rather important areas in southern Guyana and Suriname (Sipaliwini savanna, Roraima-Rupununi savannas).

The montane savannas occur on the top of the tepuis and are characterized by a very particular flora where some families, like Rapateaceae, are of considerable importance.

2.c. The herbaceous and scrub vegetation of the bare rocks occur on the rocky shores and on the rocky outcrops, principally found on crystalline rocks. The boulders of the streams, flooded in rainy season, bear a very peculiar vegetation of which the Podostemonaceae is the most noteworthy family.

The flora : some distribution patterns and floristic affinities

In his study on the American tropical forests and their phytogeography (1987), Prance discerns 18 phytochoria in the same way that those defined by White (1979) in tropical Africa. A phytochorion is an area with 50 % or more of the species confined to it and with a total of more than 1000 endemic species. The phytochoria, based on the distribution of the species, are more or less equivalent to the "regions" in the sense of Engler (1964).

Two of the 18 tropical american phytochoria concern the Guianas :

- The Guiana -Eastern Amazonian Regional Center, which includes the Amazon delta with a part of the Pará, the Amapa, the French Guiana, the Suriname and the Guyana except its western border.

- The Guayana Highland Region, particularly developed in Venezuela, South of the Orenoque, but including also the western part of Guyana.

1. The Guiana-Eastern Amazonian Regional Center includes many vegetation types but mostly lowland tropical moist forests.

It is impossible in a few pages to give a good account of the flora of such complex formations. So, we will limit ourself to some remarks about the floristic affinities.

- 1.a. The lowlands, on marine alluvia (coastal plain) have a flora generally rather poor and composed of large spread species, able to colonize new and changable, rapidly moving mediums

(mangrove, beaches, subcoastal herbaceous swamps, swamp and marsh forest, coastal savannas, seasonal ridge forests). The endemic species are *unfrequent*.

- 1.b. The uplands (interior zone) are much more interesting by their flora of considerable variety in respect of affinities and distribution types.

In what follows, we will study the distribution of the species present in the Guianas of 8 taxa of plants occurring particularly in forests : 2 families of trees of the canopy (Meliaceae, Caryocaraceae), one sub-family of shrubs of the understory (Apocynaceae Tabernaemontanoideae), the Palms, 2 families of herbs (Musaceae, Zingiberaceae), one family of lianas (Passifloraceae) and one genus of ferns (Lindsaea).

- 1.b.1. The Meliaceae (data from Pennington 1981).

31 of the 120 american species (26 %) occur in the Guianas. Their distribution can be linked to the following groups :

- 11 species (35 %) are wide spread in South and Central America or in northern South America.
- 11 (35 %) are confined to the Guianas and the Amazon Basin.
- 2 are "periamazonian" : Guarea macrophylla subsp. pachycarpa in the Guianas, Peru, Bolivia and atlantic coast of Brazil; Trichilia martiana in the Guianas, northern Venezuela, West Indies, Colombia and the atlantic coast of Brazil,
- One is found in Central America, northern Venezuela and Colombia and in the Guianas : Carapa guianensis.
- 3 occur in the Guianas and in central (Carapa procera) or lower Amazon valley (Trichilia lecointei, Trichilia surinamensis).

- 3 species are endemic to the Guianas : Guarea costata, Trichilia lepidota subsp. leucastera and T. surumuensis. Only the latter seems to be confined to the Guayana Highland.

1.b.2. The Caryocaraceae (data from France and da Silva, 1973).

7 of the 23 species occurring in tropical America (30 %) grow in the Guianas :

- None of them is a wide spread species.
- 3 are found in the Guianas and the Amazon Basin.
- 4 are endemic to the Guianas : Anthodiscus trifoliatus, Caryocar nuciferum and, exclusively on the Roraima sandstones, Anthodiscus mazarunensis and Caryocar montanum.

1.b.3. The Apocynaceae Tabernaemontanoideae (data from Allorge 1985).

15 of the 89 tropical american species (17 %) occur in the Guianas :

- 4 (27 %) are wide spread species.
- 1 lives in Central America and from northern Venezuela and Colombia to the Guianas : Stemmadenia galeottiana.
- 2 are periamazonian species : Anartia meyeri in Para (Brasil), the Guianas, Venezuela, Trinidad and amazonian Colombia. Anartia olivacea has a typical periamazonian distribution from Pará to Peru through the Guianas and Venezuela. It grows also on the atlantic coast of Brasil.
- 1 is found in the Guianas and eastern Amazonia : Bonafousia rupicola.
- 7 (46 %) are endemic to the Guianas. 6 of them belong to the genus Bonafousia : B. albiflora, B. angulata, B. disticha, B. lorifera (also once found near Manaus), B. macrocalyx, B. morettii. Anartia cerea is confined to the Guayana Highland.

1.b.4. The Musaceae (data from Maas 1985).

16 of the 100 species growing in tropical America (16 %) occur in the Guianas :

- 6 (30 %) are wide spread tropical American species. 4 of them are rain forest species and the 3 others are found in open places and secondary forest.
- 2 species occur in north-western South America : Heliconia bihai and H. stricta.
- 1 grows in the Guianas, Amazonian Brazil, Venezuela, Colombia, Ecuador, Peru : H. chartacea.
- 2 species are more or less periamazonian : H. densiflora is distributed in northern South America and south-western Amazon Basin to Peru and Bolivia, H. lourteigiae occurs in Peru, Colombia, northern Amazon Basin and the Guianas.
- 3 species are confined to the Guianas and the eastern Amazon Basin : H. acuminata, H. pendula, H. richardiana.
- 2 species only are endemic to the Guianas : H. dasyantha and H. nickeriensis.

1.b.5. The Zingiberaceae (data from Maas 1985).

20 of the 125 tropical american species (16 %) are found in the Guianas :

- 6 of them (30 %) are wide spread species.
- 5 (25 %) are north-western South American species.
- 2 occur in Central America, northern Venezuela and Colombia : Costus guanaiensis and C. villosissimus.
- 3 are found in the Guianas and eastern Amazon Basin : Costus congestiflorus, C. lanceolatus, Renealmia guianensis.
- 1 grows in northern South America from Venezuela to French Guiana : Renealmia orinocensis.
- 4 (20 %) are endemic to the Guianas : Costus claviger, C. curcumoides (restricted to French Guiana), C. aff. erythrothyrsus, Renealmia thyrsoides subsp. chrysantha.

1.b.6. The Arecaceae.

89 of the 1160 american species (8 %) occur in the Guianas. Among 80 guianan species of which we could study the distribution :

- 25 (31 %) are wide spread in northern South America. 6 of them grow in open places (mangrove, savannas, secondary vegetation), the others are primary forest species.
- 20 are confined to the Guianas and the Amazon Basin.
- 4 are periamazonian : Bactris cf. cuspidata, Geonoma euspatha, G. interrupta, G. triglochis.
- 31 (39 %) are endemic to the Guianas : Acrocomia lasiospatha, Asterogyne sp. nov., Astrocaryum sp. nov., Bactris sp. nov. 1 aff. B. acanthocarpoides, B. aubletiana, B. raphidacantha, B. sp. nov. 2, B. sp. nov. 3, Euterpe stenophylla, Geonoma bartlettii, G. oldemanii, G. poiteauana, G. stricta, G. "stricta x pycnostachys", G. sp. nov., Jessenia bataua subsp. oligocarpa, Lepidocaryum guianense, Maximiliana macro-petala, Scheelea camopiensis, S. degranvillei, S. guianensis, S. maripensis, S. passargerii, Syagrus stratincola. 7 species are found only in the Guayana Highland : Bactris ptariana, B. ulei, Euterpe aurantiaca, E. roraimae, E. tenuiramosa, Geonoma appuniana, G. fusca.

1.b.7. The Passifloraceae (data from C. Feuillet, 1986).

54 of the 400 american species (13 %) occur in the Guianas :

- 10 (18 %) are wide spread species.
- 6 (11 %) are found in the Guianas and the Amazon Basin.
- 1 is confined to the coastal area of the Guianas, Venezuela and Colombia : Passiflora foetida var. moritziana.
- 2 species live in the Guianas and north-eastern Brazil : Passiflora glandulosa and P. nitida.
- 3 can be linked to the "periamazonian" group : Mitostemma glaziovii occurs both in the Guianas and on Atlantic coast of Brazil, Passiflora riparia in the Guianas and eastern Peru, P. costata in the Guianas, Amazonian Peru and brazilian Atlantic coast.

- 32 species (59 % !)-are endemic to the Guianas : Dilkea magnifica, Mitostemma jenmanii, Passiflora acuminata, P. amicum, P. bomareifolia, P. candida, P. capparidifolia, P. cardonae, P. ceratocarpa, P. cirrhiflora, P. citrifolia, P. crenata, P. deficiens, P. fanchonae, P. fuschsiiflora, P. garckeii, P. gleasonii, P. holtii, P. laurifolia, P. leptopoda, P. lonchophora, P. longiracemosa, P. maguirei, P. nuriensis, P. ovata, P. pachyantha, P. phaeocaula, P. picturata, P. plumosa, P. quelchii, P. retipetala, P. rufostipulata, P. sclerophylla, P. securidata, P. stipulata, P. stoupyana.

1.b.8. The Dennstaedtiaceae, genus Lindsaea (data from Cremers, pers. comm. and Kramer 1957).

27 of the tropical american species and subspecies (60 %) occur in the Guianas.

- 4 are wide spread in South and Central America and generally also in the Caribbean Islands.
- 2 are found in north-western South America.
- 2 are more or less periamazonian : L. coarctata from Guyana, eastern Colombia and coastal Brasil, L. ulei from Guyana, Venezuela and south-western Amazon Basin.
- 8 species (30 %) have an area limited to the North of the Amazon Basin (Guianas, southern Venezuela and Colombia, northern Brasil. They could also have been classified as periamazonian but they have a more restricted area. These are : L. cyclophylla, L. dubia, L. javitensis, L. lancea var. elatior and var. leprieurii, L. pendula, L. semilunata, L. sphenomeridopsis, L. surinamensis.
- 2 are found both in the Guianas and the Amazon Basin.
- 2 species are confined to the Guianas and the eastern Amazon Basin : L. schomburgkii, L. lancea var. remota.
- 2 species grow in the Guiana area and the Caribbean Islands : L. quadrangularis subsp. antillensis and L. stricta var. jamesoniiformis.
- 5 (19 %) are endemic to the Guianas : L. parkeri, L. reniformis, L. sagittata, L. pleioptera, L. tenuis. Only the two latter are exclusively confined to the Guayana Highland.

The study of the distribution patterns of these 251 guianan species distributed in 8 taxa shows that (table 5) :

The most important groups are respectively the endemic species (35 %), the wide spread species (26.3 %) and the Guianas-Amazonian Basin species (17.1 %).

The endemicity vary, depending on the taxa, from 12.5 % (Musaceae) to 59.2 % (Passifloraceae). Though it would be dangerous to generalize without studying more taxa, the rather high endemicity seems to confirm the hypothesis of one or several centers of endemism in the Guianas.

Secondly, after the endemic and the wide spread species, the forest flora of the Guianas seems to have more affinities with the adjacent Amazon Basin than with the other regions. This is not surprising especially taking account of the absence of geographical barrier between these regions.

A fourth group, the one of the periamazonian species is particularly interesting although it holds only 6 % of the species : they occur in the Guianas, southern Venezuela, Colombia, eastern Peru and sometimes Bolovia. Some of them occur also on the Atlantic coast of Brazil. In the Guianas, these plants are generally found on the highest hills, in low montane forest or in cloud forest rather than in the valleys. In addition to the examples appearing in the studied families, we can mention : Hyptis pachycephala (Lamiaceae), Anomospermum chloranthum subsp. confusum (Menispermaceae), Dichorisandra sp. nov. (Commelinaceae), Mouriri oligantha (Melastomaceae), Tassadia guianensis (Asclepiadaceae), all occurring both in the Guianas and eastern Peru; Costus aff. erythrothyrus (Guianas) is closely related (may be conspecific) to C. erythrothyrus (Peru); Couepia parillo (Chrysobalanaceae) is present in Amapa, the Guianas, eastern Colombia and

Peru; Geonoma triglochis (Arecaceae) occurs in the Guianas but also in Venezuela, Colombia, Peru, Brazil except in the Amazon Basin; Geonoma euspatha is found in the Guianas, Venezuela and Colombia; Cyathea lasiosora (Cyatheaceae) grows in the Guianas and from Venezuela to the North of Bolivia.

2. The Guayana Highland Region is characterized by a very rich and highly endemic flora.

According to Maguire (1970), the total population would be "in magnitude of 8000 species of which considerably more than 50 % are endemic". 4000 endemic species had already been described in 1970 ! The proportion of endemic species is not the same at low and at high altitudes : it is estimated to be of about 70 % at middle elevation, while it would reach 90 to 95 % on the summits of the tabular mountains. This proportion seems to have been much over-estimated and more recent studies carried out by Steyermark (1982) show that the specific endemicity vary, depending on the tepuis, from 5.3 to 63 %.

The high endemicity of the Guayana Highland flora reaches the generic level : according to Steyermark (1982), 39 genera (8.5 %) are strictly endemic to the summits of the sandstone table mountains, but 40 additional genera are endemic to the surrounding area (bluffs, slopes, Gran Sabana), increasing the generic endemism to 17.2 %.

The families well represented in the Guayana Highland flora are not generally the same as the predominant ones in the Guianas-Eastern Amazonian Regional Center previously studied. The Leguminosae, for instance, have not a so large range than at lower altitudes. On the other hand, other taxa are more developed, especially those represented by numerous herbaceous or scrubby species. However, only one family seems to be confined to this region : the Tepuianthaceae (Sapindale), a new monogeneric family described a few years ago (Maguire and Steyermark, 1981).

The relationships between the Guayana Highland flora and the one of the lower altitude forests, principally the Guianas and Amazonia, has been discussed by Steyermark (1982). He distinguishes especially the constituents of autochthonous origin and those, more recently evolved, originating from Amazonian centers.

Two examples of taxa well represented on the tepuis are given below :

- 2.a. The Ochnaceae (Maguire, 1970) are represented in the Guayana Highland by 10 of the 16 genera now known : 6 are exclusively endemic to the summits of the tepuis : Adenanthe, Adenarake, Leitgebia, Philacra, Poecilandra. In the Eastern Amazonian Regional Center, 3 genera only are found : Elvasia, Ouratea, Sauvagesia.

The distribution of the 15 species of Sauvagesia (data from Sastre 1971, 1984) occurring in the Guianas indicates that :

- 50 % of the 30 american species are found in the Guianas.
- 3 only (20 %) are wide spread species growing in wet sandy savannas of northern South America, often Central America and Caribbean Islands.
- 1 species occurs in Colombia, Venezuela, the Guianas and in northern Amazon Basin : S. ramosissima.
- 4 species (26 %) are found in the Guianas and in the north-eastern Amazon Basin : S. elata and S. longifolia are forest clearing species, S. rubiginosa and S. sprengelii are savanna species. The latter is found also along the Brazilian coast.
- 7 species (46 %) are endemic to the Guianas : 4 are endemic to the Guayana Highland, at altitudes higher than 1000-1500 m , S. guianensis, S. imthurniana, S. roraimensis, S. longipes. S. tafelbergensis occurs at lower altitudes both on roraima sandstones and on

granitic outcrops in Suriname and French Guiana. S. aliciae subsp. aratayensis grows on granitic outcrops of French Guiana and S. angustifolia is a species of Gran Sabana, between 500 and 1500 m.

The wide spread species grow in savannas and in open places at low altitudes while endemic species occur in montane or submontane areas. Moreover, according to Sastre, the endemic species are generally shrubs whereas the wide spread ones are always annual herbs with high spreading ability.

Most of the Guianan species would result from a differentiation during Oligocene in consequence of the uplift of the Guiana Shield which has been the main center of differentiation of the genus.

2.b. The Rapateaceae (data from Maguire 1958, 1965, 1970)

14 of the 16 genera now known occur in the Guayana Highland. 10 are exclusively confined to this region : Amphiphyllum, Duckea, Guacamaya, Kunhardtia, Phelpsiella, Potarophytum, Monotrema, Schoenocephalum, Stegolepis, Windsorina. Thus, 62 of the 80 species are endemic to the Guayana Highland, but 16 of them only occur inside the political boundaries of the Guianas. Most of them grow in the low lying herbaceous scrub formations of the summits. According to Maguire (1958), "...perhaps no other family of flowering plants can be considered more characteristic of the phytogeographic province of Guayana than the Rapateaceae...The center of distribution and the greatest concentration of genera and species lie within the periphery of Guayana".

Conclusions

The vegetation of the Guianas is principally constituted by tropical forests differentiated in many types depending on the nature of the bedrock, the soils, the drainage conditions, the local climate and also of the paleohistory of the region.

Thus, the vegetation types may be characterized by their floristic composition only in a relatively limited area, but not in the whole Guianas.

The studies based on the species distribution on the continental scale give good informations especially on the global endemicity of the Guianas which seems rather high. The same studies limited to the Guianan scale would be hazardous because of the still considerable lacks of the floristic inventory : some regions, well prospected because they are easy to reach, look on the maps as if they were centers of endemism in opposition to other areas, poorly or not prospected by lack of tracks, airstrips or navigable rivers and which seem less species diverse because they are badly known !

Nevertheless, some areas seem to be really more species diverse and to harbour more endemic species than others. These areas are presumed to coincide rather well with the forest refuges during the dry periods of the late Pleistocene and the Holocene. Patterns of forest refuges in South America have been proposed by several scientists, especially Haffer (1969), Vanzolini and Williams (1970), Morley (1975), Prance (1973, 1982a and b), Brown (1979). The two latter, whose researches are more recent and more detailed, agree with the hypothesis of, at least, 3 endemic centers in correlation with forest refuges in the past in the Guianas (

Though the size and the shape of these refuges are not exactly the same depending on the authors, their distribution is rather similar and in agreement with the one we proposed for French Guiana (1982).

Moreover, the periamazonian disjunct species distributed in isolated populations, especially in the Guianas and in eastern Peru (and also, in a lower proportion, along the Atlantic coast of Brazil), fit rather well with the other proposed refuges and are witnesses of former continuous populations in tropical South America, divided later in patches by the forest recession.

However that may be, the floristic inventory has to be intensely continued, especially in the southern part of Guyana in order to confirm or to modify these hypothesis and to have a good estimation of the endemism of each guianan refuge and of their relationships one to the other.

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Table legends :

- Table 1 : The upland tropical evergreen moist forest types in the Guianas.
- Table 2 : Tree species of more than 15 cm in diameter occurring in French Guiana.
- Table 3 : The inundated forest types in the Guianas.
- Table 4 : The transition forests in the Guianas.
- Table 5 : Distribution patterns of the Guianan species for 8 taxa of vascular plants occurring mostly in rain forest.

Figure legends :

- Fig. 1 : The 3 Guianas; topography and relief.
- Fig. 2 : Proposed forest refuges in the Guianas, based on distribution of woody Angiosperm families (Prance 1982).
- Fig. 3 : Paleoecological forest refuges : areas of high probability for stability of tropical forest over the last 20 000 years (paleoecological forest refuges for the late Würm-Wisconsin ice-age), determined by summation of data from geomorphology, paleoclimate, soils and vegetation types. Dotted areas : 60 % probability; black areas : 80-100 % probability. (Brown, 1982)
- Fig. 4 : Endemic centers in the neotropical forests, based on subspecific differentiation in Heliconiini and Ithomiinae (aposematic Lepidoptera). Dotted areas : 1/3 of maximum isoline; black areas : 2/3 of maximum isoline. (Brown, 1982)

Table 1

RAIN FOREST ON FERRALLITIC SOILS		
<ol style="list-style-type: none"> 1. Mixed forest consociation 2. Green heart consociation 3. Morabukea consociation <p style="text-align: center;">(Davis and Richards, 1933-1934)</p>	<ol style="list-style-type: none"> 1. Eschweilera-Licania association 2. Eschweilera-Dicymbe association <p style="text-align: center;">(Fanshaw, 1952)</p>	<ol style="list-style-type: none"> 1. High rain forest on deep soils associated to the Paramaca series (Gabbros, basic laves) 2. Low rain forest on impoverished soils, conglomerate and quartzite, associated to the Orapu and Bonidoro series 3. Rain forest on soils associated to the crystalline base <p style="text-align: center;">(J.-J. de Granville)</p>
RAIN FOREST ON LATERITIC CRUSTS		

Table 2

LEGUMINOSAE	150	BURSERACEAE	20
CAESALPINIACEAE	56	CLUSIACEAE	19
MIMOSACEAE	55	MYRTACEAE	18
PAPILIONACEAE	39	APOCYNACEAE	16
LAURACEAE	56	RUBIACEAE	16
SAPOTACEAE	50	ANNONACEAE	15
CHRYSOBALANACEAE	45	SAPINDACEAE	15
MORACEAE	38	VOCHYSIACEAE	15
LECYTHIDACEAE	33	BOMBACACEAE	10
EUPHORBIACEAE	28	ELAEOCARPACEAE	10
MELASTOMACEAE	25		
MELIACEAE	23		
Other families : less than 10			

Table 3

<p style="text-align: center;"><u>MARSH FOREST</u></p> <ol style="list-style-type: none"> 1. Palm marsh forest 2. Marsh forest 3. Marsh woodland 4. Palm marsh <p style="text-align: center;"><u>SWAMP FOREST</u></p> <ol style="list-style-type: none"> 1. Mora forest 2. Swamp forest 3. Swamp woodland 4. Mangrove forest <p style="text-align: center;">(Beard, 1944) (Fanshaw, 1952)</p>	<p style="text-align: center;"><u>MARSH FOREST</u></p> <ol style="list-style-type: none"> 1. <i>Triplaris surinamensis</i>- <i>Bonafousia tetrastachya</i> type 2. <i>Symphonia globulifera</i> type 3. <i>Hura crepitans</i> forest 4. <i>Mauritia-Chrysobalanus</i> association <p style="text-align: center;"><u>SWAMP FOREST</u></p> <ol style="list-style-type: none"> 1. Mixed swamp wood 2. <i>Machaerium lunatum</i> scrub <p style="text-align: center;">(Lindeman, 1953)</p>	<p style="text-align: center;"><u>PERIODICALLY FLOODED FORESTS</u></p> <ol style="list-style-type: none"> 1. Mangrove forests 2. Tidal swamp forest (tidal varzea) 3. Seasonal swamp forest (seasonal varzea) 4. Flood plain forest <p style="text-align: center;"><u>PERMANENT SWAMP FORESTS</u></p> <p style="text-align: center;"><u>GALLERY FORESTS</u></p> <p style="text-align: center;">(Prance, 1987)</p>
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Table 4

EVERGREEN SEASONAL FOREST	
<ol style="list-style-type: none">1. Cereus ridge wood2. Intermediate ridge forest3. Typical evergreen seasonal forest4. Parinari ridge forest5. Forest on the ridges near Coronie <p>(Lindeman, 1953)</p>	<ol style="list-style-type: none">1. Open forest2. Liana forest <p>(Prance, 1987)</p>
SEMI-EVERGREEN SEASONAL FOREST (Fanshaw, 1952) or DRY FOREST (Prance, 198)	

Table 5




















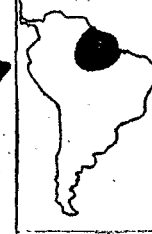

Types of distribution patterns											Endemic to the Guianas	TOTAL
												
MELIACEAE	11		1			2		11		3	3 (9.7 %)	31
CARYOCARACEAE								3			4 (57.1 %)	7
Tabernaemont.	4		1			2				1	7 (46.7 %)	15
ARECACEAE	25					4		20			31 (38.7 %)	80
MUSACEAE	6	2				2		1	3		2 (12.5 %)	16
ZINGIBERACEAE	6	5	2				1		3		4 (19.0 %)	21
PASSIFLORACEAE	10			1		3		6	2		32 (59.2 %)	54
Lindsaea	4	2			2	2	8	2	2		5 (18.5 %)	27
TOTAL	66	9	4	1	2	15	9	43	10	4	88	251
%	<u>26.3 %</u>	<u>3.6 %</u>	<u>1.6 %</u>	<u>0.4 %</u>	<u>0.8 %</u>	<u>6.0 %</u>	<u>3.6 %</u>	<u>17.1 %</u>	<u>4.0 %</u>	<u>1.6 %</u>	<u>35.0 %</u>	

Fig. 1

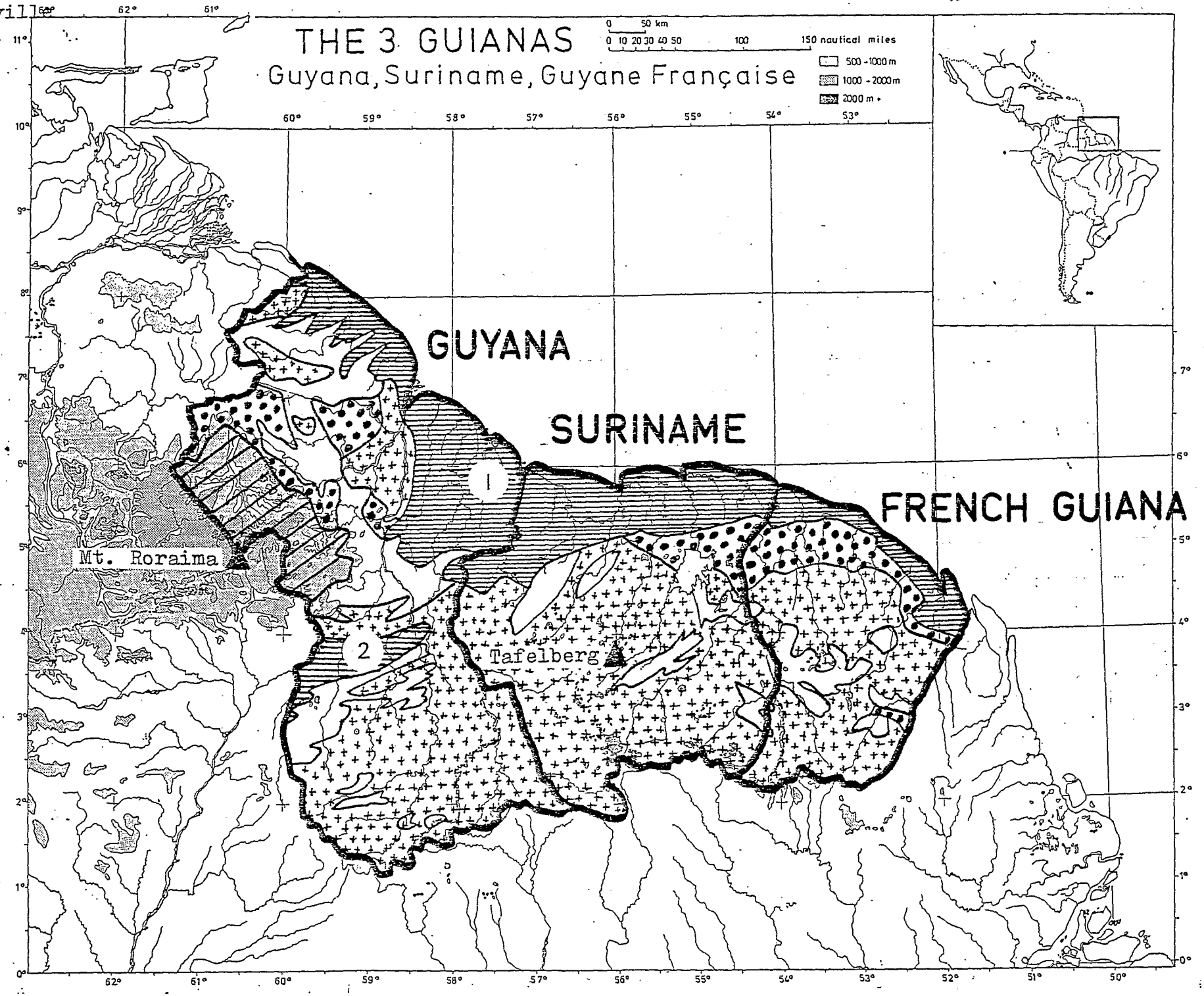


Fig. 1

Lowlands :



① Alluvial coastal plain : mangrove, savannas, herbaceous swamps, marsh and swamp forests, transition forests.

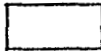


② Roraima-Rupununi savannas.

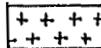
Uplands (or inlands) :



Shist, conglomerate and quartzite of the Orapu-Bonidoro series : low rain forest on impoverished soils.



Geosynclinal of the Paramaca series : high rain forest on deep soils, submontane forest, forest on lateritic crusts.



Southern peneplain on crystalline base : medium size rain forest.



Guayana Highland : forests, scrubby vegetation and savannas on sandstone table mountains.

Fig. 2

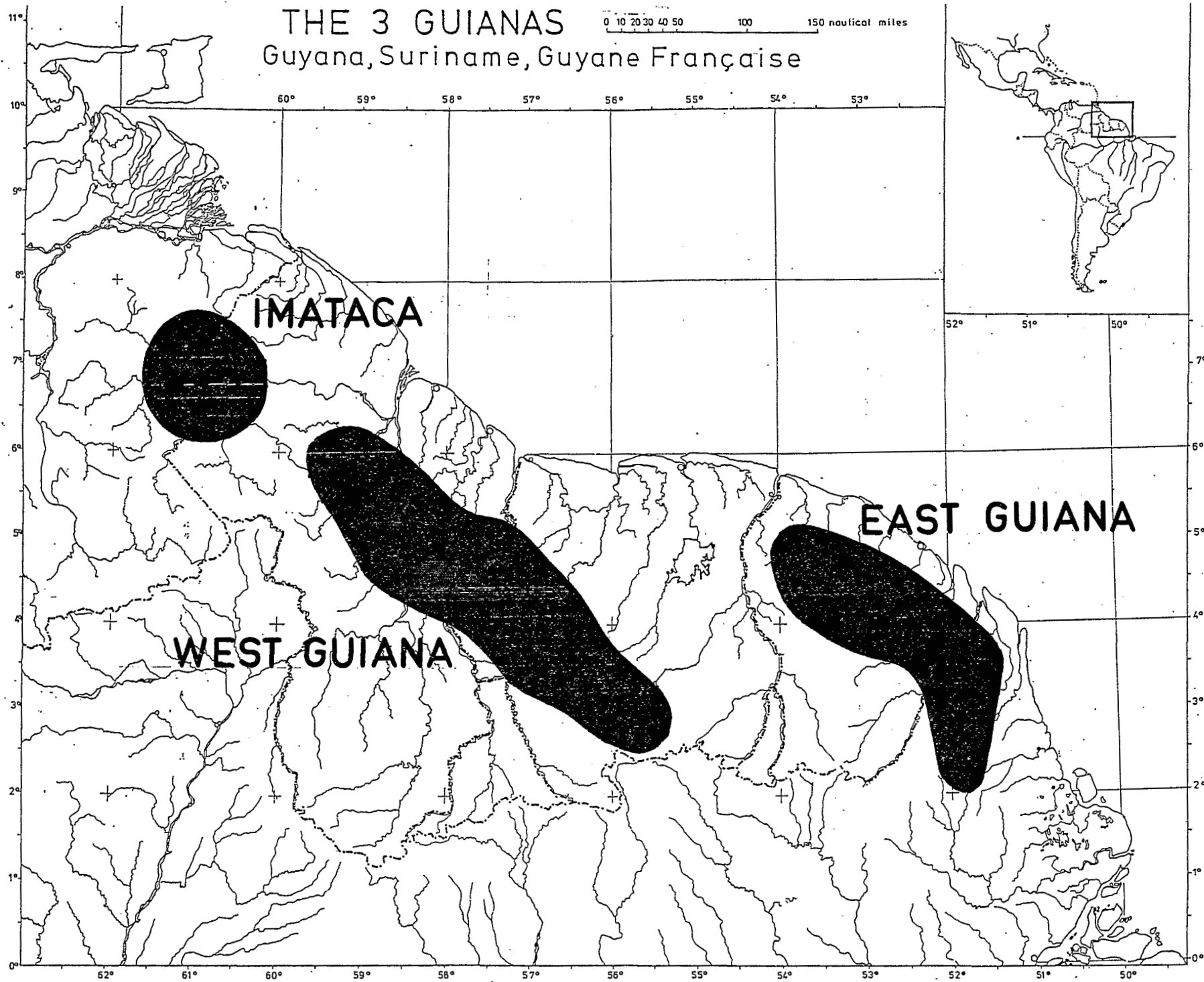


Fig. 3

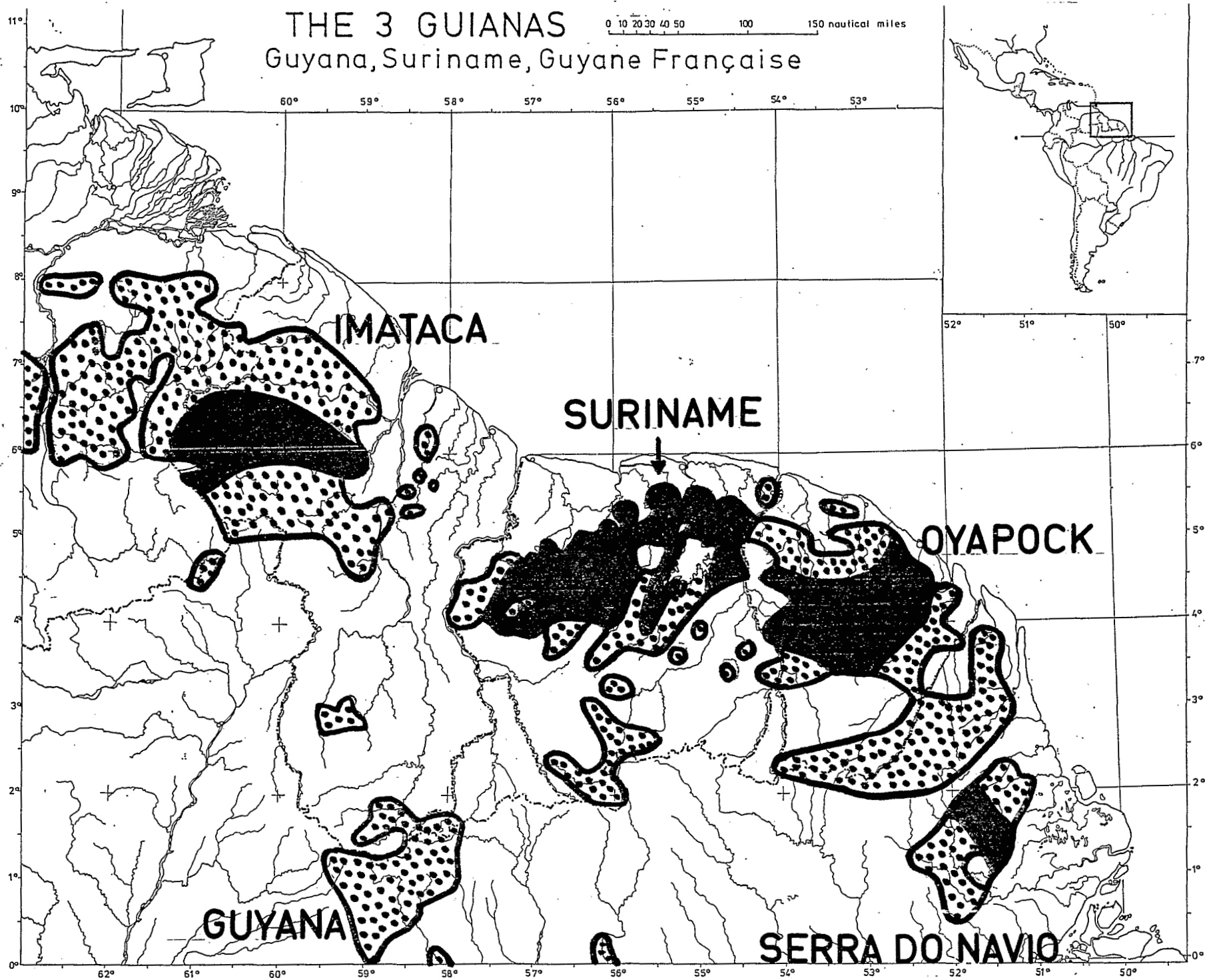
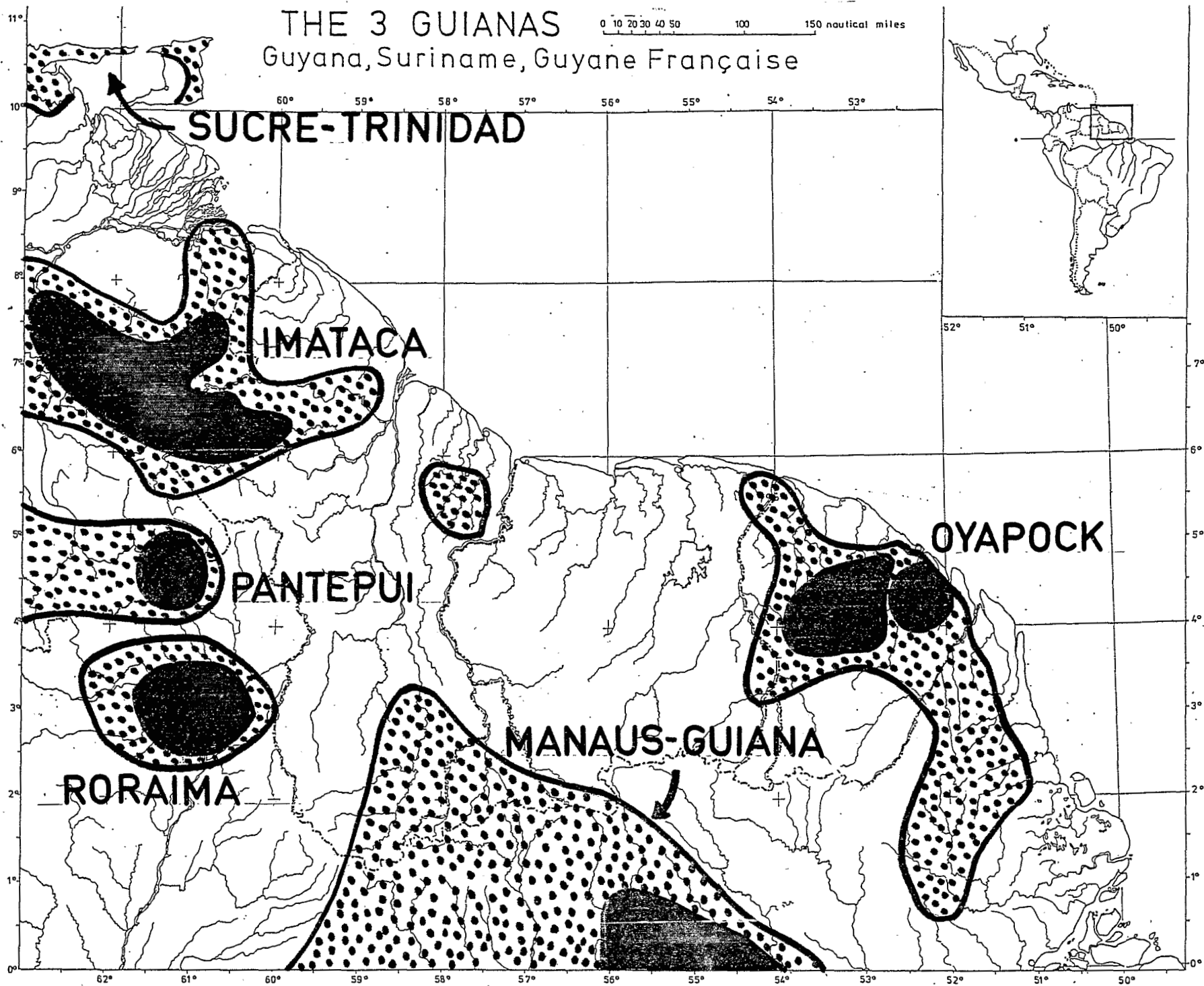


Fig. 4



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