Phytogeographic support tor the theory of Pleistocene forest refuges in the Amazon Basin, based on evidence from distribution patterns in Caryocaraceae, Chrysobalanaceae, Dichapetalaceae and Lecythidaceae

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ABSTRACT

In recent years it has generally been accepted that Amazonia was subject to long dry periods in the late Pleistocene and post-Pleistocene which reduced forest cover to a few limited areas or refuges. It has been proposed that the subsequent genetic isolation into separate populations is a major factor in the evolution of the species diversity within the lowland forest of Amazonia. Most of the previous evidence for this theory is based on studies of animals, for example: lizards, butterflies, and birds. Here data are presented to confirm the theory of forest refuges using evidence from phytogeography. Distribution patterns of the lowland species of the woody plant families Caryocaraceae, Chrysobalanaceae, Dichapetalaceae and Lecythidaceae are discussed and concur with the possibility of forest refuges. A map is given of the refuge areas that seem most likely, based on evidence from species distribution of the above plant families. The refuges proposed here correspond closely with the refuge areas proposed by Haffer and Brown rather than the extremely reduced areas proposed by Vanzolini.

INTRODUCTION

In recent years several researchers in various branches of zoology have discussed the interesting distribution patterns of organisms in Amazonia, in the light of the complex climatic history of the region.

The pioneers in this field of research are Haffer (1969), on speciation in Amazonian birds, and Vanzolini and associates in lizards, Vanzolini and Williams (1970), Vanzolini (1970) and (1973). Recently their data have been backed up by work in the Heliconian butterflies, Brown and Mielke (1972), Brown (1972). This work is also supported by the palynological evidence of Van der Hammen (1972), and most recently on linguistic and archeological evidence from Indian tribes by Meggers and Evan (1973).

This emphasis on Amazonian distribution patterns in other branches of biology prompted me to examine the various distribution patterns in the various plant families that I have been studying over the past few years. (For areas in which I have also collected plants see Fig. 25).

The study of the taxonomy of any group must include ecological and phytogeographic considerations if it is to be a true interpretation of the biology of a group. White (1971), reminds us that phytogeography has two main aspects, descriptive and historic. During the course of monographic studies in the woody plant families Chrysobalanaceae, Caryocaraceae, Dichapetalaceae and Lecythidaceae, I have been concerned with the descriptive phase, considering the present day phenotype and distribution of these families, Prance (1972a), Prance (1972b), and Prance and Freitas (1973), preparing distribution maps and pictorialising the geography of variation between and within closely related species. Since three of these families are predominantly families of trees centred in Amazonia, and the fourth, Dichapetalaceae, which contains vines as well as trees, is also well represented in the region, they provide material for the study of the vegetational history of the region which is largely covered by lowland rain-forest. The logical continuation of these monographic

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studies is to use them as an aid to phytogeographic considerations.

So far, botanists have made little comment about Haffer's theory on the contribution of forest refuges to the speciation during dry climatic periods in Amazonia. One of the few brief comments is that of Simpson (1972) who supports Haffer's generally accepted Peruvian refuges on evidence of Rubiaceae genera.

Briefly stated, Haffer has proposed that the generally accepted climatic changes of the Pleistocene and of the post-Pleistocene profoundly influenced the speciation of birds because of the severe depletion in forest during the dry periods. Haffer proposes that nine isolated areas, termed " refuges ", remained as forest while most of the rest of the area was covered with savanna. (See Figure 1). The bird species of the forest were forced into these refuges where the isolation of species occurred before the continuous forest-cover returned. By the time that the re-expanding forests came in contact again, some species were isolated genetically, and others hybridised again along the zone of contact. This theory is generally endorsed by Brown and Vanzolini, but each has his own variations.

Since the tall rain-forest is at the centre of Haffer's theory and of Vanzolini's theory, it should be possible to discuss the idea in terms of the distribution of species of trees in the present day forest. The four plant families with which I have been working are all predominantly distributed in lowland forest, and are consequently discussed here within the framework of Haffer's theory of refuges in an attempt to further our understanding of the complex plant species distribution patterns

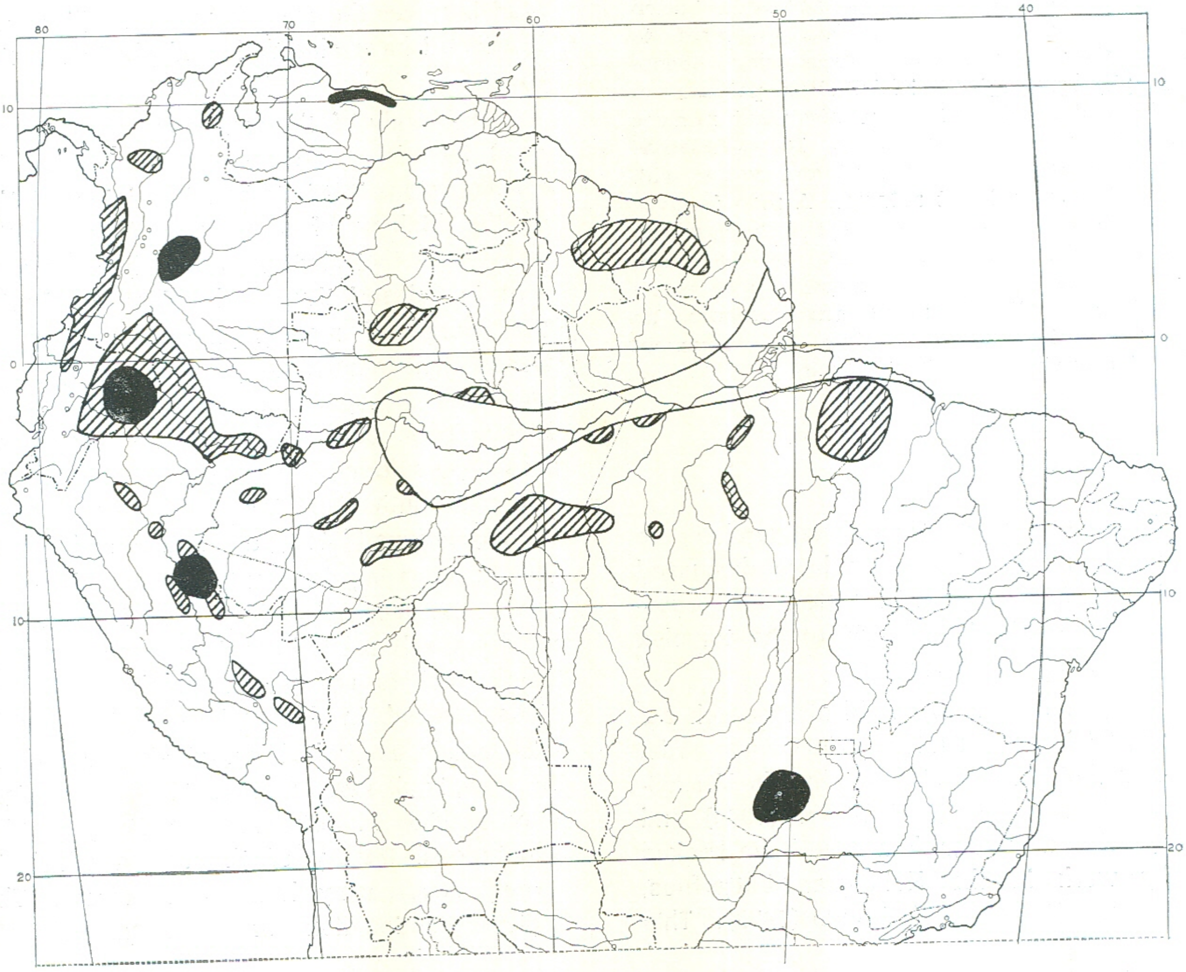

Fig. 1 — The Forest refuges proposed by Haffer (cross hatched), and by Vanzolini (black areas).

found within the Amazon Basin, and further, to show the lack of uniformity of species throughout Amazonia.

PRESENT DAY VEGETATION IN AMAZONIA

In order to discuss the vegetational history of Amazonia, it is also necessary to be familiar with the present day vegetation types and habitats of the region. The tendency is to picture the region as a rather uniform rain-forest, when there is, in fact, a great variety in vegetation types. Most of these have been discussed and summarised by previous workers, for example Ducke and Black (1954), Hueck (1966, 1972), Pires (1973), Prance (in press). Since the main purpose of this paper is to refer to the history of this region, only a brief summary of the most important vegetation types of Amazonia is given below in Table 1.

1. Forest on terra firme (non-flooded ground).
2. Varzea forest on temporarily flooded areas.
3. Igapó forest = swamp forest, permanently water-logged.
    a) river and rain water
    b) tidal influence
4. Beach woodlands and mangrove swamp.
5. Savannas on varzea.
7. Swamp savannas.
8. Caatingas of the Upper Rio Negro type.
9. Lower Rio Negro *campinas* on white sand.
10. Peripheral highland forest.
11. Xeromorphic rock outcrop areas.

Table 1. Main types of present day habitats in the Amazon Basin.

THE DIVERSITY OF THE AMAZONIAN VEGETATION

The brief summary given above of the most important vegetation types serves to show that there is considerable habitat diversity within the Amazon Region. The study of any large woody Amazonian genus shows how complex the present day distribution patterns are. Some of the habitats referred to above are highly specialised, (e. g. the Caatingas of the upper Rio Negro), and have a high rate of endemism of plants specially adapted to these areas. In this work, however, I am more concerned with the lowland rain-forest species which potentially could grow over a large part of the region. The study of the highland habitat and other specialised lowland habitats is of great interest, but is not of great relevance in considering the theory of forest refuges. The distribution of lowland species has tended to be neglected because of interest in areas of high endemism, such as mountain-tops of the Guayana Highland area or the caatingas of the upper Rio Negro. However, the distribution of any Neo-tropical species is of interest, and gives some information about the phytogeography of the region. Although there are numerous combinations of distribution patterns which could occur, the same general patterns of distribution generally appear in different groups of plants. Consequently, we can gain information about the history of the vegetation and also about present ecological factors controlling the region.

While it is difficult to present the phytogeographic patterns in a readily understandable way, the following phytogeographic breakdown of the genus *Hirtella* (Chrysobalanaceae), Table 2, should serve to demonstrate the complexity and variation in distribution in a moderately large genus (ca. 80 species). In order to find significant patterns, one must study more than one group. One would not expect exactly the same distribution in the same genus where some degree of genetic isolation must be involved to fill many niches. When we find the same pattern in many families then we may begin to draw some conclusions.

The reason for the vegetational diversity of Amazonia, a region that at first sight appears to be rather uniform, are threefold :

1. The history of the region.
2. The present climate and rainfall.
3. The habitat variety offered by a combination of factors.

The reasons are inter-related and cannot be treated entirely separately.

1. THE HISTORY OF THE REGION

As has already been pointed out, Haffer has recently attempted to explain the distribution of birds based on the climate changes of the Pleistocene. There is now much evidence from all over the world for considerable climate changes during the Pleistocene. So far little has been published for Amazonia, but there is an increasing amount of data such as Van der Hammen (1972), based on palynology. Simpson Vuilleumier (1971) gave a useful summary of data relating to climatic variation in South America during the Pleistocene. This ties in with data from Africa, a continent whose history is better known than the history of South America. Data on climatic changes in Africa were well summarised by Moreau (1966) in his study of the bird faunas of Africa. It is interesting that in both Africa and South America ornithological data have tended to precede studies of the plants, which should yield even more information because of their more static nature. However, we can now say with certainty that during the Pleistocene considerable climatic changes occurred in Amazonia. These changes included long dry periods which must have reduced the area of rain-forest and, consequently, increased the amount of savanna and other more xeric vegetation types.

2. PRESENT DAY RAINFALL AND CLIMATE

Figure 2 shows a rainfall map for northern South America based on the work of Reinke, and also reproduced by Haffer, which shows the considerable variation in rainfall over the Amazon region. It is, however, a rough estimation based on extremely variable and inconsistent data. This map was used by Haffer to help to determine the location of forest refuges. Obviously the difference between 1000mm and 3000mm of rain will have a profound effect on the vegetation. It is noteworthy that the present day large savanna

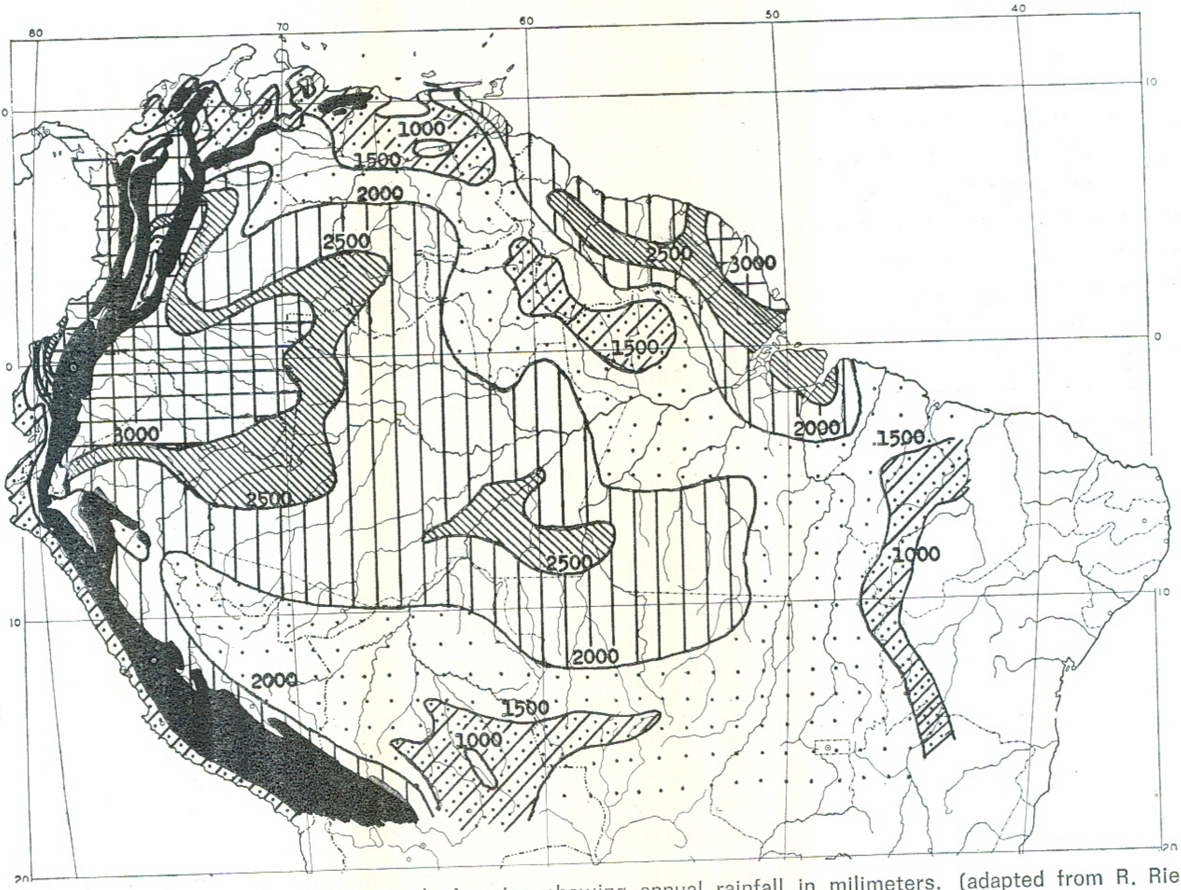

Fig. 2 — Rainfall map of northern South America showing annual rainfall in milimeters. (adapted from R. Rienke, **Das Klima Amazoniens**, thesis, University of Tubingen, 1962).

areas of Amazonia and Venezuela mostly fall within the drier areas under the 2000mm isohyet. Plant distribution studies of the region must take into consideration this rather large variation in rainfall, but at the same time we must remember that the rainfall data are scanty and we still have only an approximation of the isohyets.

3. OTHER FACTORS CAUSING HABITAT DIVERSITY

There are many other factors involved in forming habitat diversity in Amazonian species such as the geological features, e. g. the crystalline shield on the borders of the region, the distribution of sand, laterite, clay, etc. And perhaps one of the most important factors is water. My studies of woody species show that many plants grow only in temporarily flooded areas whereas others grow only in non-flooded areas. Species pairs with this type of distribution can be found in many woody families, for example the closely related species pair *Caryocar microcarpum* of flooded forest, and *Caryocar glabrum* of forest on terra firme. Looking at a distribution map based on collections made mainly near the major rivers one might assume that these two species are entirely sympatric. However this is not so, and in addition they are genetically isolated by having a different flowering season. I have found such pairs of species in all four families of plants considered here : In the Chrysobalanaceae, *Licania macrophylla* on flooded ground and its closest relative in the family, *Licania oblongifolia* on terra firme. Some of the factors contributing to habitat diversity were summed up in Prance (in press).

DISTRIBUTION PATTERNS IN THE FOUR PLANT FAMILIES

My data for the Chrysobalanaceae are presented .in the form of a phytogeographic breakdown of the species of the two largest genera in Tables 2 and 3, and in a selection of distribution maps with descriptive legends for the Dichapetalaceae, Caryocaraceae and Lecythidaceae. Many more maps could be given for the Chrysobalanaceae, but they would show much the same as the maps included. The refuge areas accepted here are based on the distribution of all lowland forest species of South America in the four families.

1. CHRYSOBALANACEAE

Data for the genera *Hirtella* and *Licania* are given in Tables 2 and 3. As is typical of the large and predominantly lowland forest genera, there is much variety of distribution pattern, indicating a complex phytogeographic history for the region. There are several areas of particularly repeated endemism in each of the genera which correspond well with refuges proposed here in the final section.

One of the interesting features in *Licania*, a large genus of over 150 species, is the relationship of the savanna species within the genus. Table 3 lists, in addition to the phytogeographic areas, the distribution within the nine sections of the genus. The sections are listed in an order which ranges from what I consider to be the more primitive (section *Moquilea*) gradually developing to section *Licania* which is more advanced, (apetalous, many fewer stamens etc.). The few savanna species of *Licania* are all members of the more advanced sections of the genus, indicating that they are derived from what are basically forest species. The predominance of lowland forest species shows that the divergence within the group has mostly taken place within the lowland forest habitat. Something like the dry climatic periods with isolation of species into separate populations, and subsequently separate species, is needed to explain this lowland species diversity in an area where there are no real geographic barriers for genetic isolation. Some of the ochlospecies (species of wide distribution and a polymorphic phenotype) are easily explained by a certain degree of isolation into populations which did not develop sterility barriers during the time of isolation. Good examples of this are *Licania heteromorpha* Benth. and *L apetala* (E. Mey.) Fritsch, see Prance (1972).

2. DICHAPETALACEAE

Fig. 3-6. All the South American species of *Tapura*.

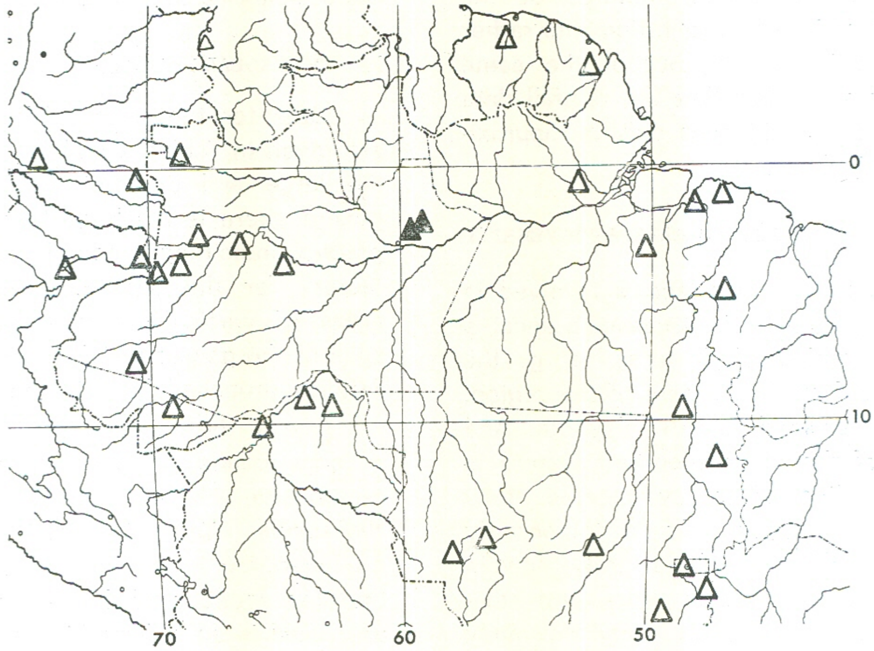

Fig. 4 — Distribution of **Tapura amazonica.** △ subsp. **amazonica** ▲ Subsp. **manausensis** Prance. This distribution shows a widespread species on the fringes of Amazonia, on high nonflooded forest. Subspecies **manausensis** only occurs in central Amazonia, and has become isolated from the rest of the species.

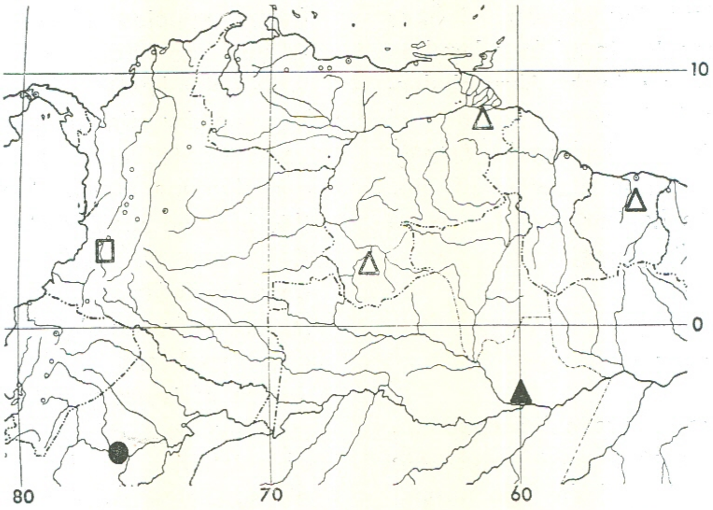

Fig. 5 — Distribution of species of **Tapura.** △ **T. capitulifera** Baill. □ **T. colombiana** Cuatr. ▲ **T. lanceolata** (Ducke) Rizzini ● **T. tessmannii** (Krause) Prance. This, and Figure 6, show how several species have developed throughout the Amazon region. Three species correspond to refuges accepted here: **T. colombiana** to Mocoa refuge **T. tessmannii** to the expanded Napo refuge, and **T. capitulifera** to the Guiana and Imeri refuges.

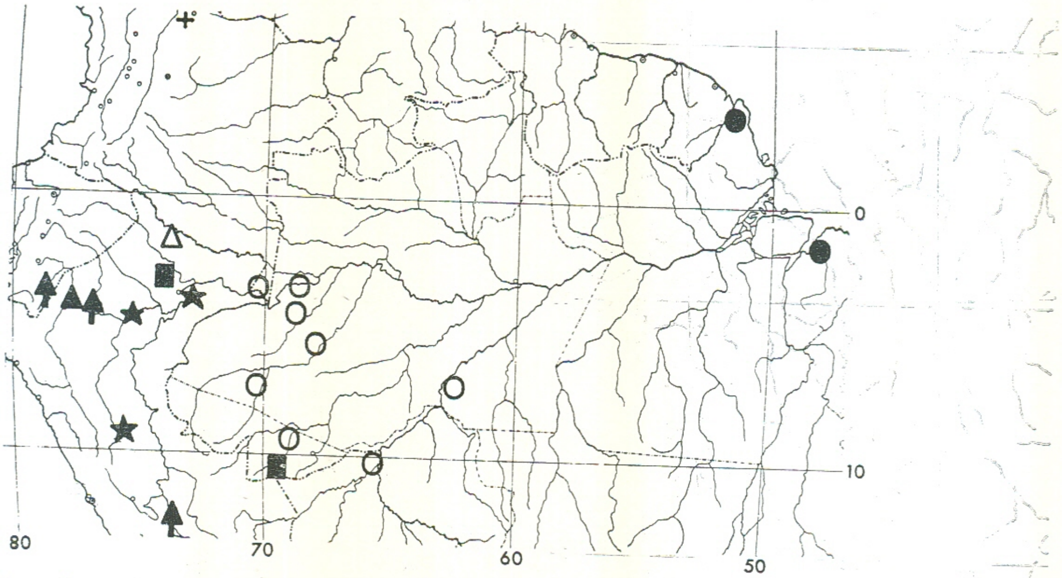

Fig. 6 — Distribution of species of **Tapura.** ○ T. **juruana** (Ule) Rizzini; ● **T. singularis** Ducke; Δ **T. Juliana** Macbr.; ▲ **T. peruviana** Krause var. **peruviana;** Δ **T. peruviana** Krause var. **petioliiflora** Prance; □ **T. acreana** (Ule) Rizzini; ✱ T. **coriacea** Macbr.. **T. juliani, T. peruviana** and **T. coriacea** correspond with the expanded Napo and eastern Peruvian refuges; **T. juruana** is a widespread eastern Amazonian species, and **T. singularis** corresponds with the Belém and Guiana refuges.

Fig. 7-8 all species of *Stephanopodium*.

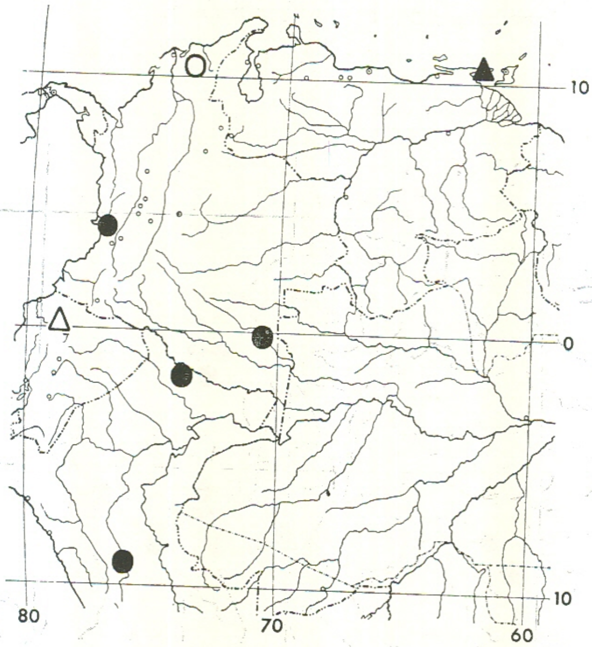

Fig. 7 — Distribution of the northern species of **Stephanopodium.** ○ **S. aptotum** Wheeler corresponds with an area of high plant endemism, the Santa Marta refuge. ▲ **S. venezuelanum** Prance is from the Paria refuge, and. Δ **S. angulatum** (Little) Prance from the southernmost part of the Chocó refuge. ● **S. peruvianum** is rather widespread in the Napo, Peruvian and Chocó refuge areas.

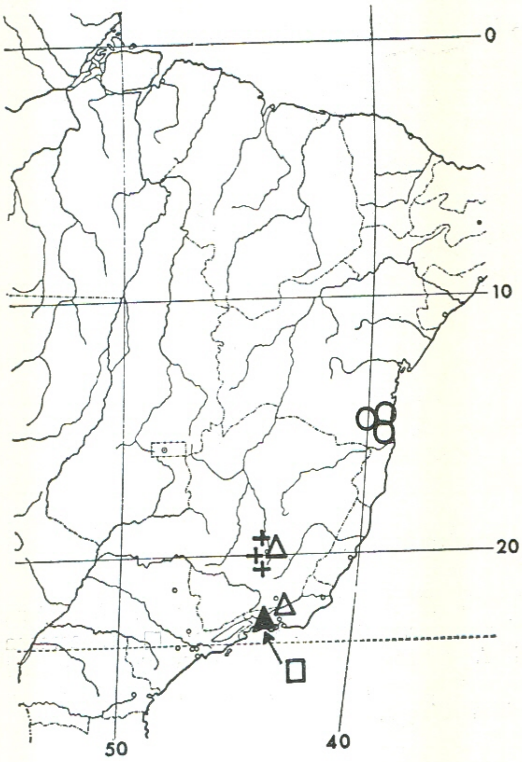

Fig. 8 — Distribution of the southern species of **Stephanopodium**. Since there are no species between those on Figure 7, there was a probable isolation of a more continuous distribution at some stage of its history, possibly by the drier climate of the Pleistocene. The present day distribution is only in some particularly wet areas of South America.

Fig. 9-12. All South American species of *Dichapetalum*.

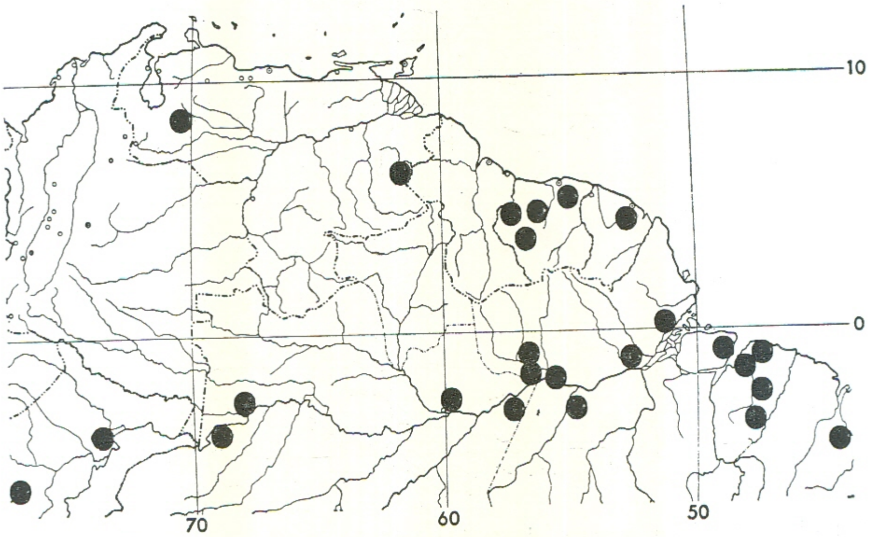

Fig. 9 — Distribution of **Dichapetalum rugosum** (Vahl) Prance, showing a widespread species of forest on high ground. There is much phenotypic plasticity in this species, typical of widespread species that have probably been scattered into isolated populations during the drier periods.

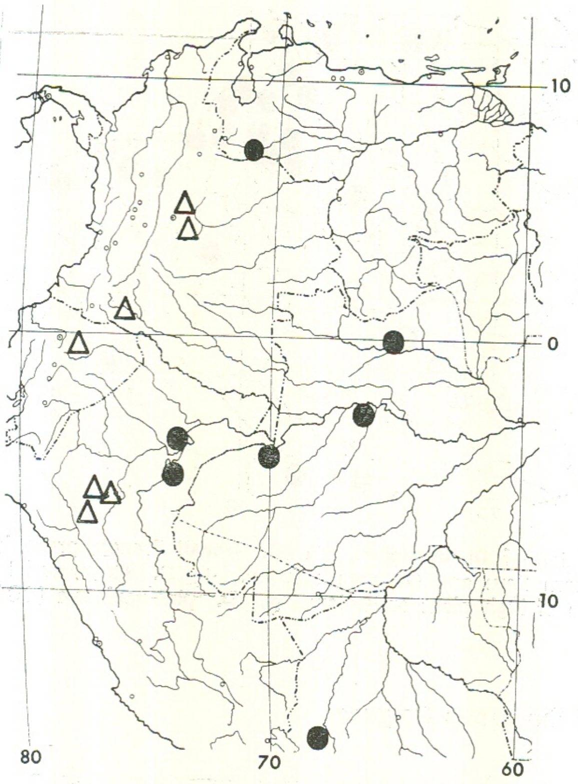

Fig. 10 — Distribution of species of **Dichapetalum**. ▲ D. **spruceanum** Baill, and ● **D. latifolium** Baill., both confined to western Amazonia.

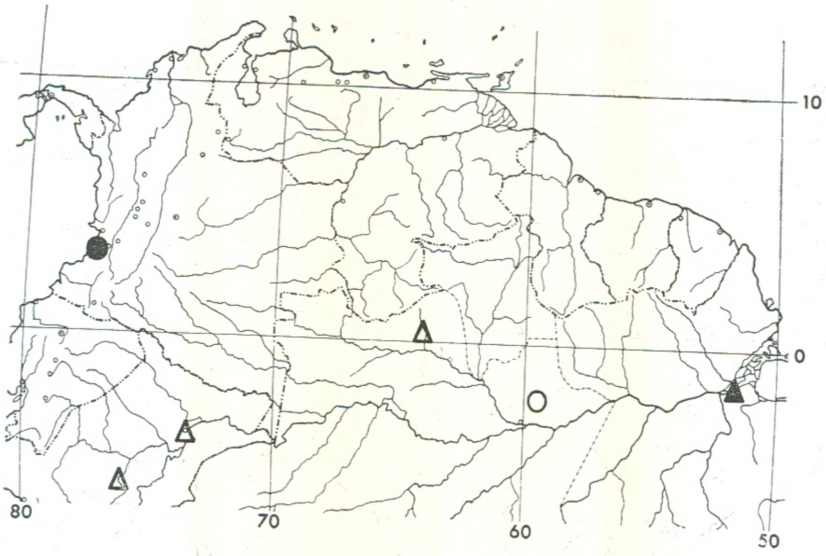

Fig. 11 — Distribution of species of **Dichapetalum**. ● **D. nervatum** Cuatr. in the Chocó refuge area. ▲ **D. stipulatum** Macbr. in western Amazonia. ○ **D. coelhoi** Prance, one of the many species known only from the Manaus area, indicating a large refuge to the immediate north of the seaflooded area and separated from the Guiana refuge. ▲ **D. pauper** Rizzini confined confined to the Belém refuge area.

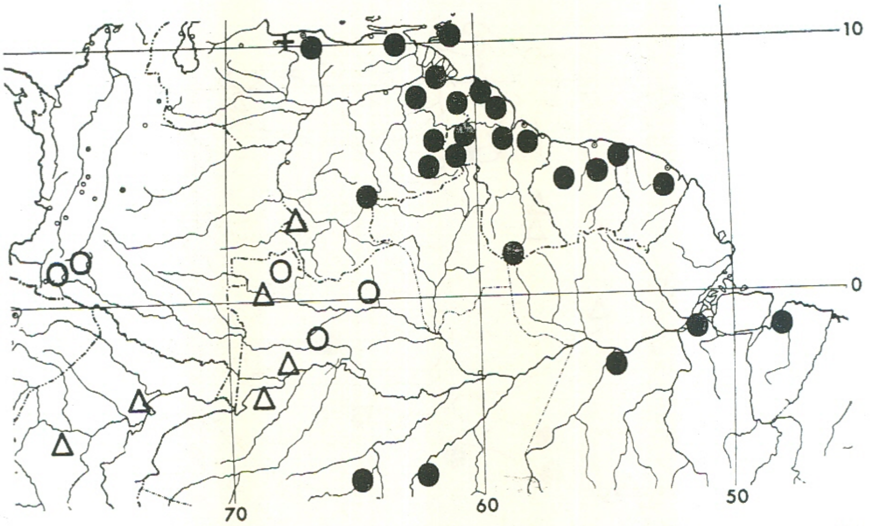

Fig. 12 — Distribution of species of **Dichapetalum.** O **D. froesii** Prance, probably originated in the Napo refuge. Δ **D. odoratum** Baill, of eastern Peru and Olivença refuges. + **D. steyermarkii** Prance confined to the Rancho Grande refuge area, an area of high plant endemism. ● **D. pedunculatum** (DC.) Baill, a widespread species.

3. CARYOCARACEAE

Fig. 13-16. All species of the genus *Caryocar.*

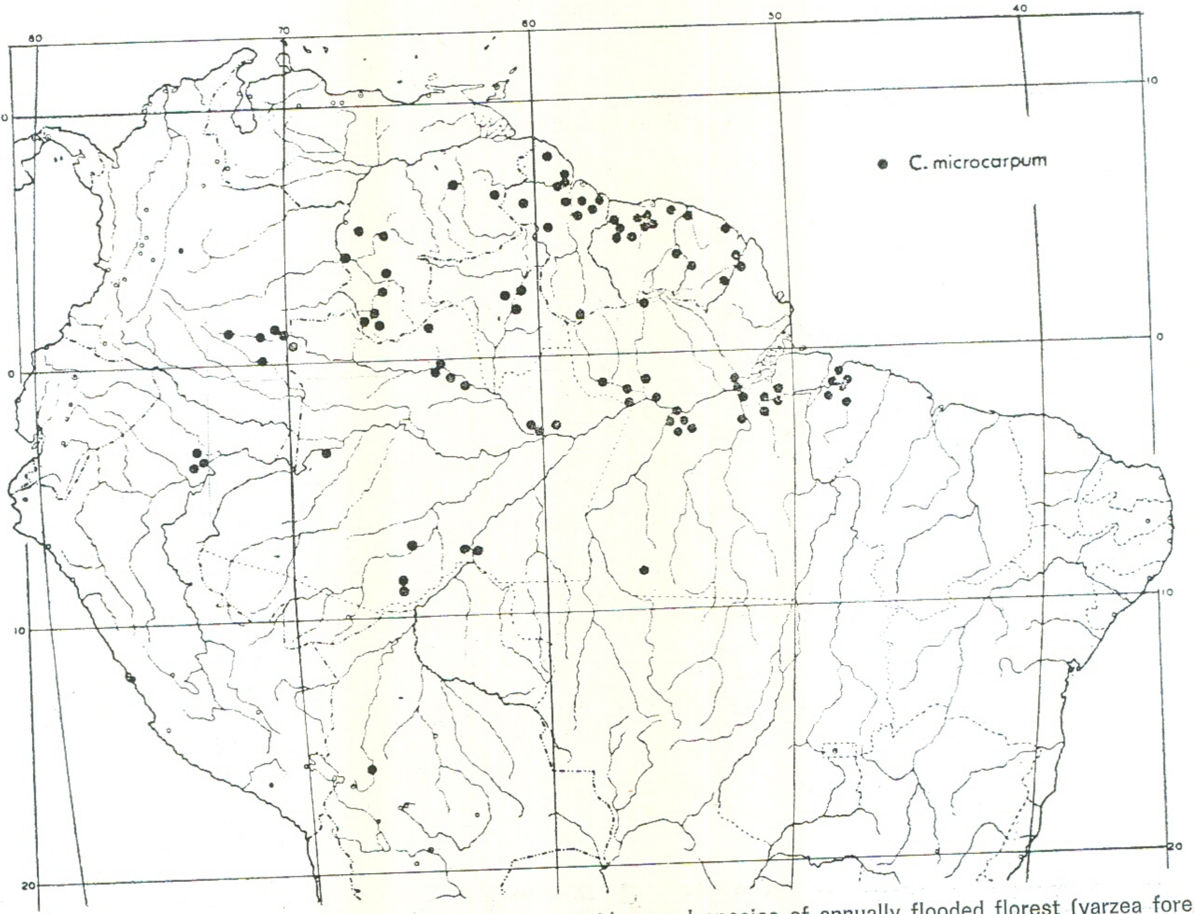

Fig. 13 — Distribution of **Caryocar microcarpum** Ducke, a widespread species of annually flooded florest (varzea forest). Species of flooded areas were not so affected by drier periods because of riverine forest and rapid ability to re-disperse by water.

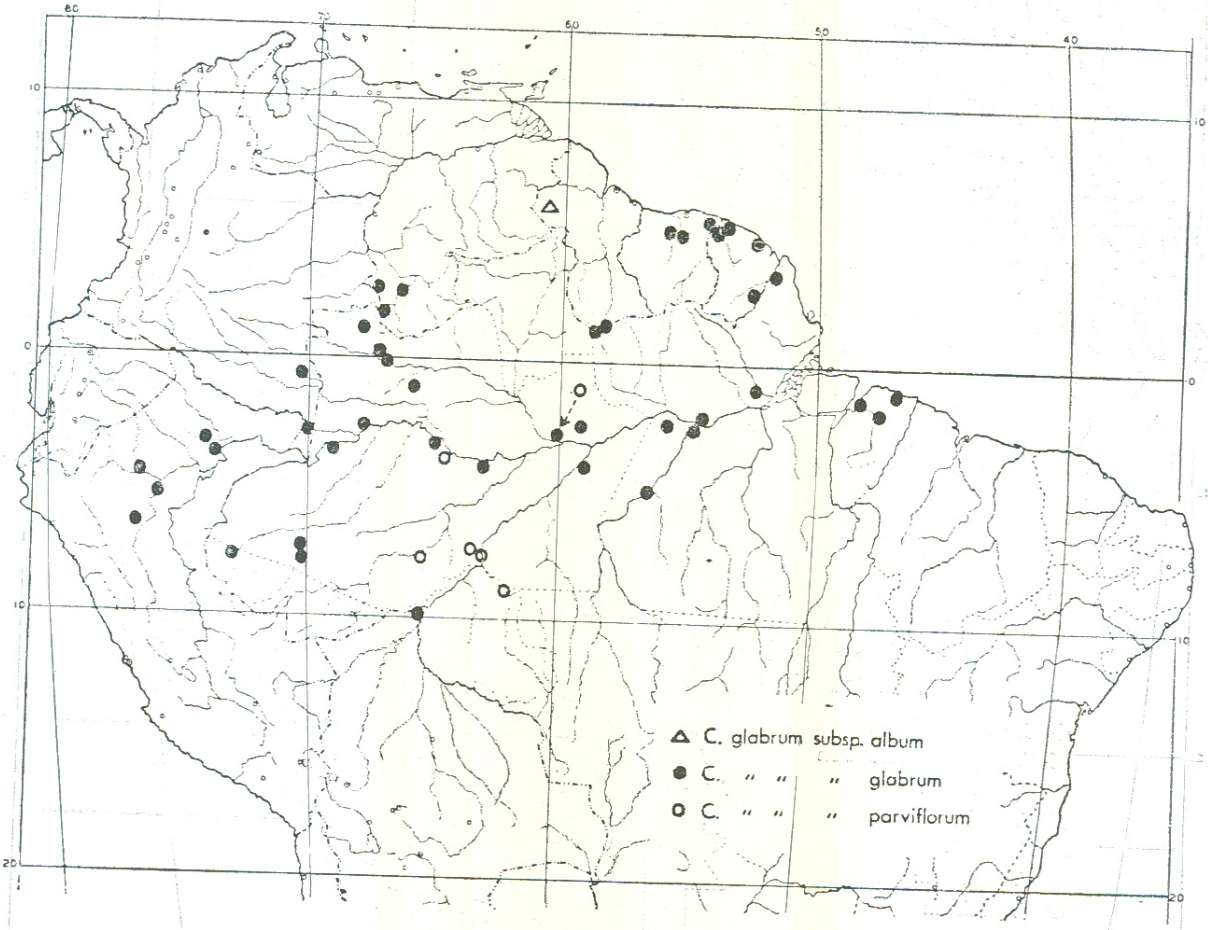

Fig. 14 — Distribution of **Caryocar glabrum** (Aubl.) Pers. a widespread species of nonflooded forest (terra firme). The sub-species indicate that some diversification has taken place through isolation of individual populations.

Fig. 15 — Distribution of species of **Caryocar.** + **C. amygdaliferum** Mutis was probably isolated in the Nechi refuge. ▲ **C. amygdaliforme** G. Don is in the eastern Peruvian refuge △ **C. gracile** Wittm, is confined to the white sand forests of western Amazonia. ⊕ **C. pallidum** A. C. Smith is a widespread species in Central Amazonia. ● **C. nuciferum** L. is in the Guiana refuge area. □ **C. edule** Casar, of the coastal forest in Brazil, shows the isolation of species in coastal forests.

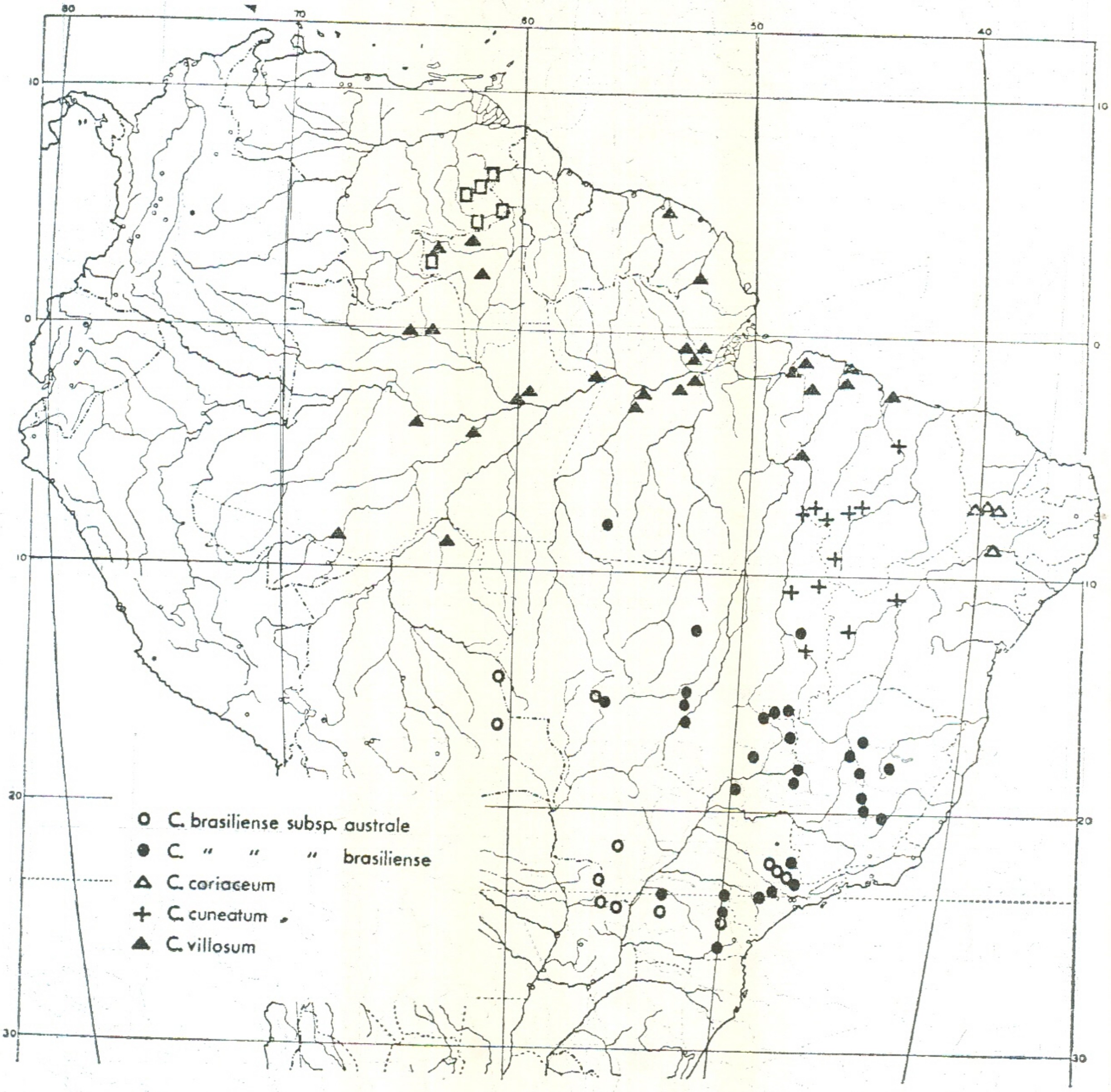

Fig. 16 — Distribution of species of **Caryocar**. □ **C. montanum** Prance is in the Imataca refuge area. ▲ **C. villosum** (Aubl., Pers). is a widespread species on non-flooded forest. The other species of the genus are outside the Amazon region in drier areas in Central and southern Brasil.

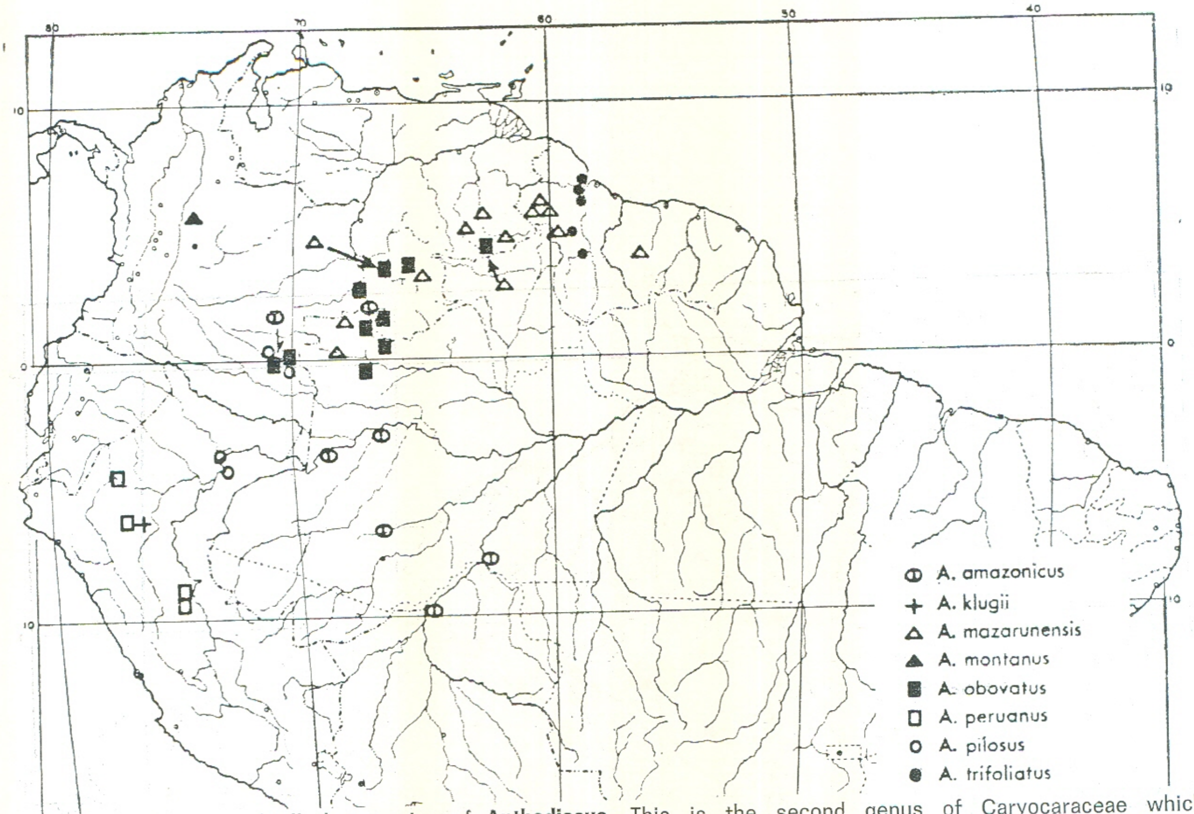

Fig. 17 — Distribution of all the species of **Anthodiscus.** This is the second genus of Caryocaraceae which is confined to north-western South America. The speciation of the eight closely-related species was probably largely due to isolation into forest refuges, and the distribution co-incides with various refuges accepted here. + **A. klugii** Sandl, ex Prance and □ **A. peruanus** Baill, with eastern Peruvian refuges. O **A. pilosus** Ducke with the enlarged Napo refuge. ▲ **A. mazarunensis** Gilly with the Imataca refuge etc.

4. LECYTHIDACEAE

Fig. 18-20. Distribution of species of *Cariniana.*

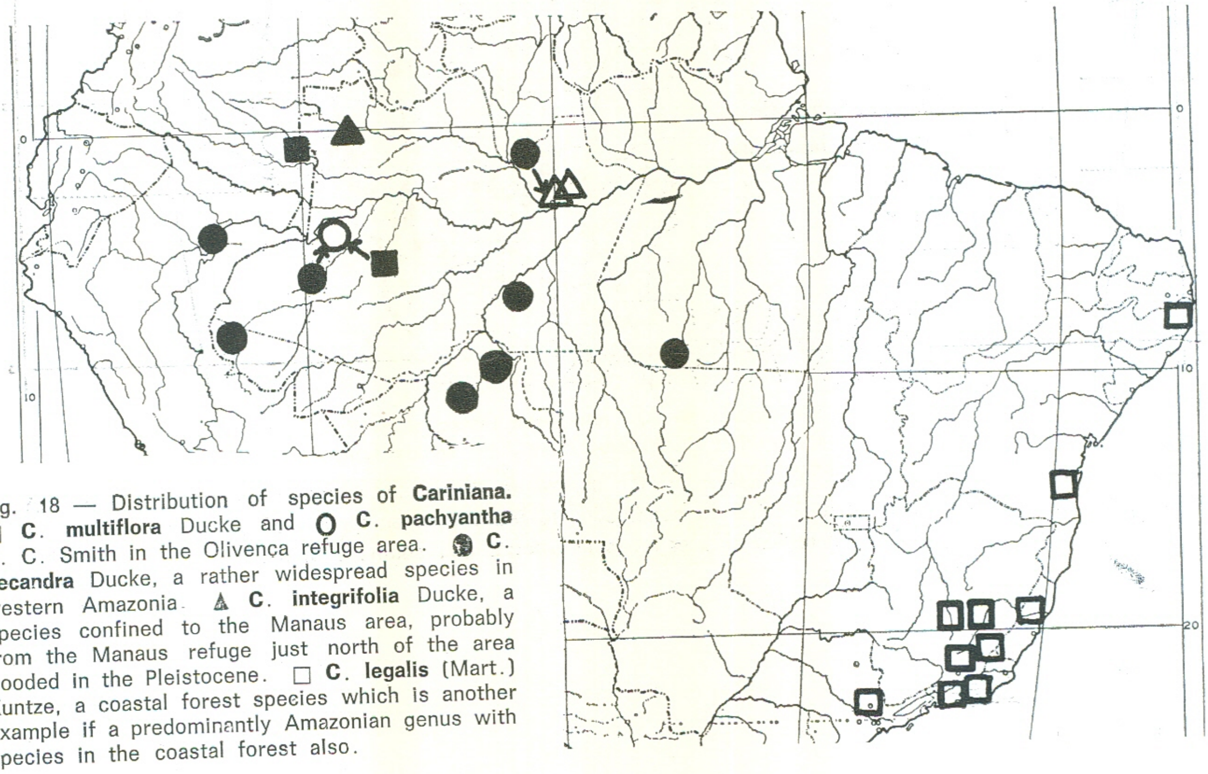

Fig. 18 — Distribution of species of **Cariniana.** □ **C. multiflora** Ducke and O **C. pachyantha** A. C. Smith in the Olivença refuge area. ● **C. decandra** Ducke, a rather widespread species in western Amazonia. ▲ **C. integrifolia** Ducke, a species confined to the Manaus area, probably from the Manaus refuge just north of the area flooded in the Pleistocene. □ **C. legalis** (Mart.) Kuntze, a coastal forest species which is another example if a predominantly Amazonian genus with species in the coastal forest also.

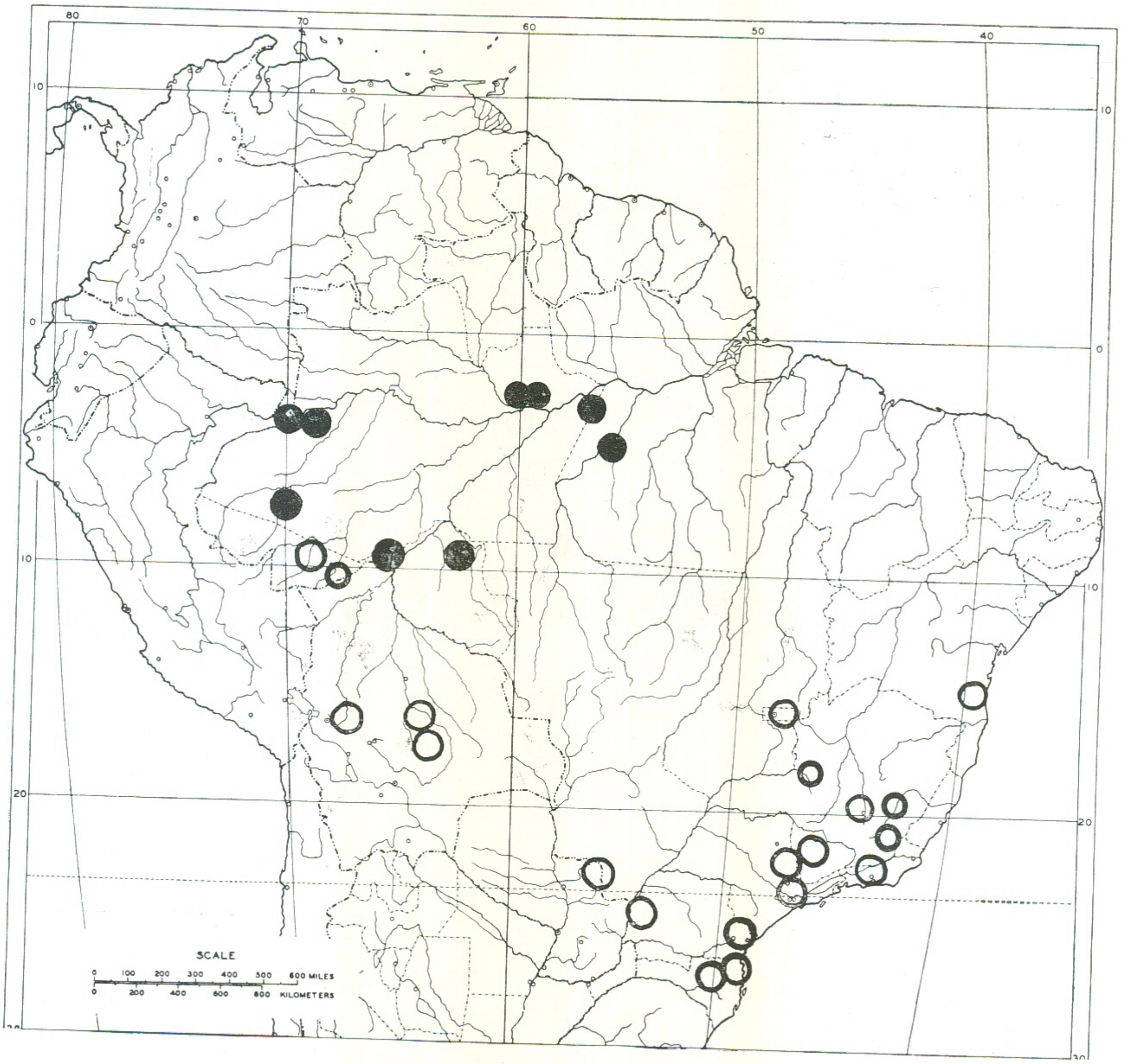

Fig. 19 — Distribution of species of **Cariniana**. ● **C. micrantha** Ducke of central and western Amazonia. ○ **C. estrellensis** (Raddi) Kuntze with the interesting distribution from Acre to southern Brazil. This is a species found in the Planalto and drier regions, and its distribution shows how it has maintained a more or less continuous distribution through gallery forest. Other species. e. g. **Couratari macrosperma** (Fig. 22), have become dis-continuous, and in others there has been further evolution resulting in speciation. e. g. in **Stephanopodium** (Fig. 7 and 8) and **Caryocar** (Fig. 15 and 16).

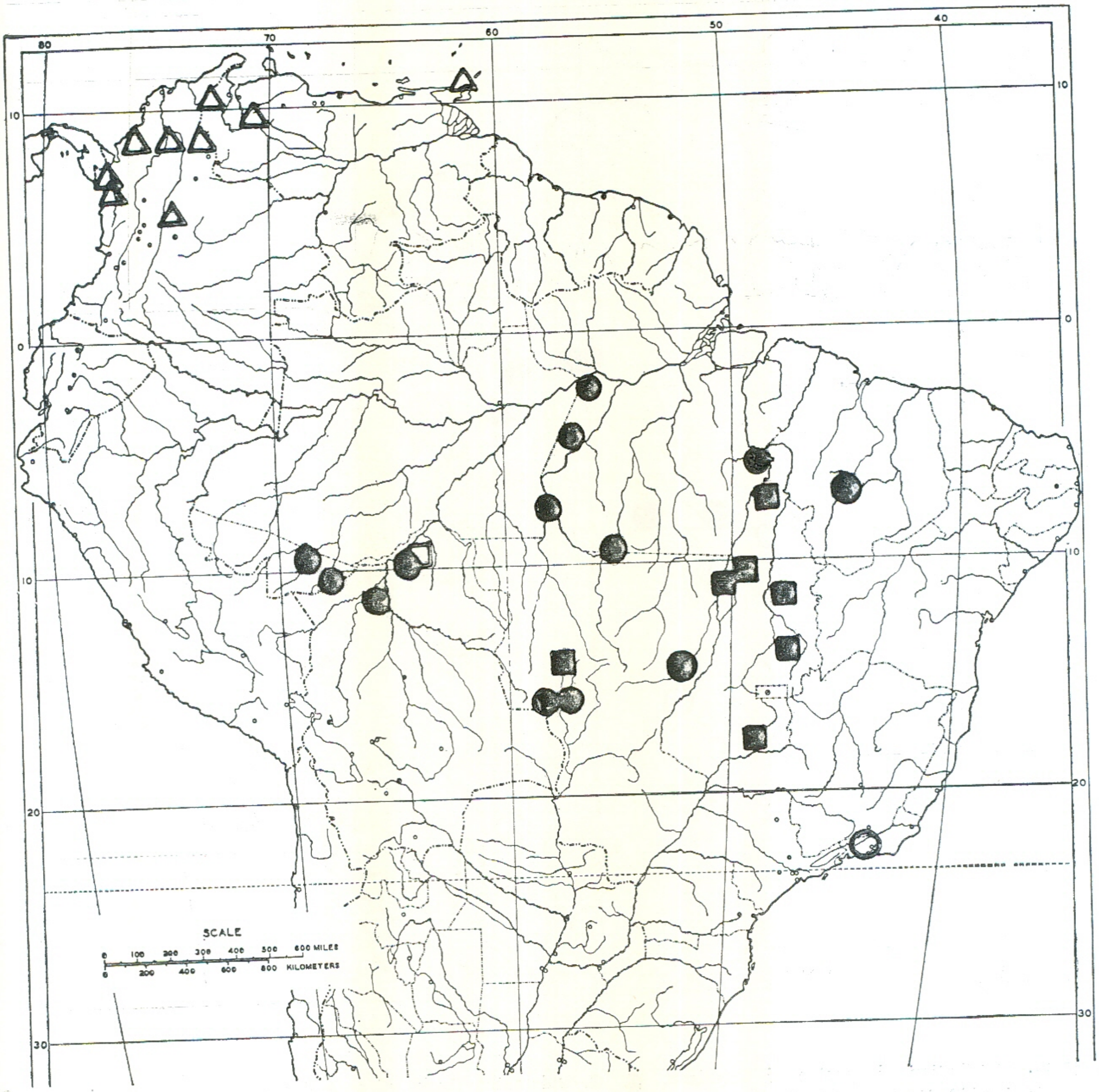

Fig. 20 — Species of Cariniana. △ **C. pyriformis** Miers a species of the Nechi and Catumbo refuge area (probably introduced to Trinidad). ● **C. domestica** (Mart.) Miers, a southern Amazon species. □ **C.** sp. nov. a species of the Rondônia refuge area. □ **C. rubra** Gardn. ex Miers a Planalto species, and. ○ **C. janierensis** Knuth, a coastal species.

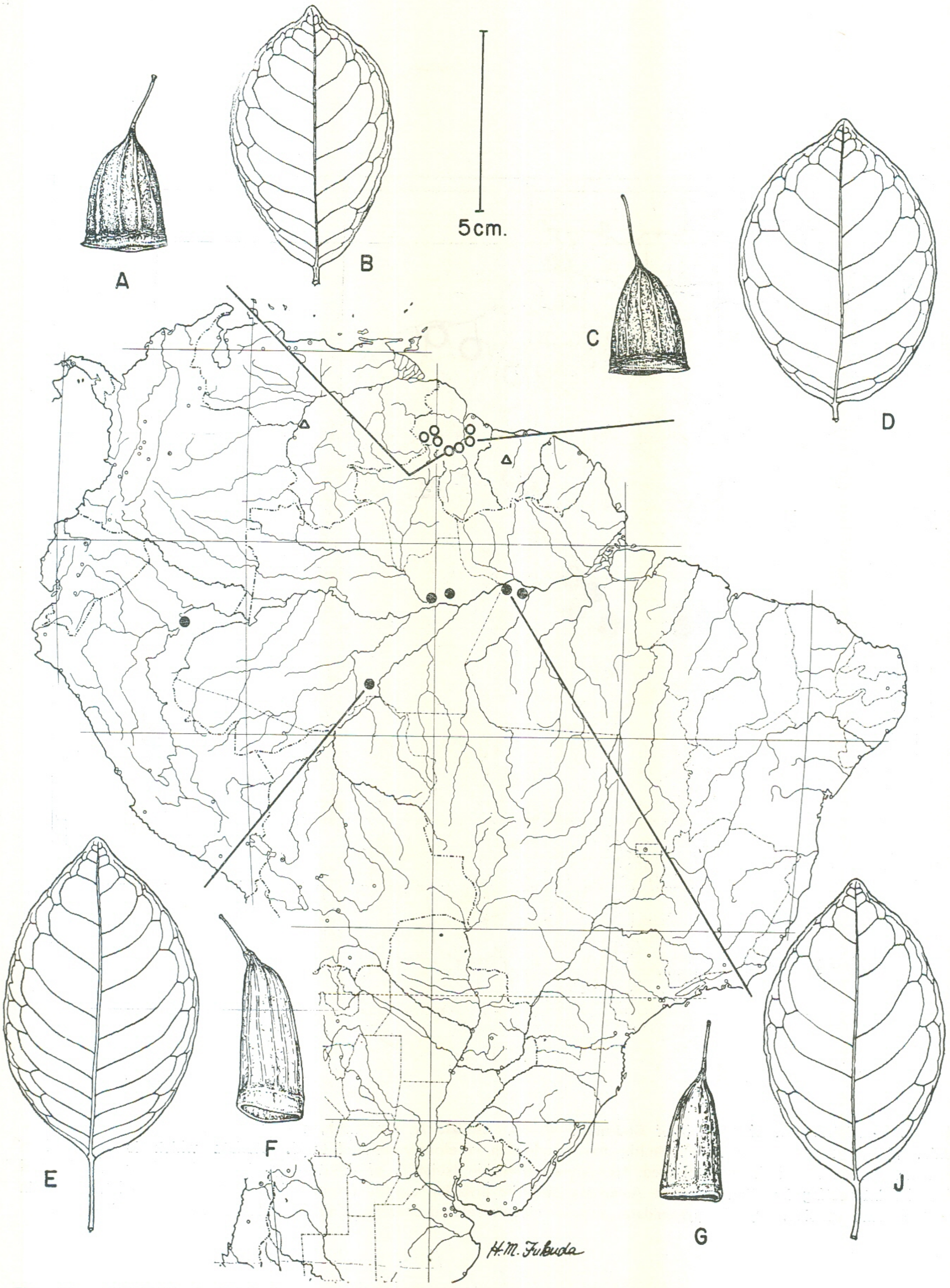

Fig. 21 — Pictorialised distribution map of **Couratari riparia** Sandw, and **C. tenuicarpa** A. C. Smith showing a pair of closely riverine species which have differentiated sufficiently to be recognized as species, and were probably isolated during drier periods.

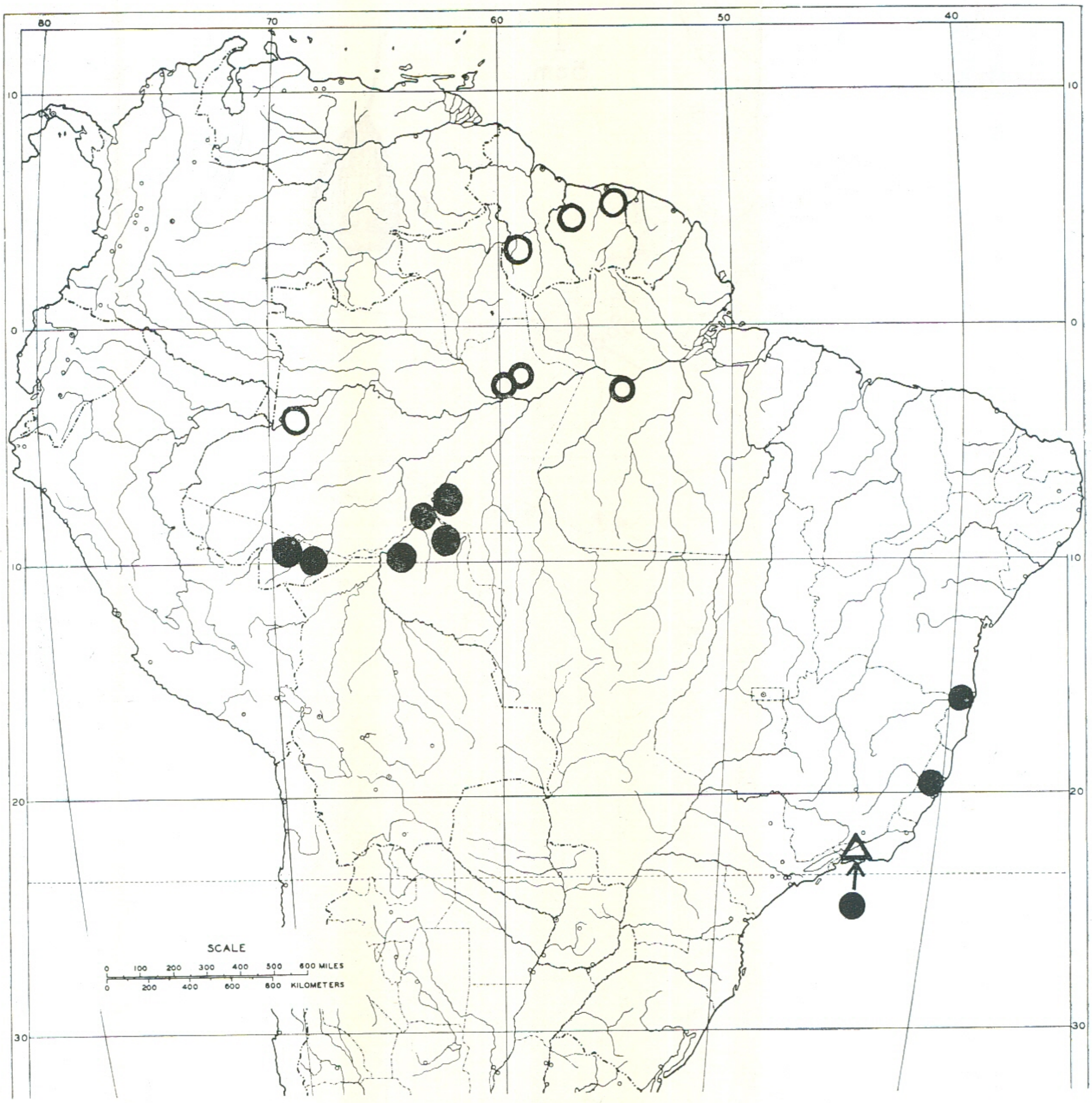

Fig. 22 — Distribution of species of **Couratari.** ○ **C. stellata** A. C. Smith, a species confined to northern Amazonia. ● **C. macrosperma** A. C. Smith, the species most closely related to **C. stellata** which is confined to southern Amazonia and the coastal area. This shows probable isolation of the two species during drier periods, and also the interesting isolation between Amazonia and the Brazilian coastal forests of two allopatric populations within the same species. Δ **C. pyramidata**, another closely related species, is endemic to the Rio de Janeiro area.

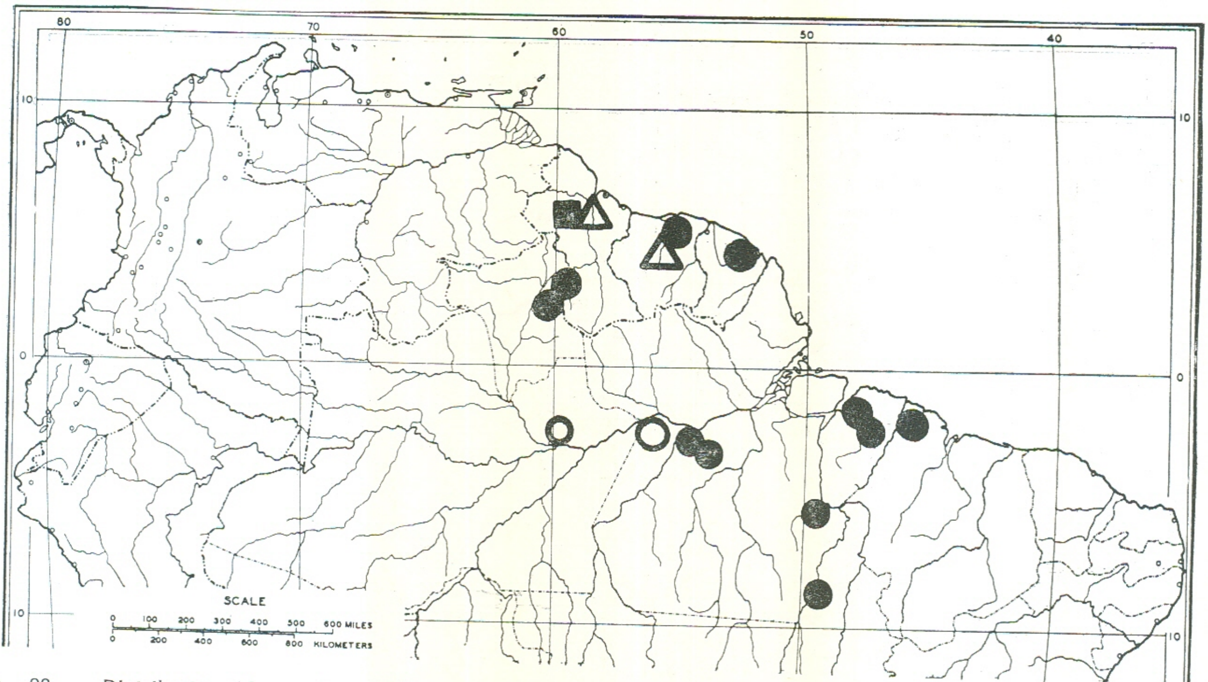

Fig. 23 — Distribution of species of **Couratari**. △ **C. gloriosa** Sandw. and □ **C. calycina** Sandw. still confined to the Guiana refuge area. ○ **C. tauri** Berg, a species probably originating from the Manaus refuge area, and ● **C. oblongifolia** Ducke & Knuth, a widespread species.

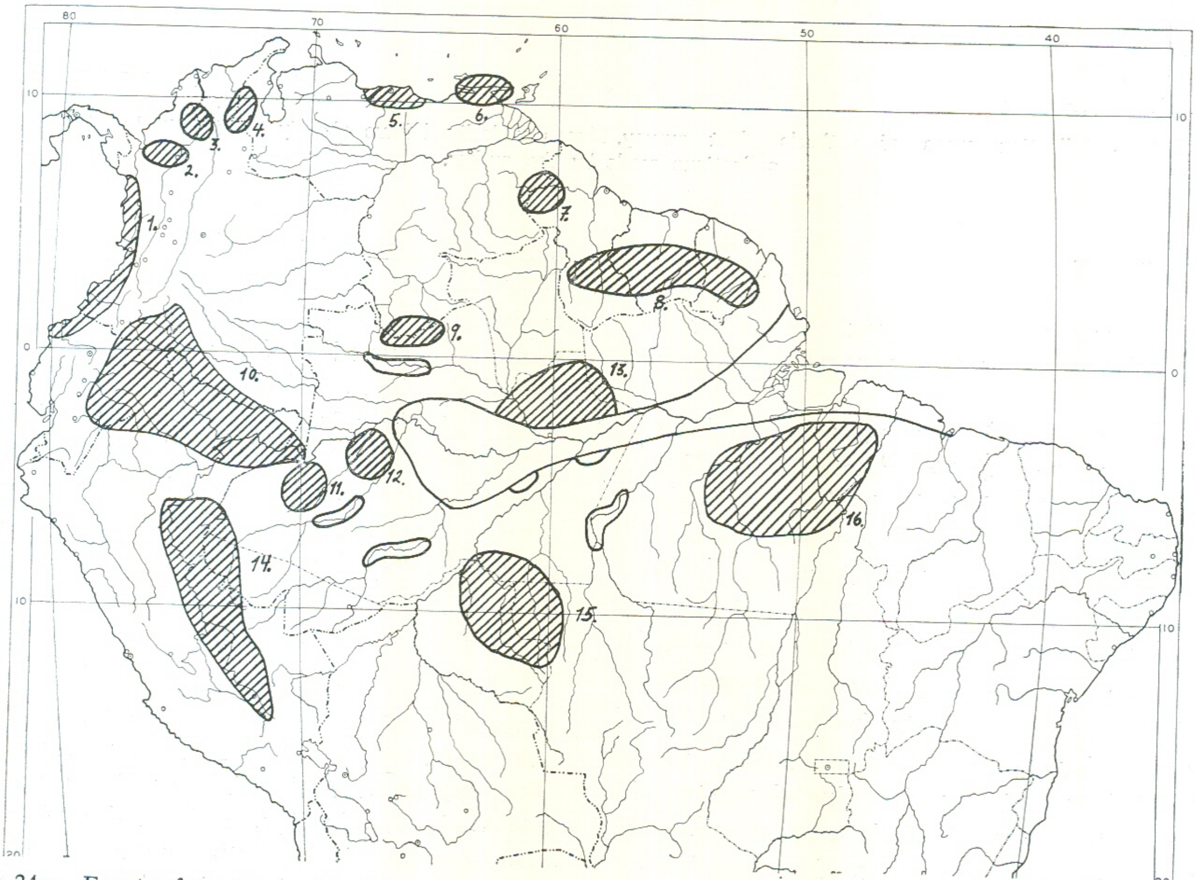

Fig. 24 — Forest refuges proposed in this paper. 1 — Chocó. 2 — Nechi. 3 — Santa Marta. 4 — Catumbo. 5 — Rancho Grande. 6 — Paria. 7 — Imataca. 8 — Guiana. 9 — Imerí. 10 — Napo. 11 — Olivença. 12 — Tefé. 13 — Manaus. 14 — East Peru. 15 — Rondônia-Aripuanã. 16 — Belém-Xingú.

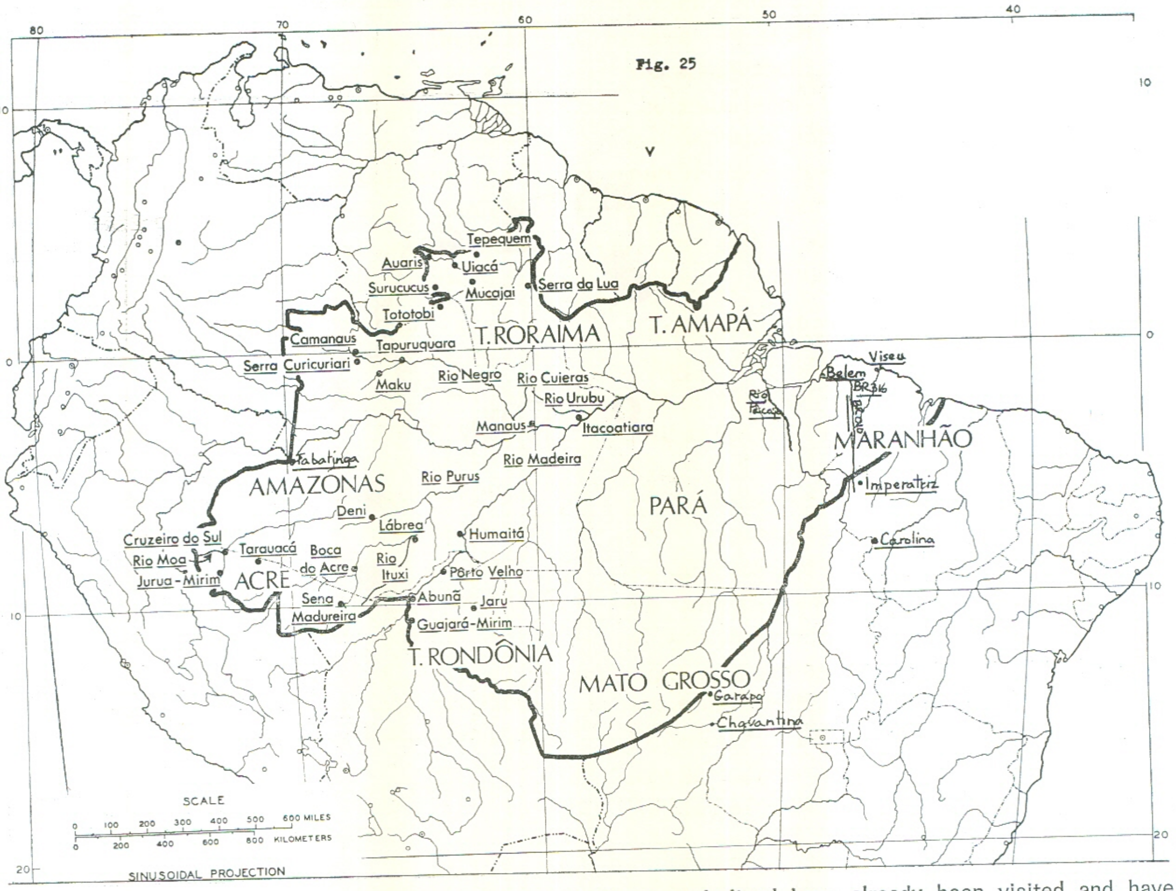

Fig. 25 — Collection areas of author's plant survey. Places underlined have already been visited and have and collections made by the author.

CONCLUSION

REFUGES PROPOSED FROM THE STUDY OF THESE FOUR PLANT FAMILIES

A summary of the refuges proposed here is given in Fig. 24. The main difference from both Vanzolini and Haffer is that I think that they both have reduced the size of the possible refuges too much, (compare Figures 1 and 24), placing too much on the periphery of Amazonia. From plant distribution it certainly seems apparent that Vanzolini's five small areas of refuges could not explain the diversity of the present day distribution, nor could it have provided opportunity for the diversity of species to evolve. Haffer's areas correspond much more to the speciation of lowland forest plant species. However, it seems dubious whether the forest was ever as reduced at any one time, in the Pleistocene and post-Pleistocene climate changes, as Haffer proposes. It should be remembered that drier periods probably occurred at least three times, and therefore it is possible that there was some variation in the refuge areas of forest, and that certain areas were smaller at different times. The sixteen refuges proposed here expand, rather than alter drastically, the refuges proposed by Haffer, and they certainly agree with his main hypothesis. The main differences which I find in plant distribution are :

1. The Napo area of Haffer is too small, and probably should be extended eastwards and to the north. Adjoining this a new refuge is proposed south of the Amazon River around São Paulo de Olivença, and another further east around Tefé. Both areas have an unusually large number of rather restricted lowland endemic species of plants.

2. In all four plant families studied there is very little endemism in or near the area of Haffer's proposed refuge Madeira-Tapajóz. Conversely, there are many local species in Rondônia and the neighbouring part of Amazonas as far as the Rio Roosevelt. Consequently, I have proposed a different refuge, Rondônia-Aripuanã, which lies to the west of Haffer's refuge of Madeira-Tapajóz.

3. There is an extremely high concentration of local species around Manaus which cannot be explained by migration of the species from the Guiana refuge. It seems likely that there was a large and important refuge just to the north of the area flooded by sea-water. This area was directly north of Manaus. The receding sea-water brought southwards migration of the species to the present day position of Manaus. There is apparently little contact with the Guiana refuge, although today there are a number of plant species found in both the Guiana and the Manaus regions. A much commoner relationship for the Guiana species is with the Belém area, extending eastwards into the Amazonian part of Maranhão. The number of local species around Manaus is unlikely to have spread from a refuge south of the river, as the water has always acted as somewhat of a barrier in this respect.

4. Haffer's map of refuges left a few small areas along some of the main rivers as gallery forest refuges. Judging from plant distributions, I suspect that these gallery forest areas played a more important part than is indicated by Haffer in providing refuges and also some genetic contact between areas, as well as a route for the dispersal of the diaspores of various species. Today many of the species of the varzea forests are the most widely distributed in Amazonia, partially because of the persistence of gallery forest in the dry times, and partly because of the ease of diaspore dispersal by water. Today we have a similar situation in the area presently covered by cerrado vegetation in the Planalto of Central Brazil. A number of Amazonian species are distributed throughout the gallery forests of the Planalto and provide a link to the coastal forests. Fig. 19 shows the distribution of *Cariniana estrellensis,* a forest species in Acre and near to the coast but also occurring in gallery forest of the Planalto. *Couratari macrospermum* (Fig. 22), on the other hand, has not maintained a continuous contact through gallery forest, and now occurs in two disjunct and isolated populations in Amazonia and the coastal forest.

In conclusion it can be observed that plant distribution appears to concur well with zoological evidence for the reduction of forest cover during the last Pleistocene and post-Pleistocene period. It is to be hoped that further investigation can be carried out in branches of botany which will produce further evidence, e. g. palynology, and perhaps in studies of the soils, and most especially investigation which will produce further comments on the distribution of other plant families widely distributed throughout the region.

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RESUMO

Nos últimos anos diversos zoólogos têm escrito sobre a história do clima amazônico e a evolução de diversas espécies de animais. Afirmam que durante o Pleistoceno e pós-Pleistoceno houve períodos de clima seco. Durante essas épocas, as áreas de mata pluvial eram reduzidas tornando-se em pequenas áreas ou refúgios de mata. Por conseguinte, dessas áreas pequenas de mata, houve algumas populações isoladas dando oportunidade para a evolução de espécies antes da volta da mata contígua. Esse fenômeno é uma das razões pela

qual há diversidades de espécies nas matas de terreno baixo da bacia amazônica. Até agora, a maior parte em evidência pela teoria dos refúgios, é baseada na qualidade dos animais, principalmente aves, borboletas e lagartos. Aqui é dada a evidência para confirmar a teoria dos refúgios, com estudos fitogeográficos. As distribuições das espécies amazônicas das famílias de plantas lenhosas, Caryocaraceae, Chrysobalanaceae, Dichapetalaceae e Lecythidaceae são usadas para confirmar a existência dos refúgios pleistocênicos. Um mapa dos refúgios indicado pelas 4 famílias de plantas é apresentado, baseado nas distribuições das espécies. Os refúgios propalados aqui, correspondem-se mais ou menos com os refúgios de Haffer e Brown, melhor que os de Vanzolini que parecem muito mais reduzidos.

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H I R T E L L A

Geographic Distribution	**Nº of species**	**Notes on Habitats**
Northern South America		
1. West of Andes, Lowlands, "chocó"	3	H. **carbonaria** — salt flooded sea; 2 in forest
2. Confined to Colombia & Ecuador east of Andes	3 + i	H. **adenophora** — montane scrub; 2 + i in forest
3. Colombian **Amazon**	1	H. **vesiculosa**
4. Venezuelan **Amazon**	5	2 savanna, 2 mountain slopes, 1 savanna & slopes
5. Venezuelan **Amazon** & Upper Rio Negro Brazil	4	2 Forest margin & open forest; 1 savanna margin & open river sand
6. Upper Rio Negro Brazil	1	H. **longifolia** known on sheet from secondary forest
7. Venezuela **Federal District**	1	H. **leonotis** from forest
8. Venezuela confined to Bolívar	1	H. **deflexa** from river banks
9. Venezuelan Guiana and/or the Guianas	5	3, forest; 1, river islands; 1, open forest margins
10. Venezuelan Guiana, The Guianas to **Brazil Pará**	5	4 forest; 1 savanna & river margins
11. Guyana and Central **Amazonia**-Manaus	1	H. **mucronata** from forest
12. Venezuela and/or Colombia, Guianas widespread **Amazonia**	1 + ii	H. **racemosa** var **racemosa, H. hispidula** & **H. bicornis** var **pubescens** from forest
13. Guyana Central & Eastern **Amazon**	1	H. **piresii** from forest
14. Guianas, eastern **Amazon** to Planalto	2	H. **ciliata** savanna & cerrado; **H. glandulosa** Gallery forest & savanna margins
15. Guianas, western & Central **Amazon**	1	H. **duckei** from forest;
16. Guyana, Venezuela, Western **Amazon**, Bolivia	1	H. **bullata** from river and savanna margins
17. Eastern **Amazonia**	4	Forest
18. Central **Amazonia**	4	3 forest; H. **glabrata** open forest, secondary forest and savanna
19. Western **Amazonia**	7	6 forest; H. **scaberula** on caatinga
20. Southern **Amazonia**	5	Forest and riverine forest
21. Widespread **Amazon** and Northern Planalto	1	H. **eriandra** in riverine forest, savanna, cerrado, secondary
22. Eastern and Central **Amazonia**	1	H. **suffulta** in forest
23. Eastern **Amazonia** and Pernambuco	i	H. **bicornis** var **bicornis** in sandy riverine localities
24. Western and Southern **Amazonia**	2	H. **pilosissima** & H. **guainieae** in forest
25. Western and Central **Amazonia**	1	H. **macrophylla** in riverine and secondary forest
26. Central America, Caribbean, Guianas, **Amazon**	i	H. **triandra** subsp. **triandra** in a variety of forest types
27. Central America, Caribbean, Guianas, **Amazon**, Eastern Brazil	i	H. **racemosa** var. **hexandra** in savanna and many open habitats
28. Guianas and widespread in **Amazonia**	1	H. **physophora** in forest
29. Terr. **Roraima Brazil**	1	H. **dorvalii** in savanna margin
Extra Northern South America		
29. Eastern Coastal Brazil	9 + i	8 + i in forest, 1 in open areas
30. Antilles & Puerto Rico	2	H. **rugosa** & H. **pendula** from forests
31. Central America	3 + i	Forests
32. Confined to Planalto of Central Brazil	2	H. **martiana** gallery & swamp forests, H. **gracilipes** Riverine & slope forest
33. Planalto to Southern **Amazon and Acre**	1	H. **burchelli** in gallery forest
34. Planalto to Southern Brazil	1	H. **hebeclada** in forests
35. Central America, Caribbean, Northern Venezuela & Colombia	1	H. **americana** in dry forests
36. Antilles, Venezuela, Guianas, Northern **Amazon**	1	H. **paniculata** in savanna and river margins
37. Bolivia	1	H. **lightioides** in forest

TABLE 2. PHYTOGEOGRAPHIC BREAKDOWN OF **HIRTELLA**

Phytogeographic Areas	MOQUILEA	LEPTOBALANUS	MICRODESMIA	PARINARIOPSIS	HIRSUTA	HYMENOPUS	CYMOSA	PULVERULENTA	LICANIA	TOTAL SP	FOREST	SAVANNA	OTHER
Northern South America													
1. West of Andes, Lowland Forest, "Chocó"	3	2	2	—	—	1	—	1	—	9	9	—	—
2. Santa Marta "Catumbo"	—	1	—	—	—	—	—	—	—	1	1	—	—
3. Confined to Colombia east of Andes	—	—	2	—	—	—	—	—	1	3	3	—	—
4. Colombia and Venezuela	—	—	—	—	—	—	—	—	1	1	1	—	—
5. Confined to Venezuela other than Venezuelan Guiana	—	—	—	—	—	—	—	—	5	5	1	2	c/s
6. Venezuela and Caribbean	2	—	—	—	—	—	—	—	—	2	2	—	—
7. Venezuelan Guiana and/or The Guianas	—	3	—	—	1	7	1	2	8	22	22	—	—
8. Venezuelan Guiana, The Guianas and Brazil-Roraima	—	—	—	—	—	1	1	—	2	4	3	—	s
9. Venezuelan Guiana, The Guianas to Brazil-Pará or Maranhão	1	—	—	—	—	1	1	2	4	9	8	1	—
10. Guianas and eastern Peruvian Amazon	1	—	—	—	—	—	—	—	—	1	1	—	—
11. Guianas and Central Amazonia	—	1	—	—	—	—	—	1	—	2	2	—	—
12. Guianas and Amazonia widespread	—	2	—	1	1	2	1	2	2	11	11	—	—
13. Upper Rio Negro Venezuela and/or Brazil	—	1	—	—	—	—	—	1	3	5	2	2	ca
14. Widespread within Amazonia	2	1	—	—	—	3	2	—	5	13	13	—	—
15. Confined to Eastern Amazonia	1	—	—	—	—	—	1	—	1	3	3	—	—
16. Confined to Central Amazonia	1	—	—	—	1	1	1	—	2	6	6	—	—
17. Confined to Western Amazonia Ecuador, Peru, Colombia, Brazil (expanded Napo)	4	1	—	—	1	—	—	1	3	10	9	1	—
18. Southern Amazonia widespread	1	1	—	—	—	—	—	1	1	4	4	—	—
19. Southern Amazonia Rondônia, Mato Grosso	—	1	—	—	—	—	—	1	1	3	3	—	—
20. Extremely widespread over several of above areas	—	2	—	—	—	—	1	—	1	4	—	—	—
Extra Northern South America													
21. Southeastern U.S.A	1	—	—	—	—	—	—	—	—	1			
22. Mexico and Central America	3	1	1	—	1	1	—	—	—	7			
23. Lesser Antilles	—	—	—	—	—	—	—	—	1	1			
24. Planalto of Central Brazil	—	2	1	—	—	—	1	—	2	6			
25. Northeastern Brazil	1	2	—	—	—	—	—	—	—	3			
26. Coastal Brazil Bahia - São Paulo	1	—	1	—	—	2	—	—	6	10			
27. Central Bolivia, La Paz Dept.	1	—	—	—	—	—	—	—	—	—			
	23	21	7	1	5	19	10	12	49	147			

TABLE 3. PHYTOGEOGRAPHIC BREAKDOWN OF **LICANIA**

c = cloud forest
s = slope forest
ca = caatinga