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FOREST FLORA AND XERIC FLORA REFUGES IN FRENCH GUYANE DURING THE LATE PLEISTOCENE AND THE HOLOCENE

par

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ABSTRACT

After a short description of the natural environment in French Guyane and of the chronology of the recent climatic variations, the probable evolution of the flora and vegetation due to these fluctuations is analysed in terms of climatic, topographic and mainly pedologic and floristic data. So, the approximative limits of a rainforest refuge in French Guyane during the great arid phase of the late Pleistocene are postulated. On the other hand, the present day situation, corresponding to the end of a wet period, support the evidence of isolated refuges with a xeric herbaceous flora (coastal savannas, outcrops, forest canopy).

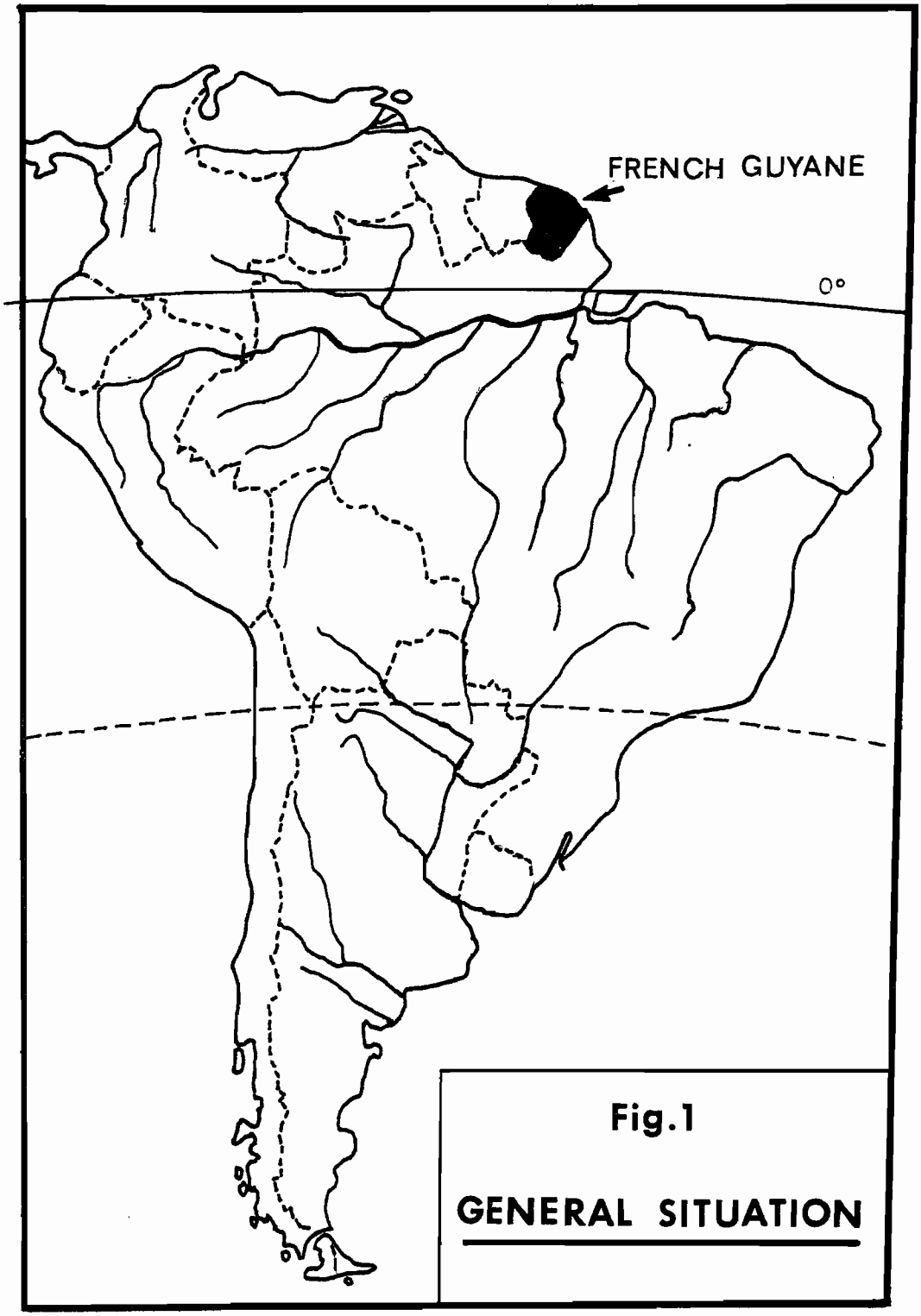


Fig.1

GENERAL SITUATION

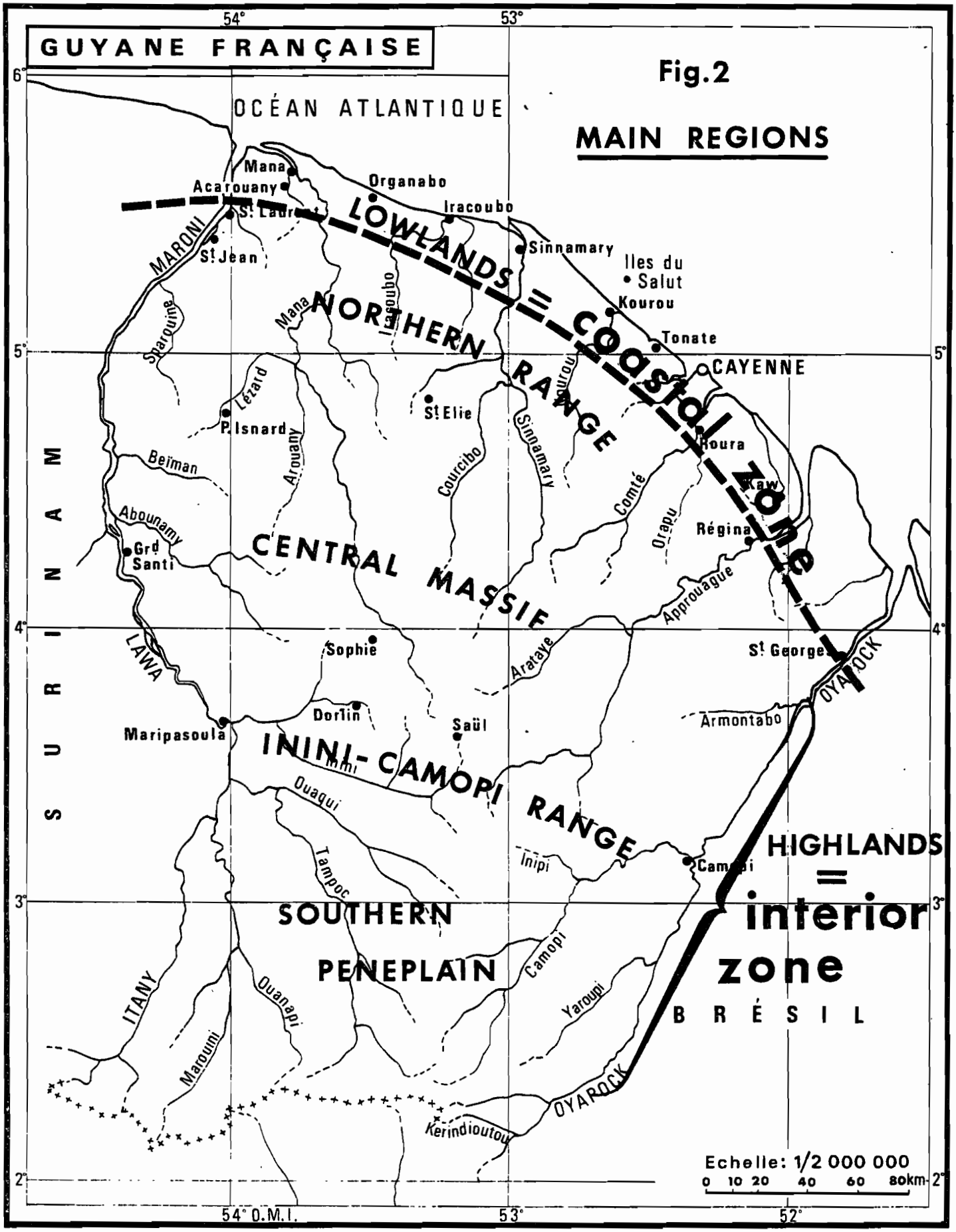
I INTRODUCTION TO FRENCH GUYANE

Situated between 2° and 6° latitude north on the precambrian base of the "Guianian shield", French Guyane covers an area of 90 000 km^2 approximately (fig. 1).

The natural environment of Guyane, compared with other South American territories covered with rainforest, has been relatively well studied, but is still much less well known than the temperate regions. Maps depicting the topography, geology, geomorphology, pedology, hydrography, vegetation and the climate (Atlas de la Guyane, 1979) have been drawn up. The human impact on the natural ecosystems is negligeable, due to the very low population density which is essentially urban (50 000 people of which 30 000 are in Cayenne), the lack of industry, agriculture and penetration roads.

Only the very narrow coastal zone (fig. 2) where the Quaternary marine sediments overly the precambrian base, does a non forested vegetation exist. This is made up of mangrove (0.6 % of Guyane), savannas and coastal swamps (1.7 % of Guyane).

The interior zone which covers almost completely French Guyane corresponds to the position of the precambrian base. Today, this zone is covered with dense equatorial rainforest which occupies more than 97 % of the total area of Guyane. Its physiognomy is in general fairly uniform in spite of an unequal distribution of the rainfall which varies, according to the region, from less than 2 000 mm to more than 4 000 mm/year (fig. 3). It is an evergreen forest which grows on ferralitic soils on a sloped but rarely steeply inclined relief, and where the multiconvex pattern


GUYANE FRANÇAISE
Fig.2
MAIN REGIONS
OCÉAN ATLANTIQUE
54°
53°
52°
6°
5°
4°
3°
2°
Mana
Acarouany
Organabo
Iracoubo
Sinnamary
Iles du Salut
Kourou
Tonate
CAYENNE
St Jean
MARONI
LOWLANDS = coastal zone
NORTHERN RANGE
Mana
Iracoubo
Sinnamary
Kourou
Sparouine
Lézard
P. Isnard
St Elie
Roura
Beïman
Arouany
Courcibo
Comté
Kaw
Orapu
Régina
Abounamy
Grd Santi
CENTRAL MASSIF
Approuague
SURINAM
LAWA
Sophie
Arataye
St George
OYAPOCK
Dorlin
Saül
Armontabo
Maripasoula
ININI-CAMOPI RANGE
Inini
Ouaqui
Tampoc
Inipi
Camopi
HIGHLANDS = interior zone
SOUTHERN PENEPLAIN
ITANY
Ouanapi
Camopi
Yaroupi
Marouini
OYAPOCK
Kerindioutou
BRÉSIL
Echelle: 1/2 000 000
0 10 20 40 60 80km
54° O.M.I.

called "demi-oranges", on granite, is the most common.

The rainforest which grows on well drained soils, is only very locally replaced by other vegetation types or communities i.e. white sand forests, swamp forest or "pinotières" ("Igapo" forest in Brazil) along certain water courses, "cambrouses" or thickets of bamboos, "savanes-roches" ("rocky savannas") on denuded granite outcrops, low lying scrub forest rich in lianas on the lateritic crust of the summits of the plateaux, "cloud forest" rich in epiphytes covering the summits above 500 m (although relatively hilly Guyane doesn't have any very high peaks (fig. 4).

The forest flora is rich. The botanists from O.R.S.T.O.M. (Office de la Recherche Scientifique et Technique Outre-Mer), after more than 20 years of research and exploration in Guyane, reckon the number of vascular species to be between 6 000 and 8 000. A precise inventoty is in the process of being made, but there is still no specific flora in Guyane which enables easy identification of species. Up to the present, research has dealt mainly with the collection of herbarium specimens, the phytoecology of the savannas, the dynamics, ecology and architecture of the forest and regeneration of the vegetation after cutting and burning.

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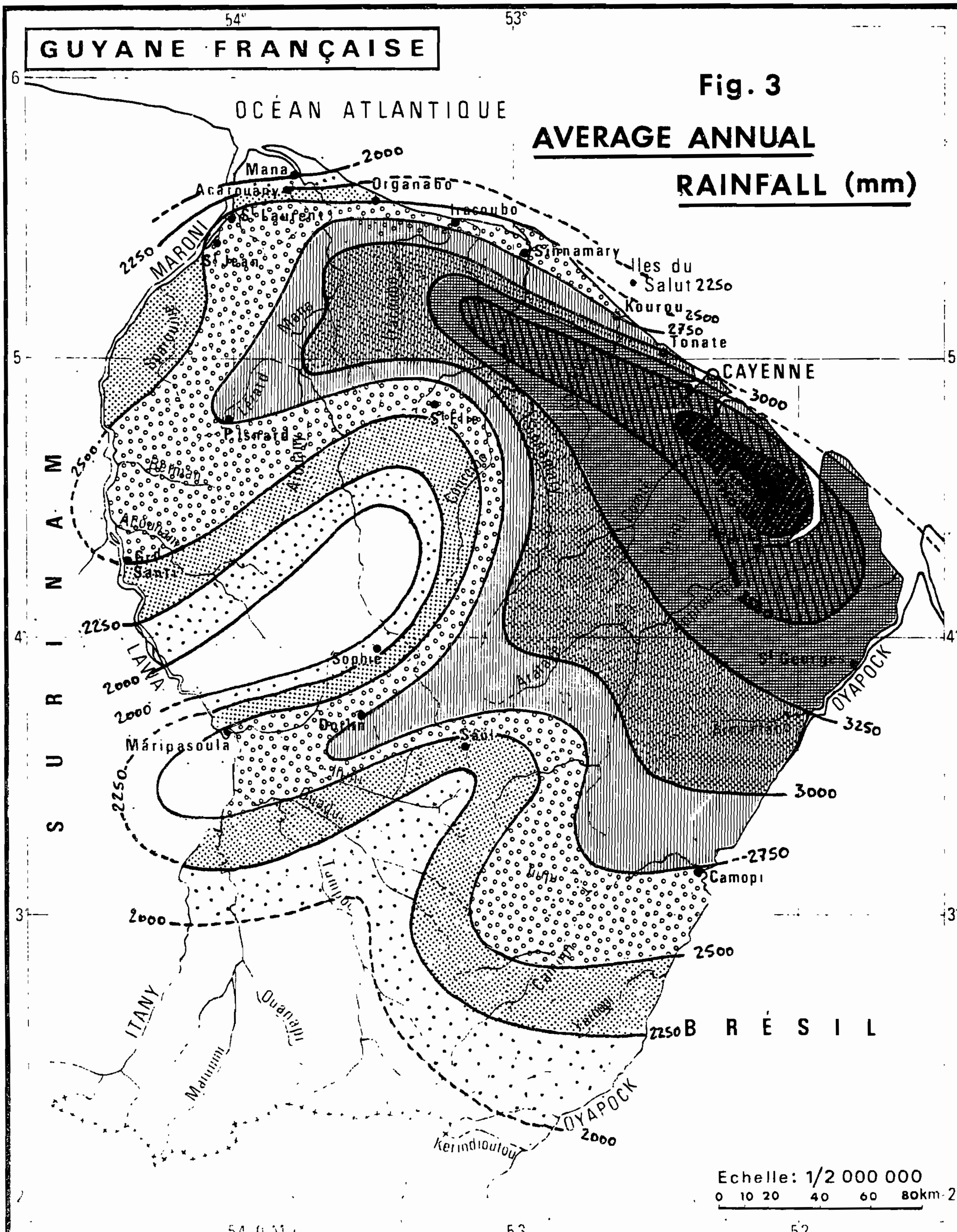
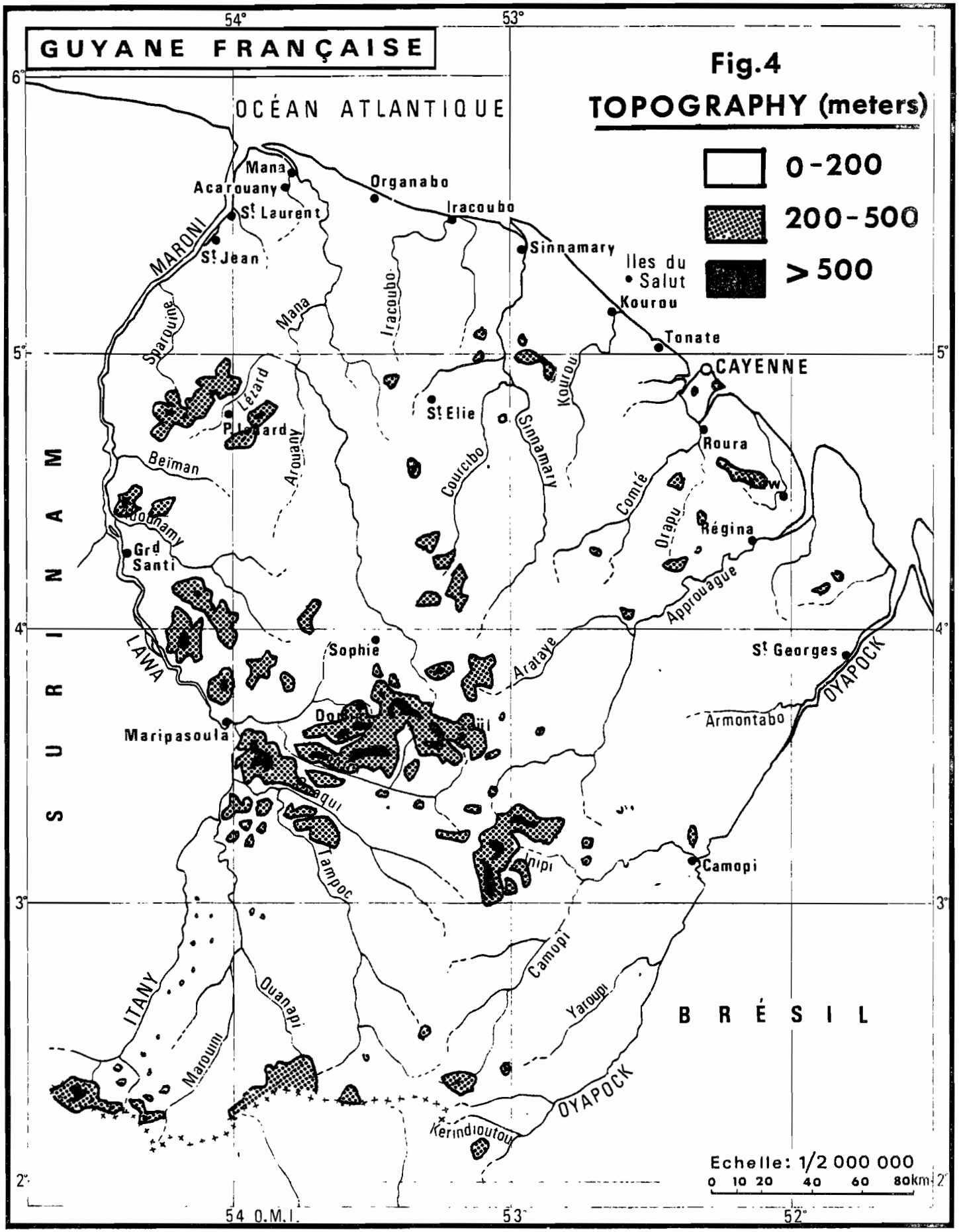

GUYANE FRANÇAISE
Fig. 3
AVERAGE ANNUAL RAINFALL (mm)
OCÉAN ATLANTIQUE
Mana
Acarouany
Organabo
Iracoubo
St Laurent
St Jean
Sinnamary
Iles du Salut
Kourou
Tonate
CAYENNE
MARONI
SURINAM
P. Sparouine
St Élie
Sophie
Saül
Maripasoula
Camopi
St Georges
OYAPOCK
LAWA
ITANY
BRÉSIL
2000
2250
2500
2750
3000
3250
Echelle: 1/2 000 000
0 10 20 40 60 80km
54°
53°
52
6
5
4°
3°


GUYANE FRANÇAISE
Fig.4
TOPOGRAPHY (meters)
0-200
200-500
> 500
OCÉAN ATLANTIQUE
SURINAM
BRÉSIL
54°
53°
52°
6°
5°
4°
3°
2°
Mana
Acarouany
St Laurent
MARONI
St Jean
Organabo
Iracoubo
Sinnamary
Iles du Salut
Kourou
Tonate
CAYENNE
Sparouine
Mana
Iracoubo
Kourou
Lézard
Léopard
St Elie
Sinnamary
Roura
Beïman
Arouany
Courcibo
Comté
Orapu
Régina
Gd Santi
LAWA
Approuague
Sophie
Arataye
St Georges
OYAPOCK
Armontabo
Maripasoula
Camopi
Tampoc
Inipi
ITANY
Ouanapi
Camopi
Yaroupi
Marouini
Kerindioutou
Echelle: 1/2 000 000
0 10 20 40 60 80km
54 O.M.I.

II CLIMATIC FLUCTUATIONS AT THE END OF THE QUATERNARY AND THE PROBABLE EVOLUTION OF THE FLORA AND THE VEGETATION DURING THESE FLUCTUATIONS

Palaeoclimatic research undertaken by numerous different disciplines (geology, geomorphology, palynology, biogeography, studies in solar radiations, analysis of the isotopic composition $^{18}O/^{16}O$ of marine sediments) have permitted the establishment with remarkable precision of the climatic variations on earth during the Quaternary (1).

We know in particular that the last of the 6 important Pleistocene glaciations, the Würm (70 000 to 10 000 B.P.), was marked by a succession of 4 glacial stages broken by interstadials. During the glacial stages, part of the water of the oceans was immobilized in the polar ice-caps, the climate in general was colder and dryer, including the intertropical regions. During the interstadials, the warming up of the climate was accompanied by an increase in the rainfall and in the amount of water contained in the atmosphere at saturation point (TRICART, 1974).

The last big glacial episode of the Würm occuring between 22 000 and 13 000 B.P. is the one which has particularly interested scientists because of the importance of its biogeographical consequences : the drying

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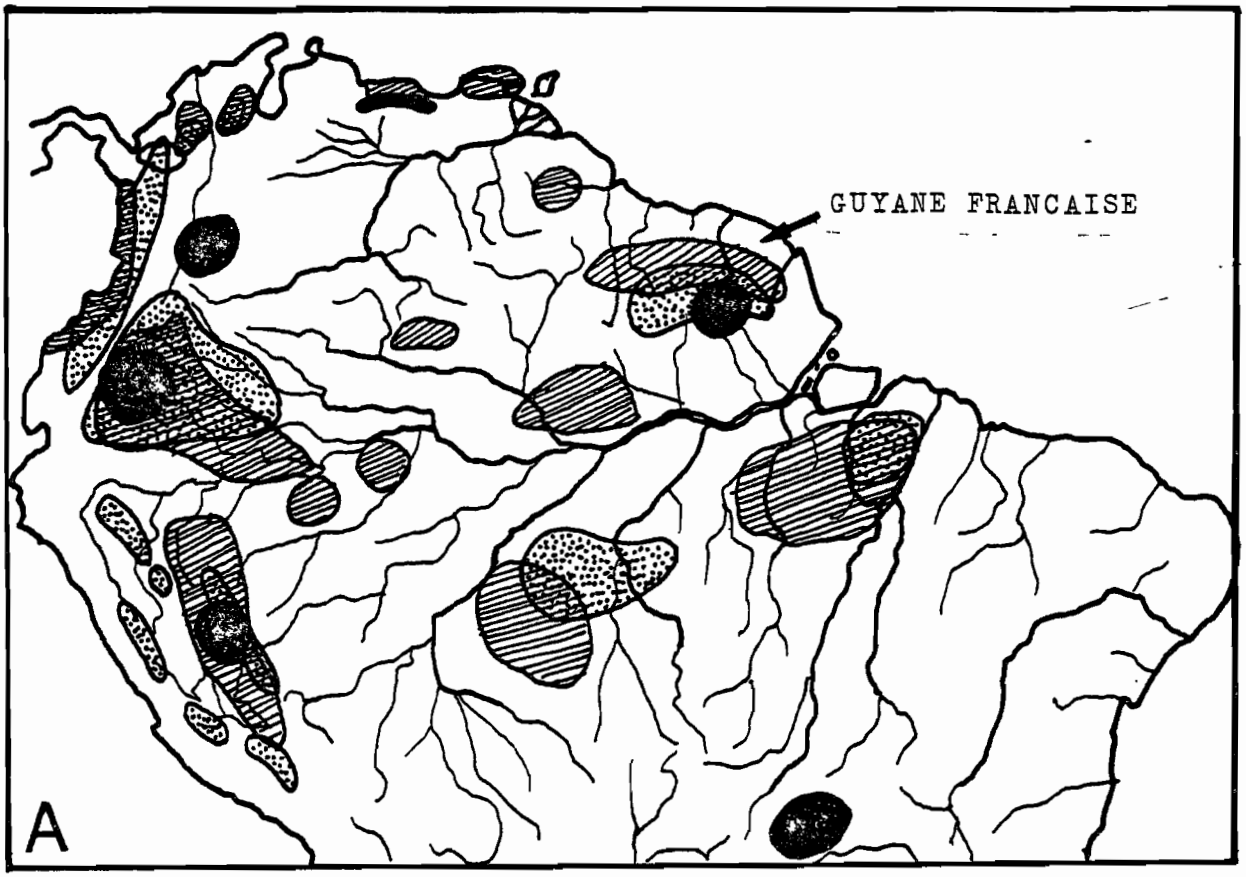
(1) Among the very many authors who have approached this subject, we can mention : Ab'SABER, ABSY, BIGARELLA, de BOER, DAMUTH & FAIRBRIDGE, GATES, IMBRIE & KIPP, JOURNAUX, LAMB, LORIUS & DUPLESSY, MALEY, MEGGERS, MILANKOVITCH, MÜLLER, TRICART, Van GEEL , Van der HAMMEN, VANZOLINI, VUILLEUMIER, WIJMSTRA.


GUYANE FRANCAISE
A

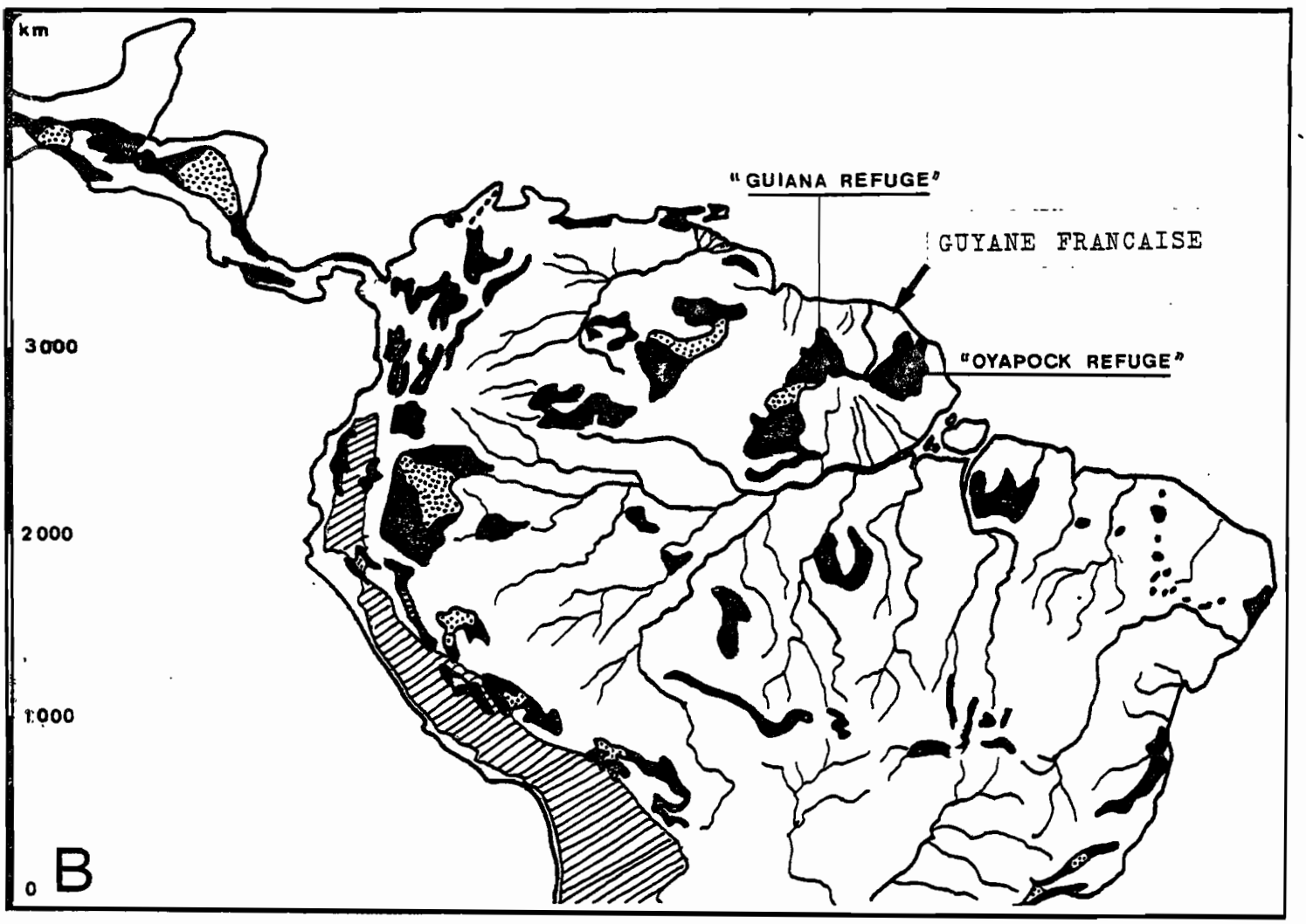

km
"GUIANA REFUGE"
GUYANE FRANCAISE
"OYAPOCK REFUGE"
3000
2000
1000
0
B

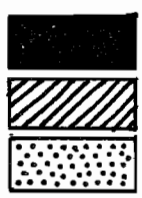
Fig. 5

up of the climate gave rise to an important retreat of the forest which, notably in South America, was situated at this time in a certain number of refuges where the local climatic conditions favoured its maintainance. These refuges acted as centers of diversification. On the other hand, during the interglacial periods, the recoalescence of the forest gave rise to the contact and hybridisation of species and subspecies which were genetically isolated. Although the number and area of the refuges proposed by different authors may differ (fig. 5), it is a fact that their distribution on the periphery of the Amazon basin is on the whole the same in all cases and that in each case there exists a Guianian refuge which is partially situated in French Guyane.

Other dry episodes, which have been much shorter and less intense, have marked the Holocene, especially between 11 000 and 9 500 B.P. (recent Dryas or " El Abra ") and between 3 500 and 2 800 B.P. According to BROWN (1977), they didn't last long enough to give rise to an important fragmentation of the flora. ZONNEVELD (1975)

Fig. 5 : RAIN FOREST REFUGES IN TROPICAL AMERICA

DURING THE LATE PLEISTOCENE (22 000 - 13 000 B.P.)

A.  according to VANZOLINI (1970, 1973).

according to PRANCE (1973).

according to HAFFER (1969).

B. According to BROWN (1977).

estimates however that, between 5 000 and 2 400 B.P., the american rainforest was largely replaced by savanna and JOURNAUX (1975) suggests that the "... savanes "incluses" fréquentes au nord de l'Amazone sont des témoins peut-être attardés de la dernière phase sèche ou d'une ultime oscillation climatique se situant alors vers 4 000 - 2 200 ans B.P. ". We think also that these recent dry periods during the Holocene, without having the consequences of the break up of the forest during the Pleistocene, did exert a certain impact on the vegetation by delaying the advancement of the forest and also in inducing local small savannisations and in the uncovering of granitic outcrops.

It suffices to say that each dry period didn't necessarily affect the tropical regions in the same way : BROWN (1978) notes that the distribution of the forest refuges has been very different during each climatic cycle. It is probable that, during the short dry periods of the Holocene, the maximum rainfall wasn't geographically the same as that during the end of the Pleistocene. Both ZONNEVELD (1975) in Surinam and JOURNAUX (1975), in his geomorphological study of the Brazilian Amazonia, showed that <u>the phenomenon of " climatic pulsations " must be considered along with the phenomenon of displacement of climatic zones in space</u> : " Les savanes du Roraïma et du pays des Tirios se sont étendues aux dépens de la forêt; cette conquête s'est effectuée du nord au sud dans le pays des Tirios " (JOURNAUX, 1975).

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III FRENCH GUYANE IN THE CONTEXT OF CLIMATIC FLUCTUATIONS

In what follows, we intend to analyse briefly the information we have obtained on the natural environment of Guyane which may give us some general indication of the existence, location and extent of the forest refuges during the glacial periods and of the low lying xeric vegetation refuges during the interglacial periods.

1 - THE RAINFOREST FLORA REFUGES DURING THE ARID PERIODS

We will limit ourselves to the period from 22 000 B.P. up to the present.

a) The areas of study which can supply useful information for the construction of a model of refuges :

Biogeography, alone, cannot provide information which is sufficiently complete to construct such a model. At present, the establishment of an area of distribution of certain plant species on a relatively precise map is unlikely. In fact, the floristic data collected on explorations are much too fragmentary because :
- certain regions are still little or not at all explored;
- other regions have been explored during a single season of the year such that the species flowering or fruiting during other seasons have not been collected;
- and, although a special effort has been made toward the identification of herbarium specimens in recent years, it is still incomplete especially where it concerns rare species, with a small distribution, new or endemic.

But in considering the information as a whole, even though fragmentary, on the natural environment of French Guyane which has been provided by different areas of study, it is possible to draw up an approximative map of the zones which have been probable forest refuges during the most recent dry periods.

We know that the geographic distribution of rainfall during dry periods of the past cannot in general be extrapolated from data concerning present day climatic conditions (TRICART, 1974; ZONNEVELD, 1975).

However, there are regions in Guyane where, because of the topography, the rainfall remained continually abundant. These are found in mountain massifs the ones which are the most important in terms of area and altitude, and where there exists microclimates which are very humid because of convection currents and dew. The mountains of this type, in Guyane, are mostly situated along the " Inini-Camopi range " (fig. 2 & 4) on table summits of 500 to 900 m in altitude, covered with a thick lateritic or bauxitic crust. They are witnesses of dry and humid episodes long before the Würm : the most recent crust of this category dates from the Eocene (BOULET, pers. comm.). It is the "first peneplain" of CHOUBERT (1957) and corrseponds, in Surinam, to the "Kopinang surface" of which the Nassau mountains make up part of it (Mc CONNEL, 1966; de BOER, 1972). These crusts, at a relatively high altitude, have therefore no connection in their formation with the events of the late Pleistocene. The forest which covers them is very hygrophilic in spite of a scruby aspect due to the mechanical difficulties encountered by the big trees in rooting.

The pedological map of French Guyane (fig.6), narrowly linked to the physiognomy of the vegetation, provides only a few indices which can give information on the soils which stayed under forest during the recent arid

phases, and on the soils which indicate savannisations.

From among the possible forest refuges, one can eliminate the following zones :

1. The lowland soils of the recent coastal plain (fig. 6 : 1 to 3), saline, silty, hydromorphic, flooded during the flandrian transgression corresponding to the climatic optimum of the present interglacial which occured around 6 000 B.P. and which, today, is covered at high tide. They are overlaid with mangrove and subcoastal marshes. These sediments were laid down in the course of 3 stages : Mara (2 700 B.P.), Moleson (1 600 to 1 000 B.P.), Comowine (800 to 0 B.P.).

2. The soils of the former coastal plain (fig. 6 : 4), composed of more or less sandy leached clays, sometimes hydromorphic, of which the summit doesn't excede the ordinance datum level + 5 m. They have been also covered by the sea 6 000 years ago to a level of about 10 m higher than it is today (2). Now, these soils are covered either with dry coastal savannas or swamp forest rich in palms, therefore belonging to recent implantations and with a fragile equilibrium (de GRANVILLE, 1978) : " In South America, following the establishment of herbaceous swamps, palms appear to enter as "initial stages" in the formation of seasonal swamp forest or of true swamp forest " (MOORE, 1973).

3. The precoastal sandbars, sometime rising above the clays of the former coastal plain (maximum altitude : + 13 m), which were also partially submerged 6 000 years ago and which, today, are covered by savanna and forest with xeric tendancies.

(continuation p.19)

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(2) 10 to 50 m according to CHARLESWORTH & EMILIANI, in VUILLEUMIER (1971) ; 5 to 12 m according to Ab'SABER, in BROWN (1977).

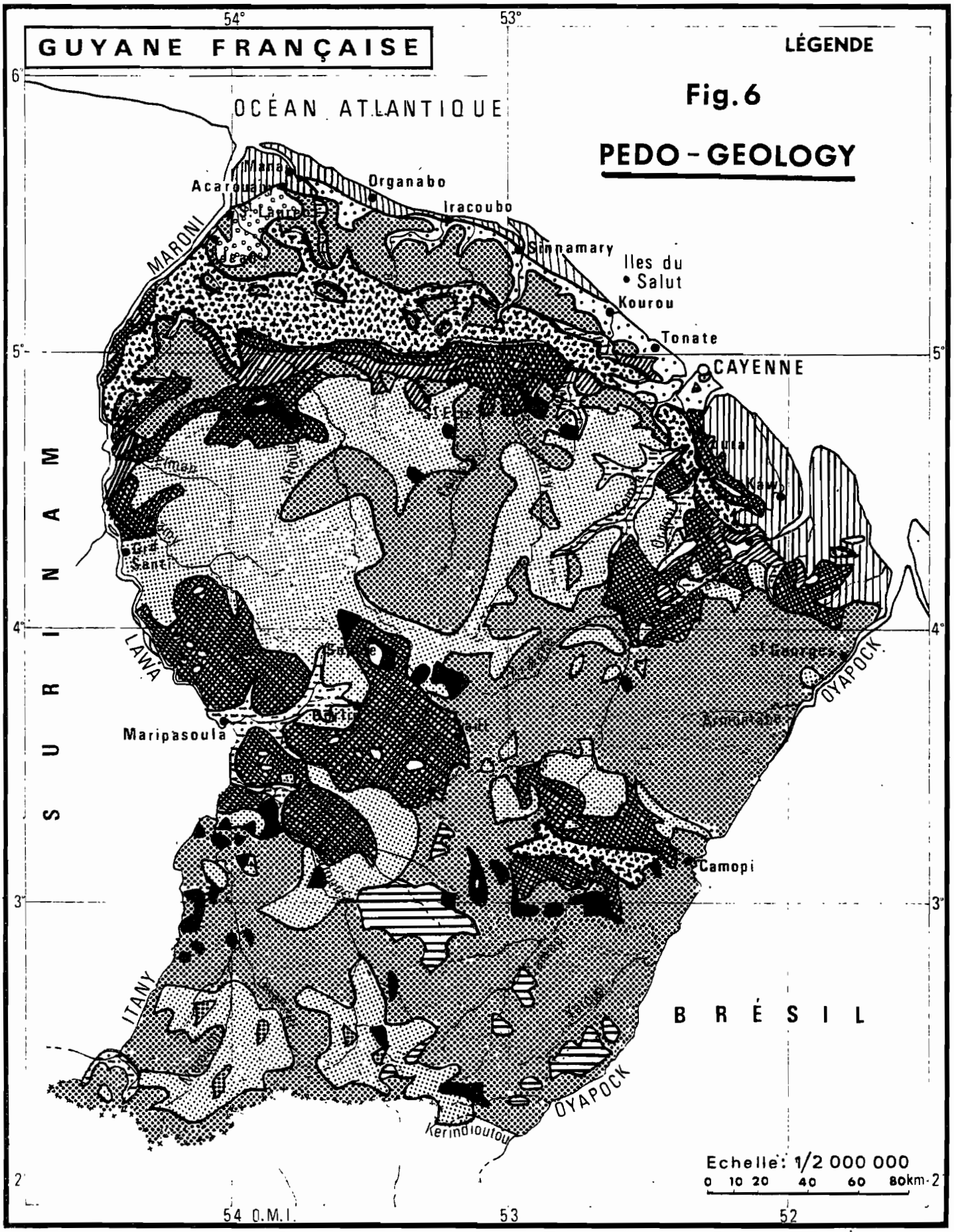
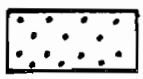

GUYANE FRANÇAISE
LÉGENDE
Fig.6
PEDO - GEOLOGY
54°
53°
6°
5°
4°
3°
2°
OCÉAN ATLANTIQUE
Organabo
Iracoubo
Sinnamary
Iles du Salut
Kourou
Tonate
CAYENNE
MARONI
SURINAM
LAWA
Maripasoula
OYAPOCK
Camopi
ITANY
BRÉSIL
Kerindioutou
Echelle: 1/2 000 000
0 10 20 40 60 80km
54 O.M.I.
53
52

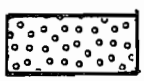
Fig. 6 : PEDO - GEOLOGY

LOWLANDS :

1 - 3  Soils of the recent coastal plain (mineral and unevolved non climatic soils) on marine alluvia and sandy silt.

4  Soils of the former coastal plain (ferralitic leached and/or impoverished soils, podzols, hydromorphic soils) on former sandbars and marine alluvia.

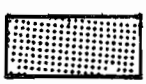
HIGHLANDS :

5  Soils of the "série détritique de base" (ferralitic soils, highly desaturated in B, leached and/or impoverished, podzols) on white sands and yellow sands.

Ferralitic soils, highly desaturated in B, on precambrian base :

6  Characteristic reworked, rejuvenated, impoverished soils on : "schistes de l'Orapu" (schist, conglomerate, quartzite).

7  Characteristic crusted, rejuvenated, impoverished soils on : "schistes de Bonidoro" (schist, conglomerate, quartzite).

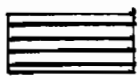
8  Characteristic reworked, impoverished, rejuvenated soils on : "granites guyanais" (granites, granodiorites, migmatites).

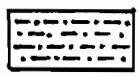
9  Characteristic soils, reworked, rejuvenated, leached and/or impoverished in clay, on : "granites Caraïbe et Galibi" (granite, granitogneiss, gneiss, migmatites, feldspar).

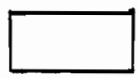
10  Characteristic reworked, rejuvenated soils on : "roches vertes de la série de Paramaca (schist, basic laves, rhyolithes, tufs).

Fig. 6 (2)

11  Characteristic reworked, rejuvenated soils on igneous rocks associated to "Paramaca" (gabbros, peridotites, pyroxenolites, amphibolites).

12  Characteristic leached and/or impoverished soils, hydromorphic soils, on sandy-clayey continental eluvia.

13  Characteristic leached and/or impoverished soils, hydromorphic soils on fluviatile alluvia (valley floors)

14  Lateritic crusts.

(According to J.-C. BLANCANEAUX,
in : Atlas de la Guyane, 1979)

4. The leached, hydromorphic soils of fluviatile alluvia (fig. 6 : 13), at present occupied by swamp scrub forest, probably flooded 6 000 years ago and made up at that time of little interior lakes.

5. The podzols of the "série détritique de base" (fig. 6 : 5), situated in the S^t - Laurent region.

It is unlikely that, among the upland soils, which today are completely covered with forest, the following categories have remained permanently forested during the last 20 000 years :

1. The continental sandy-clayey eluvia which are leached or hydromorphic, badly drained (fig. 6 : 12), and which harbour a scrub forest of mediocre physiognomy and with a rather poor flora.

2. All soils in which there is a compact B horizon more or less impermeable, having a lateral drainage with a lot of superficial water, and which favour savannisation (HUMBEL, pers. comm.). These soils, according to BOULET (pers. comm.), are found principally on the migmatites.

On the other hand, one is led to believe that the upland soils with free vertical drainage, i.e. in which the B horizon is not impermeable, are characteristic of the zones which favour the maintainance of the forest during dry climatic periods. At present, the "finest" forests are found growing on these deep, chemically rich and well drained soils. These forests contain tall trees with hard wood which are witnesses of advanced sylvigenetic phases (BUDOWSKI, 1963, 1965). It seems that such soils, associated with a highly stable forest, rich in species, predominate in the interior of Guyane, principally in the central region (the Saül region is a very good example of this). These soils are found on moderate slopes of either

granite (multiconvex relief in "demi-oranges" of "granites guyanais") or schist and also even on steep slopes whose rock type is basic. The basic lavas of the "Paramaca" series (fig. 6 : 10), called "roches vertes", seem to be the most favourable for the maintainance of "fine" forests.

According to BOULET (pers. comm.), the cristalline rocks of certain northern plateaux, as well as those of the southern peneplain, would be covered by soils with moderate vertical drainage and, therefore, one wouldn't be able to affirm that they had remained completely wooded.

The pedological map of French Guyane doesn't show the existence of "stone-lines", conglomerates etc... which could provide evidence of former deforestations (Ab'SABER, JOURNAUX, in : BROWN, 1977).

The pedological information is to be used with much caution and reserve because the paleoclimatic influences, not only have they not been tested with precision, but also have, in a large part, been obliterated by the tectonic movements (BOULET, pers. comm.) : the gentle uplifting of French Guyane induces a complete transformation of the ferralitic soil cover. It is these intermittent epeirogenic movements (CHOUBERT, 1957; Mc CONNEL, 1966 ; Van der HAMMEN, 1969; de BOER, 1972) which gave rise to various peneplains which have been successively eroded and reconstructed.

The tectonic movements have also had a greater influence on the geomorphology of Guyane than the recent climatic variations. This is why one cant expect too much information on the recent paleoclimatology from the geomorphological map which is in the process of being published (Atlas de la Guyane, 1979). However, ZONNEVELD (1975), in his geomorphological study of southern Surinam, (Sipaliwini region) reckons that the fossil forms of erosion

are proof of a savannisation which dates from a few thousand years ago. The region studied by ZONNEVELD, adjacent to the south-west of Guyane, have been affected by the recent savannisations. This is a region which falls within the annual isohyete of 2 000 mm, below which the growth of dense rainforest is precarious.

The relative richness and the affinities of the flora, which have been estimated very roughly, are represented on the map of fig. 7. This must be considered as a working hypothesis only.

In keeping with the topographical and pedological information mentioned above, certain region have floristic characteristics which do not argue in favour of a continuous forest refuge since the end of the Pleistocene. These are : the existing savannicole flora of lowlands, the relatively poor flora of the southern peneplain and of the flat zones covered with continental eluvia, the presence of savannicole species in the white sand forests in the north-west of Guyane, that one finds in the "savanna bushes" of Surinam (Clusia fockeana Miq. - Clusiaceae -, Humiria balsamifera St Hil. - Humiriaceae -, Matayba opaca Radk. - Sapindaceae -, Myrcia sylvatica Dec. - Myrtaceae -) according to Van DONSELAAR (1965).

Even though nowhere in Guyane are there a high number of endemics, it seems, according to our observations, that the region which is most rich floristically, which has the greatest number of endemic species and which must habe been part of the Guianian forest refuge corresponds roughly to the zones with the greatest rainfall (fig. 7 : zone II b) and to the mountains in the "Inini-Camopi" range (fig. 7 : zone III). The Saül region, where we have carried out regular collections of herbarium specimens during the past number of years, has revealed a certain number of new

(continuation p.26)

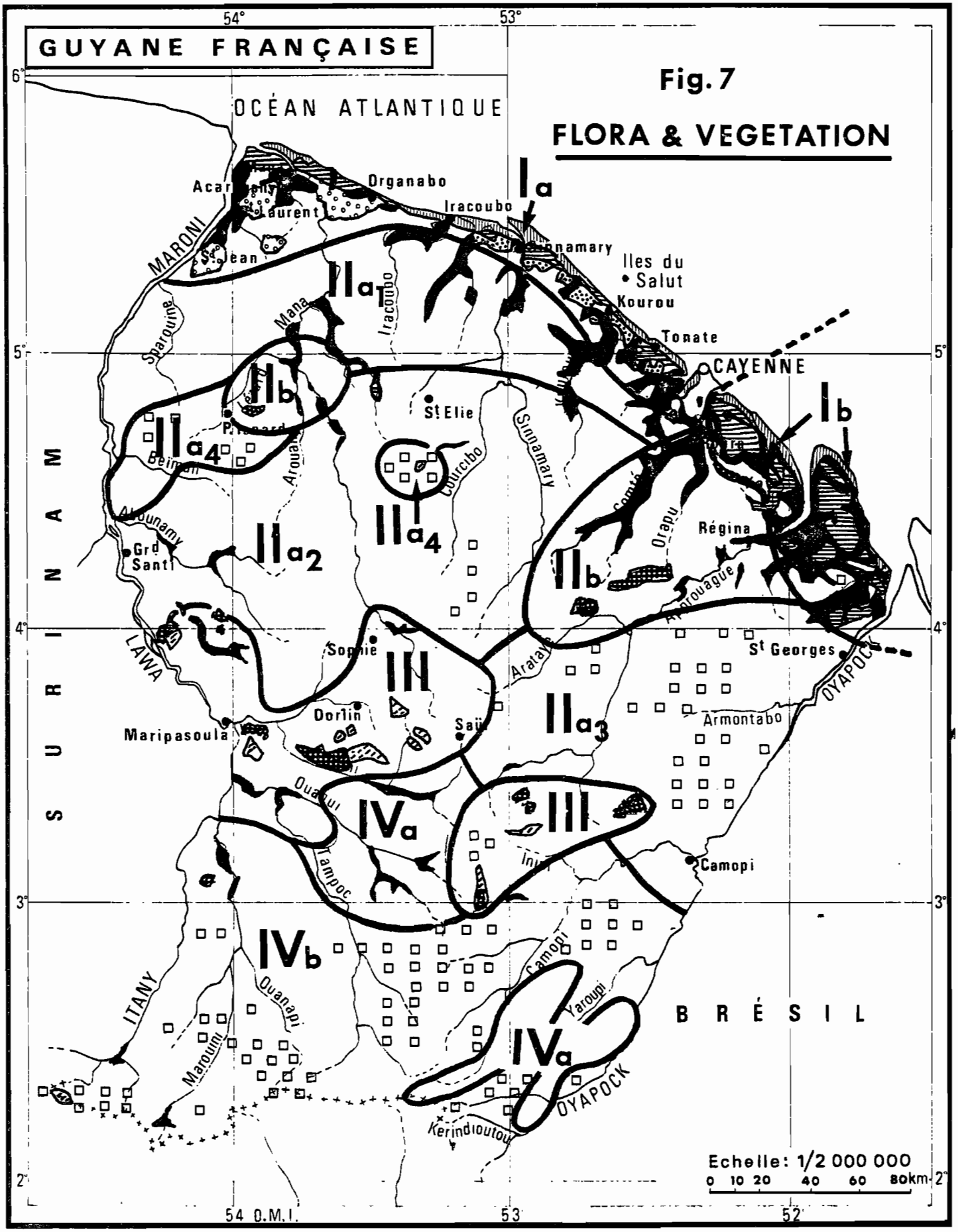
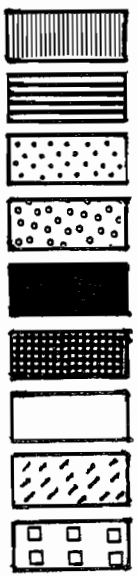

GUYANE FRANÇAISE
Fig. 7
FLORA & VEGETATION
OCÉAN ATLANTIQUE
SURINAM
BRÉSIL
54°
53°
6°
5°
4°
3°
2°
Organabo
Iracoubo
Sinnamary
Iles du Salut
Kourou
Tonate
CAYENNE
St Elie
Régina
St Georges
OYAPOCK
Sophie
Dorlin
Saül
Maripasoula
Armontabo
Camopi
Grd Santi
LAWA
MARONI
ITANY
Kerindioutou
Echelle: 1/2 000 000
0 10 20 40 60 80km
54 O.M.I.
53
52

Fig. 7 : FLORA AND VEGETATION



Mangrove

Herbaceous swamps

"Dry" savannas

White sand forests

Marsh forest and swamp forest

Forest on lateritic crusts

Rainforest on well drained ferralitic soils (alt. 500 m)

Cloud forest (alt. 500 m)

Zone rich in rocky slopes and outcrops

I. COASTAL SECTION : LOWLANDS , on marine alluvia (mangrove, savannas, swamps and marshes, coastal forests and transitional zones).

I a. Lowland zones which have a tendancy to be dry, west of Cayenne.

Vegetation : mangrove, savannas, secondary vegetation and cultivation, forests on sand with some xeric tendancies.

Flora : very varied, particularly with surinamian affinities; pantropical species frequent.

I b. Humid zones in the lowlands, east of Cayenne.

Vegetation : mangrove, large marshes, swamp forests, "pinotières".

Flora : varied, with amazonian affinities.

II. MEDIAN AND SUBCOASTAL SECTION : NORTHERN RANGE AND CENTRAL MASSIF (forest).

II a. Zone with mean rainfall.

Fig. 7 (2)

Vegetation : dense rainforest, more or less "fine".

Flora : fairly species rich; varied affinities.

II a 1. Subcoastal forests on "Orapu" shists, generally "fine" and species rich; Guianian-Surinamian floristic affinities.

II a 2. Forests on the western median zone on cristalline base, "fine" to mediocre, fairly species rich; varied floristic affinities, mainly surinamian.

II a 3. Forests of the eastern median zone on cristalline base, "fine" to mediocre, fairly species rich; varied floristic affinities, mainly amazonian.

II a 4. Forests of submountains zones on uneven bases, generally very "fine" and species rich; floristic affinities very varied, sometimes mountainous.

II b. Zones with very high rainfall on varied bases and transitional zones. Extensive lateritic crusts of low altitude.

Vegetation : dense rainforest, generally very "fine".

Flora : very rich due to the rainfall and the variety of habitats; very diverse floristic affinities.

III. THE "ININI-CAMOPI" RANGE SECTION (forest), mostly on "roches vertes". Zone of the extensive altitudinal crusts; habitats varied and contrasting; soils generally deep.

Vegetation : dense rainforest, generally very "fine" and magestic and submountainous scruby forest on lateritic crusts.

Flora : very rich, bearing endemic hygrophile species on the summits; very diverse affinities, often surinamian and mountainous.

Fig. 7 (3)

IV. MERIDIONAL SECTION : SOUTHERN PENEPLAIN (forest).

IV a. "Flats" zones and extensive eluvial plains.

Vegetation : dense rainforest, often mediocre and scruby.

Flora : generally poor.

IV b. Hills and outcrops zone on cristalline base.

Vegetation : dense rainforest, more or less "fine"; mesophilic forest, bush and xeric herbaceous vegetation on the rocky slopes and outcrops.

Flora : fairly poor, becoming rich in the higher irregular zones and on the outcrops. Presence of endemic species on the latter. Very diverse floristic affinities (especially amazonian for the forest species and coastal or mountainous for outcrop species).

species which are presumed to be endemics (fig. 8). These are, for example, Episcia sp. nov. (Gesneriaceae), Elephantomene eburnea Barneby & Krukoff (Menispermaceae) - new genus - as well as 4 non described Psychotria species (Rubiaceae), in particular :

P. sp. nov. aff. poeppigiana, exclusively localised on the "La Fumée" mountains, 5 km north of Saül, which is sympatric with P. poeppigiana Müll. Arg., species distributed all over tropical America.

P. sp. nov. aff. urniformis, which grows on the Galbao mountains (alt. : 600 m approx.), 10 km west of Saül, on the other hand, is not sympatric with P. urniformis Steyerm. which is an endemic species of Guyana (ex British Guiana), where it grows on the Ayanganna mountains, at an altitude of 800 m. These 2 last species with orophilic tendancies are probably the result of an isolation on the mountains which remained wooded during the dry phases in Guyana and French Guyane.

Among the endemic species of Guyane which have recently been described, we note Anomopaegma granvillei Gentry (Bignoniaceae), on the Ouaqui river, and Geonoma oldemanii J.-J. de Granville (Arecaceae) which is found in the swamp forests around St Georges, on the high Sinnamary river and to the north of St Elie. This last species would be taxonomically closer to G. chococola W. Boer (Choco refuge) as compared with the others (de GRANVILLE, 1975).

It would be of greater interest to study, in the other neotropical refuges, the species resembling these endemics which have been genetically individualised following their isolation. The counting of the chromosome number in the study of hybrids would also help in determining the regions where forest floras have come into contact with each other at the time of recoalescence of the forest.

Other species, growing in the primary forest in Saül, are found also in regions far away from French Guyane. These areas, which are very disjointed, could provide evidence of isolation, both in Guianian and other refuges, of species which havn't sufficiently evolved during this isolation that the beginings of speciation are discernable. These species are :

Adiantum cordatum (Adiantaceae) : Saül + Panama (Brown's Chiriqui or Darien refuge, 1977);

Anomospermum chloranthum ssp. confusum (Menispermaceae) : Saül + Peru - Huanuco, Loreto - (Napo refuge);

Heliconia lourteigii L.E. de Mello Filho (Musaceae) : Saül & Camopi + Peru (Napo refuge ?) ;

Oedematopus octandrus (Guttiferae) : Saül + Rio Negro (Manaus refuge).

However, just because of these few forest species which have a disjointed distribution, one cant completely eliminate the hypothesis (which is unlikely given that these species grow in primary forest) of a recent dispersal by man, neither the fact that insufficient botanical exploration in Amazonia may not have brought to light the presence of these species between the central region of French Guyane and the localities further away where they are found.

As far we know, no palynological research has been undertaken in French Guyane.

Within the domaine of zoology, the batracologist LESCURE (1975), studying the biogeography of the amphibians in French Guyane, concludes that there probably existed "... un centre de spéciation qui, dans sa partie de Guyane Française, était situé au nord du Tumuc-Humac, entre le Tampoc et le Camopi, autour de Saül, et entre la Comté et l'Approuague" (fig. 9). Colosthetus degranvillei (Dendrobatidae) is a characteristic example of an endemic

(continuation p. 32)

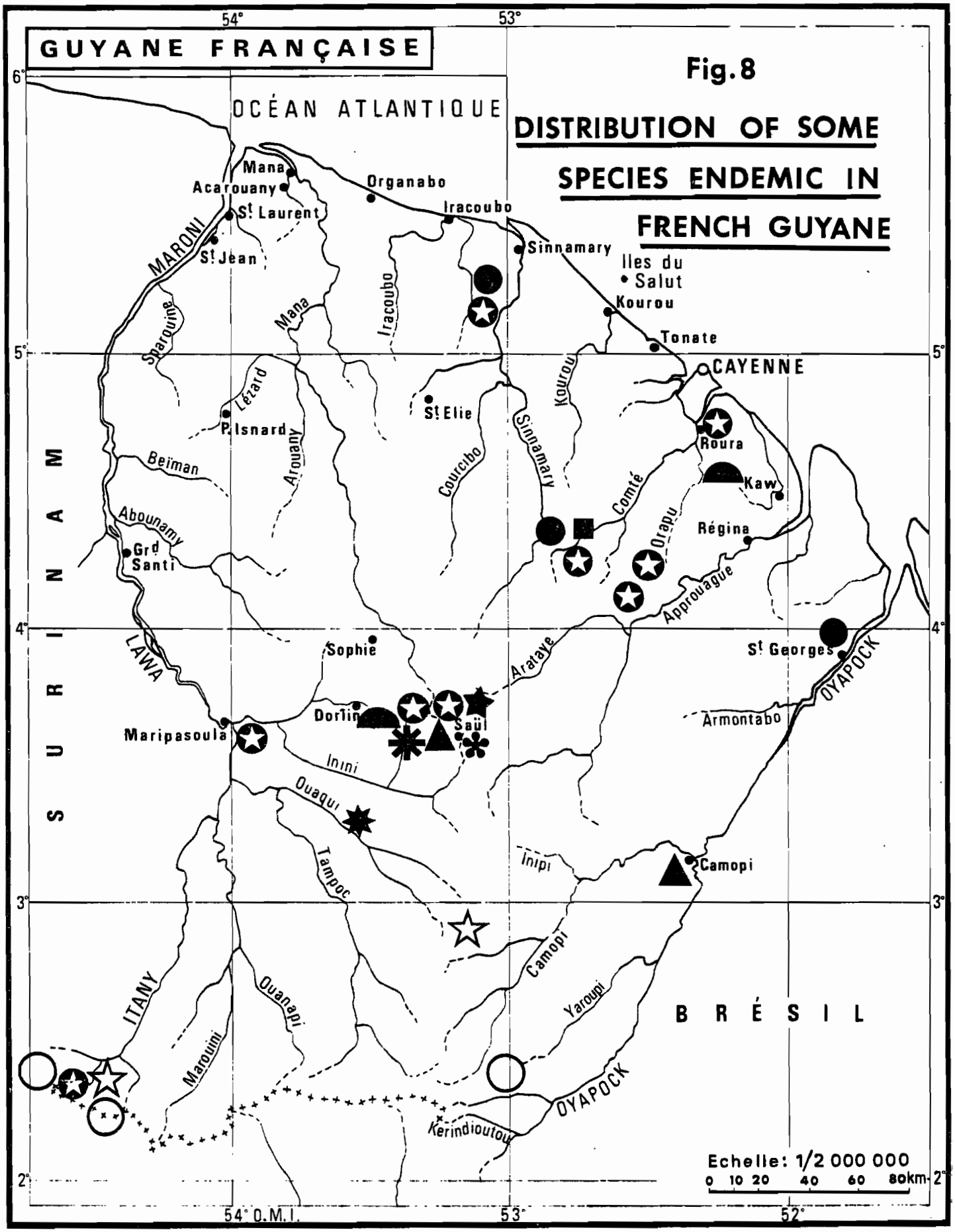

GUYANE FRANÇAISE
Fig.8
DISTRIBUTION OF SOME SPECIES ENDEMIC IN FRENCH GUYANE
OCÉAN ATLANTIQUE
SURINAM
BRÉSIL
54°
53°
52°
6°
5°
4°
3°
2°
Mana
Acarouany
St Laurent
St Jean
MARONI
Organabo
Iracoubo
Sinnamary
Iles du Salut
Kourou
Tonate
CAYENNE
Sparouine
Mana
Iracoubo
Lézard
P. Isnard
St Elie
Kourou
Sinnamary
Roura
Kaw
Beïman
Arouany
Courcibo
Comté
Orapu
Régina
Abounamy
Grd Santi
Approuague
LAWA
Sophie
Arataye
St Georges
OYAPOCK
Dorlin
Saül
Armontabo
Maripasoula
Inini
Ouaqui
Tampoc
Inipi
Camopi
ITANY
Ouanapi
Camopi
Yaroupi
Marouini
Kerindioutou
Echelle: 1/2 000 000
0 10 20 40 60 80km
54° O.M.I.

Fig. 8 : DISTRIBUTION OF SOME SPECIES

ENDEMIC IN FRENCH GUYANE

I. RAIN FOREST : HUMID FLORA

Vascular plants :

- *Anomopaegma granvillei* (Bignoniaceae)
- *Elephantomene eburnea* (Menispermaceae)
- *Episcia* sp. nov. (Gesneriaceae)
- *Geonoma oldemanii* (Arecaceae)
- *Heliconia lourteigii* (Musaceae) , also found in Peru.
- *Palmorchis prospectorum* (Orchidaceae)
- *Psychotria* sp. nov. aff. *urnifera* (Rubiaceae)
- *Psychotria* sp. nov. aff. *poeppigiana* (Rubiaceae)

Amphibian :

- *Colosthetus degranvillei* (Dendrobatidae)

II. OUTCROPS : XERIC FLORA

- *Pitcairnia geyskesii* (Bromeliaceae)
- *Pitcairnia sastrei* (Bromeliaceae)

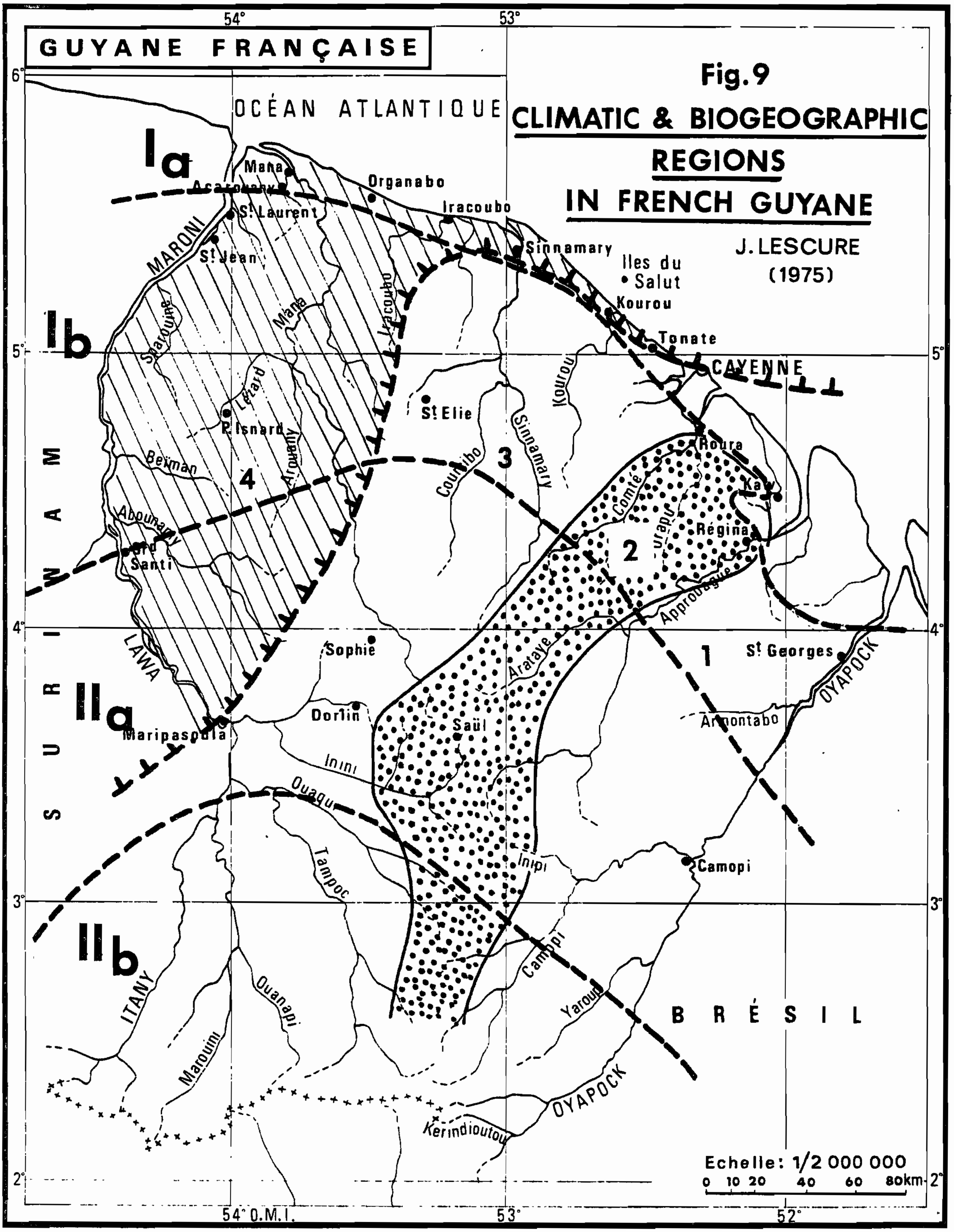

GUYANE FRANÇAISE
Fig.9
CLIMATIC & BIOGEOGRAPHIC REGIONS IN FRENCH GUYANE
J. LESCURE (1975)
OCÉAN ATLANTIQUE
Ia
Ib
IIa
IIb
1
2
3
4
Mana
Acarouany
St Laurent
St Jean
Organabo
Iracoubo
Sinnamary
Iles du Salut
Kourou
Tonate
CAYENNE
St Elie
Roura
Kaw
Régina
St Georges
Sophie
Dorlin
Saül
Maripasoula
Camopi
Antontabo
P. Isnard
Gd Santi
MARONI
LAWA
ITANY
OYAPOCK
SURINAM
BRÉSIL
Echelle: 1/2 000 000
0 10 20 40 60 80km
54°
53°
52°
6°
5°
4°
3°
2°
54° O.M.I.

Fig. 9 : CLIMATIC AND BIOGEOGRAPHIC REGIONS

IN FRENCH GUYANE

— — — — — Climatic zones

I. Coastal region :

I a. Coastal zone.

I b. Middle zone : 1. Eastern group.
2. Roura group.
3. Cayenne group.
4. Western group.

II. Interior region :

II a. Southern zone.

II b. Extrem southern zone.

 Zone with surinamian affinities

 "Forest refuge"

(according to J. LESCURE, 1975)

species in French Guyane whose area of distribution corresponds to that of the proposed refuge. LESCURE relates this species, from the taxonomic point of view, with C. infraguttatus (Andes south of the Ecuador), C. inguinalis (Colombia and notably in the Choco refuge) and especially with C. bocagei (Ecuador). It seems therefore that there are species resulting from isolation both in the north Andes refuges and in the french part of the Guianian refuge.

b) Probable limits of the Guianian refuge in French Guyane (fig. 10) :

By way of conclusion, we propose, with fair certainty, the existence of a forest refuge between 22 000 and 13 000 B.P. which occupied the central and eastern zone of French Guyane, limited to the north by the Kaw mountain and to the south by the Inini-Camopi mountain range. (cf. arguments concerning the climate, topography, pedology, botany and zoology which have been outlined in the text). The eastern and western limits of this refuge are still not well defined :

- To the west, the refuge reached the Maroni river at the level of the Atachi Bacca mountains, but it is possible that it also covered the multiconvex cristalline base to the north of the Inini-Camopi mountain range, near the 5° parallel.

- To the east, it is quite likely that this refuge reached Brazil beyond the Oyapock river, between St Georges and Camopi.

On the other hand, it is not absolutely certain that the northern mountain range, on schist, conglomerate and quartzite ("Bonidoro" series) as well as the southern peneplain rich in outcrops were part of this continuous forest refuge.

To be excluded are : the coastal lowlands, the alluvium and eluvium zones of the interior, the podzols of the St Laurent region at the extreme north-west, as well as the south-west region where traces of deforestation are still visible in the relief and in the vegetation (HURAULT, 1973 ; de GRANVILLE, 1978).

Besides, we reckon that just as the rainfall gradient of the isohyetes in space exists, the limits of the refuge between forest and savanna cant be precisely defined in a linear fashion, except in the north where it abuts against the alluvial coastal plain, between Cayenne and St Georges : as one moves further towards the regions which are wholly savanna, one must cross vast transition regions of a forest-savanna mosaic, where the forest takes refuge along the water courses (gallery forests) and on hill slopes exposed to the trade winds, in order to reach the savannas and the dry forests which encroach progressively on the dense rainforest. Such was probably the case in the southern peneplain and, in general, in the zones adjacent to the continuous forest refuge.

The geomorphology of Guyane doesn't seem to indicate the presence, in the past, of vast regions completely covered with savannas. Also we reckon that the greater part of French Guyane remained covered, even if only partially, with forest during the last big glacial period at the end of the Pleistocene.

The more recent dry periods (11 000 to 9 500 B.P. and especially from 3 500 to 2 800 B.P.), less intense and much shorter as well as higher (§ II), must not have affected a large part of the vegetation cover in Guyane. It suffices to recall, however, that the regions deforested during the most recent dry periods havn't necessary a spatial distribution which is identical to that

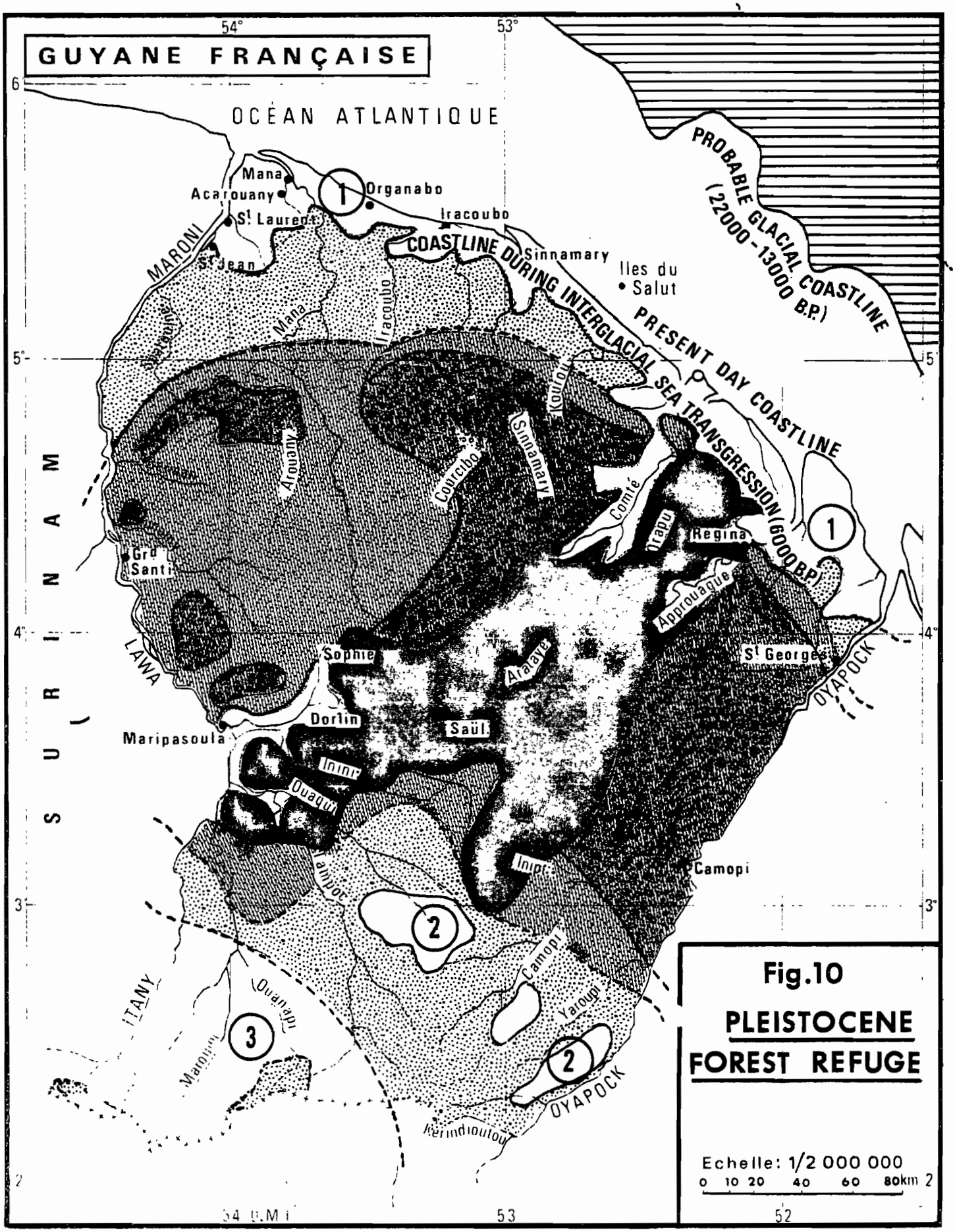
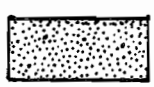

GUYANE FRANÇAISE
OCÉAN ATLANTIQUE
PROBABLE GLACIAL COASTLINE (22000 - 13000 B.P.)
COASTLINE DURING INTERGLACIAL SEA TRANSGRESSION (6000 B.P.)
PRESENT DAY COASTLINE
SURINAM
Mana
Acarouany
St Laurent
Organabo
Iracoubo
Sinnamary
Iles du Salut
MARONI
St Jean
Oyapock
Mana
Iracoubo
Kourou
Arouany
Counibo
Sinnamary
Comté
Iracoubo
Regina
Grd Santi
Approuague
St Georges
OYAPOCK
LAWA
Sophie
Araraye
Dorlin
Saül
Maripasoula
Inini
Ouaqui
Camopi
Inipi
Tampok
ITANY
Ouanapi
Camopi
Yaroupi
Manpiry
Kerindioutou
OYAPOCK
Fig.10
PLEISTOCENE FOREST REFUGE
Echelle: 1/2 000 000
0 10 20 40 60 80km
54°
53°
52
6
5
4
3
2

Fig. 10 : PRESUMED RAIN FOREST REFUGE DURING THE LAST GLACIAL STAGE (22 000 - 13 000 B.P.)

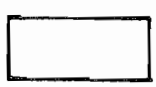
Very high probability continuous refuge zone.

High probability continuous refuge zone.

Average probability continuous refuge zone (or very high probability mosaic and network refuge zone).



Low probability continuous refuge zone (or high probability mosaic and network refuge zone).



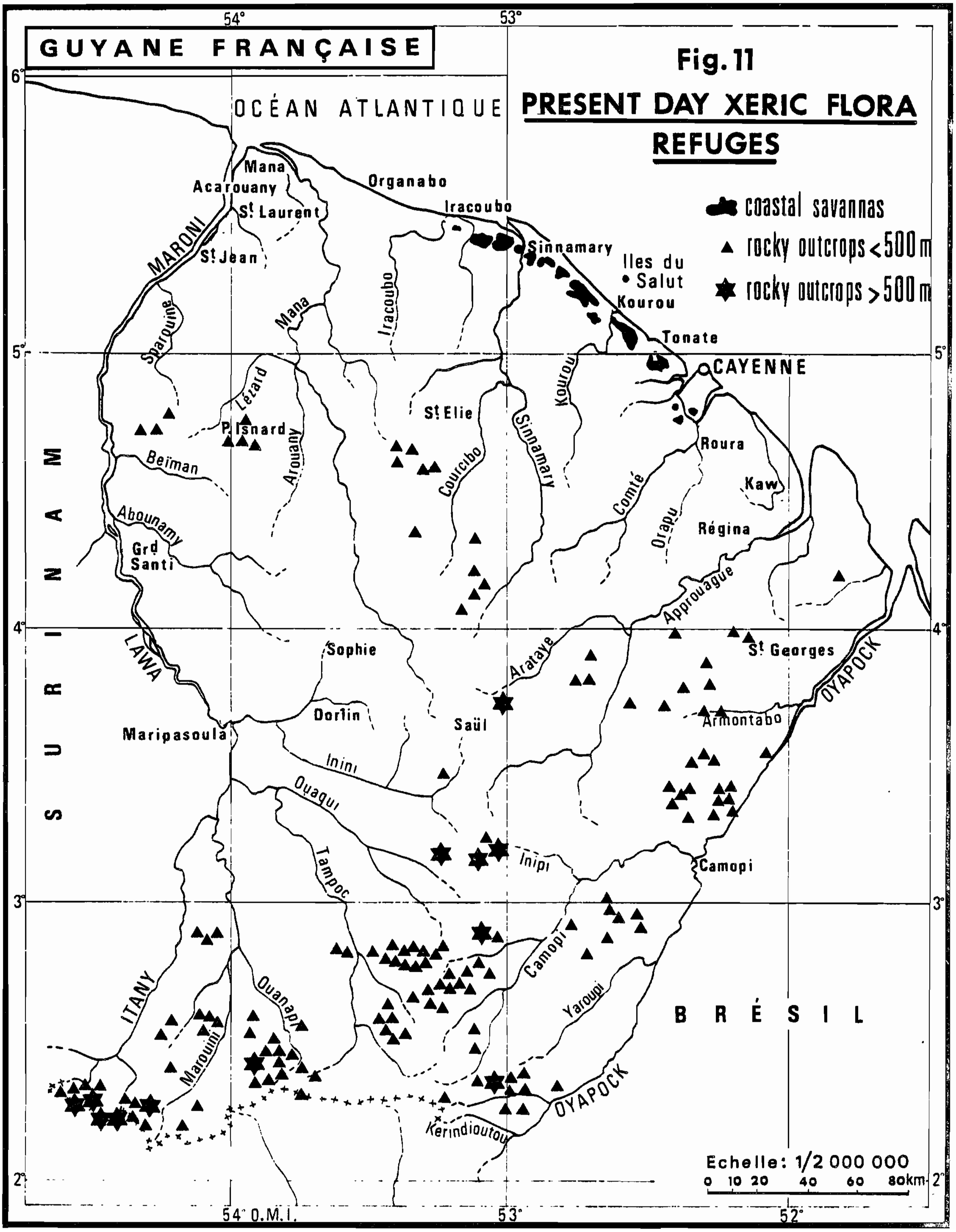
Very low probability continuous refuge zone (or average probability mosaic and network refuge zone):

1. Coastal zone, flooded in 6 000 B.P.
2. Continental eluvia.
3. Zone which could have been part of a continuous forest refuge during the Pleistocene but probably savannised in the Holocene (3 300 - 2 800 B.P.).

which existed during the arid period at the end of the Pleistocene : because of the important number of outcrops in the south and by the way in which the vegetation evolves to recover the bare rocks in spite of an annual rainfall of less than 2 000 mm, it would seem that the most recent dry episode has mainly affected the extreme south of French Guyane. " Dans le sud de la Guyane Française et, plus spécialement dans le massif du Mitaraka, on observe sur les crêtes des boules de granite tandis que d'autres ont roulé le long des versants et se sont accumulées dans le fond des thalwegs. Leurs formes sont remarquablement fraiches : il est permis d'y voir les preuves d'une phase climatique sèche très récente (quelques milliers d'années, peut-être quelques siècles) ayant entrainé la destruction de la forêt. Celle-ci est actuellement en nette progression, témoignant d'un accroissement de la pluviosité " (HURAULT, 1973). This confirms what we said above, following the research of ZONNEVELD (1975) in Surinam and agrees with the study which was carried out in the Tumuc-Humac region (de GRANVILLE, 1978). We think that the zone with a dryer climate above the relic savannas in the Tirios country (to the south of Surinam) has recently touch upon the south-west of French Guyane in the course of its displacement towards the south (JOURNAUX, 1975).

2 - THE ARID FLORA REFUGES DURING THE WET PERIODS

The present day situation corresponds to the end of a warm and humid interglacial period. The study of the vegetation in Guyane shows the presence of discrete sites, isolated from each other (with the exception of epiphytic communities in the canopy), which act as refuges for a more or less xeric flora, which is essentially herbaceous and heliophilic (fig. 11).


GUYANE FRANÇAISE
Fig.11
PRESENT DAY XERIC FLORA REFUGES
coastal savannas
rocky outcrops < 500 m
rocky outcrops > 500 m
OCÉAN ATLANTIQUE
54°
53°
52°
6°
5°
4°
3°
2°
Mana
Acarouany
St Laurent
Organabo
Iracoubo
Sinnamary
Iles du Salut
Kourou
Tonate
CAYENNE
MARONI
St Jean
Sparouine
Mana
Iracoubo
Kourou
Lézard
P. Isnard
St Elie
Sinnamary
Roura
Beïman
Arouany
Courcibo
Comté
Kaw
Orapu
Régina
Abounamy
Grd Santi
Approuague
SURINAM
LAWA
Sophie
Arataye
St Georges
OYAPOCK
Dorlin
Saül
Armontabo
Maripasoula
Inini
Ouaqui
Tampoc
Inipi
Camopi
Camopi
Ouanapi
ITANY
Marouini
Yaroupi
BRÉSIL
OYAPOCK
Kerindioutou
Echelle: 1/2 000 000
0 10 20 40 60 80km
54° O.M.I.

a) The coastal savannas :

The"dry" savannas, distributed along the coastline between Cayenne and Iracoubo are not the same as"humid" savannas or coastal swamps which are mainly situated to the east of Guyane, between Roura and the Oyapock delta.

The flora and phytoecology of the dry savannas, in which the Gramineae and Cyperaceae predominate, has been studied by HOOCK (1971) in the Kourou region. This author distinguishes the "low savannas" growing on podzols, with a low lying very discontinuous vegetation and a relatively poor flora, and "high savannas" on ferralitic soils, with a higher more continuous and less xeric vegetation, and with a somewhat richer flora.

Their origin is due to a number of interacting factors : edaphic, microclimatic (ventilation, dry season more accentuated than in the interior), human (presence of important amerindian populations in the past, at present annual fires). As well, we have already remarked that the savannas were submerged by the ocean 6 000 years ago approx, at the time of the interglacial climatic optimum. This considerably limits their role as a refuge which cannot be continuous with time. This is why their flora, very poor in endemics, is composed of elements with a generally vast area of distribution which have undergone a selection of the r type.

Relic savannas in the interior of French Guyane which are comparable to those of Surinam and of Venezuela don't exist.

b) The outcrops ("rock savannas") and the emergent rocks in the rivers :

Both the outcrops and the emergent rocks in the rivers have a discontinuous, xeric, saxicole vegetation and their floras are fairly similar.

We have studied the vegetation of outcrops in the Tumuc-Humac region (south-west of Guyane) where it is possible to show several features of the vegetation depending on the slope, the drainage conditions and the aspect. The most xeric facies is made up of thick clusters of succulent orchids, the least xeric one, on slight slopes and thin soils, have a continuous vegetation with a much richer flora dominated by Ischaemum guianense Kunth. (Gramineae). Between these 2 extremes, the facies with Pitcairnia geyskesii L.B. Smith (Bromeliaceae) occupies by preference the ridges and summits of the outcrops.

The analysis of the Tumuc Humac flora shows that a certain number of vascular species are equally saxicole and savannicole, and can also grow on the coastal savannas (25 % - de GRANVILLE, 1978 - ; 40 % - SASTRE, 1976 -), for example, Borreria latifolia (Aubl.) K. Schum. (Rubiaceae), Chelonanthus uliginosus (Griseb.) Gilg. (Gentianaceae), Heliconia psittacorum L.F. (Musaceae), Stylosanthes hispida Rich. (Papilionaceae), Xyris fallax Malme (Xyridaceae) ... These are species which will partially contribute, during the next dry climatic phase, to the restocking of the territories lost by the forest.

Other strictly saxicole species grow on outcrops as well as on the rocks of the rivers.

Certain ones which only grow on the highest outcrops (greater than 500 m), on the Tumuc-Humac, show orophilic affinities, for not only are they absent in the plains but they are found also on the summits, often much higher, in the south of Guianas and Venezuela. Such is the case for Clusia kanukuana Maguire (Clusiaceae), Pitcairnia

geyskesii L.B. Smith (Bromeliaceae) and Mandevilla surinamensis (Pulle) Woodson (Apocynaceae), endemics on the Guianian outcrops between 500 and 1 000 m. Some species are found both on the sandstone Roraïma formations (sometimes up to 3 000 m) and on certain outcrops of Tumuc-Humac. These are : Clusia annularis Maguire (Clusiaceae), Sauvagesia tafelbergensis Sastre (Ochnaceae), Doryopteris sagittifolia (Raddi) J. Smith (Cheilanthaceae). Most of these species reach the Tumuc-Humac which is the lower limit of their present day altitudinal distribution. One must bear in mind the fact that, on an outcrop of 700 m during the arid phase at the end of the Pleistocene, where the altitudinal thermic gradient was more "compressed" (Van der HAMMEN, 1974), the temperature was the same as the one prevailing now on the summit of a 1 700 m mountain (de GRANVILLE, 1978).

Xeric species, at the time of the warming up of the climate during the interglacial, must have adapted themselves to the higher temperatures in order to survive, or else must have taken refuge in sites where the mean temperature was lower than in the intertropical plain, that is to say at higher altitudes or latitudes or both at the same time. In this last case, the isolation has produced geographically disjointed species at a time when evolution was too slow to produce genetically distinct species : Trilepis kanukuensis Gilly (Cyperaceae), Asplenium pediculariifolium St Hil. (Aspleniaceae), Doryopteris sagittifolia (Raddi) J. Smith (Cheilanthaceae) growing both on the rocky summits of Guianas (on Tumuc-Humac and on Roraïma formations) and in the region of Rio de Janeiro and southern Brazil. On the other hand, when the evolution was sufficiently rapid, the speciation which had been taking place since the moment of isolation ended up in related but distinct species as with Rhynchospora subdicephala Koyama (Cyperaceae), endemic on the outcrops of south Guyane but taxonomically close to R. lapensis C.B. Clarke from Minas Gerais. All these species provide evidence of a former dry flora which was much more extensive.

Lastly, it is important to note that, like the forest refuges during the dry glacial periods, the xeric flora refuges during the warm humid interglacial periods (which are in particular the rocky outcrops) have also acted as centers of speciation.

c) The forest canopy :

The forest canopy is a permanent dry flora refuge of which certain elements equally epiphytes or saxicoles are able to contribute to the colonisation of the rocky slopes and outcrops exposed to the sun and cleared by erosion during the recession period of the forest. These elements are, for example, Aechmea setigera Mart. (Bromeliaceae), Epidendrum nocturnum Jacq. (Orchidaceae), Topobea parasitica Aubl. (Melastomaceae). It is not suprising that such species have very extensive areas of distribution because they cant be isolated in distinct populations in the course of climatic fluctuations.

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RESUME ET CONCLUSIONS

L'ensemble des données, même très fragmentaires, disponibles dans les différents domaines de l'étude du milieu naturel guyanais, permet de préciser la localisation et l'étendue probables du refuge forestier, en Guyane Française, pendant les phases climatiques arides les plus récentes.

Des arguments empruntés principalement à la topographie, à la pédologie et à la biogéographie, plaident en faveur de l'existence, au Pléistocène tardif (22 000 à 13 000 B.P.), d'un refuge forestier continu s'étendant sur le centre et l'est de la Guyane, de la montagne de Kaw à la région de Saül et tou le long de la "chaine Inini-Camopi".

Les zones adjacentes à cette région, en particulier le nord-ouest et la pénéplaine méridionale, n'ont pas nécessairement été un refuge continu mais ont pu constituer un refuge en mosaïque et en réseau (forêts-galeries).

Il est, par contre, très peu probable que la plaine côtière sur alluvions marines, submergée il y a 6 000 ans, les podzols de l'extrême nord-ouest, les éluvions continentales et la région des Tumuc-Humac aient fait partie de ce refuge.

Les épisodes secs plus brefs et récents de l'Holocène, eu égard au nombre des inselbergs dans le sud de la Guyane et aux traces de savanisation encore visibles autour de ceux-ci, ont dû affecter principalement la péné-

plaine méridionale et notamment l'extrême sud-ouest.

L'étude de l'aire de répartition des espèces végétales et des affinités floristiques, la recherche d'hybrides et d'endémiques, devrait permettre de confirmer ou de modifier ces hypothèses.

Les refuges de flore xérophile, à prédominance herbacée, pendant les périodes humides, sont actuellement les savanes côtières, la voûte forestière (épiphytes) et surtout les inselbergs. Ces derniers jouent un rôle de centres de diversification d'espèces xérophiles pendant les périodes interglaciaires, de manière comparable à celui des refuges forestiers sur la flore "humide" durant les épisodes glaciaires.

Il semble que les espèces forestières à aires disjointes, ou endémiques de Guyane mais ayant des vicariantes taxonomiques non sympatriques, aient des affinités prépondérantes avec l'Amazonie occidentale (ex-refuge de Napo, notamment) et non avec l'Amazonie méridionale. Ceci pourrait s'expliquer par la présence de la barrière écologique constituée par l'Amazone, principalement au maximum de la transgression flandrienne où elle formait une véritable mer intérieure de plus de 100 km de large.

Par contre, les espèces xérophiles des inselbergs, endémiques ou à aires disjointes, paraissent avoir des affinités avec la flore orophile des "Guyana highlands" d'une part, le sud du Brésil d'autre part : pendant les périodes sèches, la largeur de l'Amazone était réduite et de nombreux îlots refuges émergés servaient de relais aux espèces xérophiles pouvant migrer aisément du nord au sud et vice-versa.

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