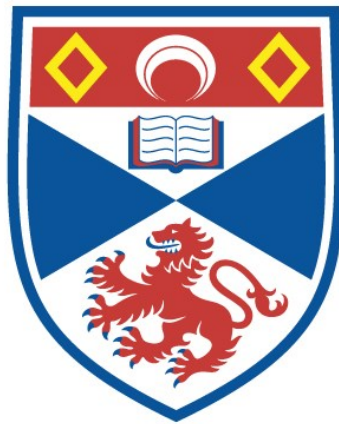


A CRITICAL EVALUATION OF THE FLORISTIC LINKS  
BETWEEN CHACO AND CAATINGAS VEGETATION IN  
SOUTH AMERICA

Darien Eros Prado

A Thesis Submitted for the Degree of PhD  
at the  
University of St Andrews



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TR B 8

**"Eu não sei mais nada.  
Vou ter que começar de novo"**

Prof. Dárdano de Andrade-Lima, back  
in Brazil after his visit to the Chaco of  
Argentina and Paraguay and shortly  
before his untimely death.

[Prof. Severino do Monte Prazeres, pers. comm.]

To Fe and Eros, my beginnings and my principles  
To Marta, my life  
To Efraín, my future  
To Paul Lewis, my mentor

I, **Darién Eros Prado**, hereby certify that this thesis has been composed by myself, that it is record of my own work, and that it has not been accepted in partial or complete fulfilment of any other degree or professional qualification.

Signed.....Date.....

I was admitted to the Faculty of Science of the University of St. Andrews under Ordinance General N<sup>o</sup> 12 in October 1986 and as a candidate for the degree of Ph.D. in October 1987.

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I hereby certify that the candidate has fulfilled the conditions of the Resolution and Regulations appropriate to the Degree of Ph.D.

Signature of the Supervisor.....Date.....<sup>17<sup>th</sup></sup> Aug 1991



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## ABSTRACT

The present study critically evaluates the alleged close floristic links between Chaco and Caatingas vegetation in South America. A reassessment of the phytogeography of these areas has been made by (a) comparing species lists in virtually all of the available literature, and (b) plotting dot-map distributions of relevant taxa based on the author's own herbarium studies and recent monographs. The environmental factors, geology and geomorphology, climate and soils of both areas were also analyzed to assess their degree of internal coherence. The prevailing concept of the Chaco itself proved to be a broad geographical entity rather than a well defined geobotanic unit in vegetational terms, and a redefinition of the Chaco *sensu stricto* and a new map of the province has been proposed. Several forest communities have been excluded from the Chaco *s.s.* since their floristic composition clearly link them to other neighbouring provinces. Although the Caatingas province vegetation is not so well known, the area appears to be a consistent natural region, and a new vegetation type has been briefly described.

Detailed floristic lists of the main woody and succulent species of the Chaco *s.s.*, the Caatingas and the Subandean Piedmont Forests are presented, which provide the basis for a subsequent phytosociological analyses (classical and numerical approaches) of these vegetation units vis-à-vis the rest of the seasonal forests and woodlands of South America. The results suggest that the alleged affinities Chaco-Caatingas are very feeble indeed, particularly when they are compared to the actual links between the Caatingas and other seasonal communities in the continent: the Guajira province in N Colombia and Venezuela, the dry forests of W Ecuador, and very particularly the Subandean Piedmont Forests in NW Argentina and SW Bolivia.

Some basic patterns of distribution of the floristic elements of seasonal forests in South America have been identified and found to form coherent trends in a series of accurate dot maps: a) Chaco endemics; b) Caatingas endemics; c) Neotropical seasonal forests pattern, including c.1- Residual Pleistocenic Seasonal Formations Arc (or 'Pleistocenic Arc'), extending from the Caatingas through some Planalto forests and calcium-rich localities in the Cerrados, SW Mato Grosso do Sul and the

Santiago and Chiquitos Sierras, to the Paraná-Paraguay river system and the Subandean Piedmont Forests; c.2- Tropical and Subtropical Seasonal Forests in South America; and c.3- Amphitropical Seasonal Forests pattern. The zoological evidence regarded until present as further proof of the Chaco-Caatingas links is also analyzed and mapped, and the results are sharply coincidental with those found for plant distribution.

An attempt has also been made to interpret the origin of the Caatingas flora; a hypothetical framework of probable ancient connections across South America between present-day seasonal woody communities is postulated, which have been interpreted here as migratory routes during the wet-dry climatic fluctuations of the late Pleistocene (18-12 ka BP). It is therefore concluded that the floristic links between the Chaco and the Caatingas are very weak and negligible when compared to other relationships, such as those between Chaco-Monte or Caatingas-Subandean Piedmont Forests. It is proposed that the Caatingas should be removed from the Chaquenian Dominion and placed in the Amazonian Dominion, with which they show much stronger affinities.

## 1. INTRODUCTION

Many authors have drawn attention to the physiognomic, floristic and faunistic connections between the Caatingas of NE Brazil and the Gran Chaco region of Bolivia, Paraguay and Argentina (Fig. 1.1), e.g. Smith & Johnston (1945), Beard (1953, p. 195), Andrade-Lima (1954, 1964a, 1967, 1981, 1982), Castellanos (1958), Rizzini (1963, 1979), Veloso (1964), Schnell (1966), Veloso & Strang (1970), Müller (1973), Vanzolini (1974, 1976), Bigarella et al. (1975), Short (1975), Cabrera (1976), Webb (1978), Cabrera & Willink (1980), Bucher (1982a), Prance & Schaller (1982), Ratter (1984), Haffer (1985), and Ratter et al. (1988b). For the most part the alleged floristic links comprise pairs of species (presumed vicariads), present in Chaco and Caatingas, such as *Ziziphus mistol* - *Z. joazeiro*, *Schinopsis quebracho-colorado* - *S. brasiliensis*, *Copernicia australis* - *C. cerifera*, *Aspidosperma quebracho-blanco* - *A. pyrifolium*, *Caesalpinia paraguariensis* - *C. pyramidalis/bracteosa*. A number of genera common to the two areas have also been cited: *Croton*, *Bumelia*, *Capparis*, *Mimosa*, *Acacia*, *Maytenus*, etc. Furthermore, some of the above mentioned authors cite Hueck (1972) as having remarked on the impressive degree of physiognomic similarity of the Chaco and Caatingas, and also for a list of disjunct species with large populations in the two areas (Andrade-Lima, 1982). However, from a careful reading of Hueck (1972) the only relevant observations with regard to the physiognomy of the Caatingas seem to be his comment: "Na sua aparência lembra principalmente as matas do Chaco do centro da América do Sul" (p. 309). And describing typical Caatingas forest Hueck wrote: "El aspecto del bosque recuerda mucho al bosque seco del Chaco" (Hueck, 1959, p. 9). These casual references to physiognomic similarities seem to have been transformed into deep floristic relationships.

Cabrera & Willink (1980) included the Chaco and Caatingas, together with the Espinal, Monte, Prepuna and Pampean provinces, in their 'Chaquenan Dominion'. According to these authors, this Dominion was quite homogeneous and characterized by the predominance of Leguminosae (*Prosopis*, *Acacia*, *Caesalpinia* and *Cercidium*), Zygophyllaceae (*Larrea*, *Bulnesia* and *Plectrocarpa*), Anacardiaceae (*Schinopsis* and *Lythraea*), Rhamnaceae (*Ziziphus* and



Fig. 1.1: Position of the Gran Chaco and the Caatingas in South America.



*Scutia* ), Capparidaceae (*Capparis* and *Atamisquea*) and numerous genera of Bromeliaceae and Cactaceae. However, only five out of these 13 genera can be actually found in the Caatingas: *Acacia* , *Caesalpinia* , *Capparis* , *Schinopsis* and *Ziziphus* , and the other genera have been excluded from that province in all of the most detailed surveys of caatinga vegetation (Luetzelburg, 1922-23; Egler, 1951; Andrade-Lima, 1954, 1960 & 1981; Figueiredo Gomes, 1981; Emperaire, 1983; Carvalho, 1986). Against this background the present study has aimed to attempt a more critical evaluation of the floristic links between these two areas.

Axiomatic to any study of 'floristic similarity' is the question of what is a phytogeographical province as an abstraction. In this study, the concept proposed by Braun-Blanquet (1919, *sub* 'Domaine'), later modified by Takhtajan (1986), is followed. This system consists essentially of the subdivision of the World flora into areas ordered in hierarchical categories according to their degree of floristic endemism and their 'taxonomic' rank. Thus, the system comprises 'kingdoms', characterized by endemic families, subfamilies and tribes; 'regions', established on the basis of high numbers of generic and specific (and sometimes even small family) endemisms; 'provinces' are subdivisions of the regions in which generic endemism is less relevant and usually consists of a reduced number of monotypic or oligotypic endemic genera, but in which specific endemisms are abundant and characteristic; the lowest category is the 'district', mainly established by subspecific endemism and where specific endemism is absent or weakly expressed (Takhtajan, 1986). Castellanos & Pérez-Moreau (1944) widened the 'province' to an ecological concept, such that it has to comprise not only the characteristic generic and specific endemics but also several edaphic communities and at least one climax community.

It is important to note that phytogeographical provinces do not necessarily coincide with geographical regions which may bear the same name. Thus, in South America the geographical areas denoted by Pampa, Monte, Caatingas, Patagonia, Amazonia or Chaco do not imply a homogeneous vegetation or equivalence with phytogeographical provinces. The danger of the misuse of geographical regions as synonyms of vegetation units has been pointed out by Castellanos & Pérez-Moreau (1944) for the Argentine vegetation and emphasized by

Castellanos (1960), and also as regards the Brazilian vegetation by Kuhlmann & Correia (1982).

To assess the degree of relationship between Chaco and Caatingas the following approaches were adopted in the course of this study:

**a-** An exhaustive search of the literature for floristic lists and phytogeographical observations on both areas and related ones was carried out.<sup>1</sup>

**b-** The present author has accumulated field experience for parts of the Chaco, based on many ecological and floristic surveys carried out from the University of Rosario (Argentina) in areas of Santa Fe, Córdoba, Chaco and Santiago del Estero provinces, and subsequent surveys in riverine vegetation in the river Paraná valley and tributaries.

**c-** During the course of this thesis further brief but very important fieldwork in NE Brazilian Caatingas (Pernambuco and Ceará states) was undertaken. The core Cerrado area near Brasilia and calcareous forest remnants in the Federal District were visited, and also similar outcrops around Corumbá in Mato Grosso do Sul. A preliminary survey of the alleged Chaco intrusion in the latter area was carried out.

**d-** An exhaustive check on taxonomic literature and verification of identity of those species cited in floristic lists and phytogeographic accounts was made by repeated visits to Royal Botanic Gardens, Kew and RBG Edinburgh, and also with exsiccata obtained on loan from various Herbaria.

**e-** Elaboration of a series of accurate distribution dot maps based only on verified specimens or on trustworthy modern revisions (solid black dots), and also on citations in reliable vegetation surveys of the areas involved (open circles).

**f-** Statistical (numerical) analysis of floristic lists on a basis of presence-absence of species was performed (Complete Linkage Algorithm-CLINK, in Wishart, 1987, and Principal Components Analysis-PCA, in JUMP IN<sup>TM</sup>), and this compared to classic phytosociological analysis (Braun-Blanquet modified by Mueller-Dombois & Ellenberg, 1974).

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<sup>1</sup> Abundant references to be found in the Chaco and Caatingas chapters (Ch. 2 & 3).

**g-** Finally, an attempt was made at a synthesis of the biogeography of certain parts of South America linked by related types of dry vegetation which form an arc across the continent.

## 2. THE GRAN CHACO VEGETATION

Within the framework of Southamerican phytogeography the term Chaco or Gran Chaco has been applied to the vegetation covering the vast plains of north-central Argentina, western Paraguay and SE Bolivia, and entering into Brazil as a narrow strip parallel to the river Paraguay in Mato Grosso do Sul (Fig. 1.1). Covering about 800,000 km<sup>2</sup> (Hueck, 1972) or 1,000,000 km<sup>2</sup> (Bucher, 1982a), it is one of the few areas in the world where the transition between the tropics and the temperate belt does not occur in the form of a desert but rather as semiarid forests and woodlands (Morello & Adámoli, 1968). For most authors the Chaco phytogeographical province has simply been equated with the Chaco Geographical Region, as shown in Hauman (1931), Kanter (1936), Ragonese & Castiglioni (1970), Cabrera (1953, 1971, 1976), Morello & Adámoli (1968, 1974), Hueck (1972), Hueck & Seibert (1981), and Zellweger et al. (1990), and no attempt has been made to date to critically evaluate the homogeneity of the resulting vegetation.

In the following sections the environmental factors modelling the vegetation of the Gran Chaco, and the floristics and structure of the vegetation itself, will be analyzed. The actual geographical area encompassed by this analysis corresponds to the broadest one, i.e. that of Ragonese & Castiglioni (1970). They described the plant cover extending from the gallery forests on the islands of the river Paraná in the east to their 'Subandean Sierra Chaco' in the west (which seems to be simply an impoverished version of the 'Palo blanco' forest). The rationale of choosing the broadest possible concept as starting point for this analysis arises from the need to take into account every vegetation unit susceptible to being regarded as chaquenian, and then test the validity of its inclusion within the province vis-à-vis both the core area of the Chaco itself and the rest of the South American phytogeographical framework. The present-day most widely accepted concept of the phytogeographical province is that of Cabrera (1976), that is to say from the forests close to the river Paraná in the east (but excluding the gallery forests and 'Selva de ribera' units), to the Sierra Chaco in the west (but excluding the 'Palo blanco', i.e. the so-called Transitional forests). There are other relevant but not widely accepted ideas of what the Chaco is, such as that of Hueck (1972) which simply includes the 'Palo blanco'

unit. The limits set by Ragonese & Castiglioni for the 'Chaquenian Park' (1970) most closely equate with the Chaco Geographical Region as defined by Kanter (1936). The map of the Chaco region in Morello & Adámoli (1968) is a similar case. These latter authors nevertheless provide the most useful phytogeographical subdivisions of the Chaco to date (Fig. 2.1), which were later slightly modified by Marlange (1972).

### **2.1- The usage of the word Chaco:**

In all likelihood the word 'Chaco' is from quechua origin. When the first Spanish Conquistadores arrived to present-day Peru, the quechua-speaking Inca civilization used the term 'chacu' or 'chaku' to designate the method of hunting by surrounding a piece of land with a large number of natives, shouting and producing noises so as to frighten the game and progressively closing the circle. Cobo (1964, p.269) described a 'chacu' involving some 10,000 indians and spreading over leagues of land in honour of Pizarro by mandate of Manco Inca. This meaning has been widely accepted by most scholars (Middendorf, 1890; Lira, 1942; Castellanos & Pérez-Moreau, 1944; Métraux, 1946; Morínigo, 1966) and by the Dictionary of the Royal Academy of Spanish, and usually accepted in a shortened version as 'hunting land'.

However, it seems that the Inca dominium never spread into the geographical Chaco or if it did it was very sporadically and in short-lived settlements, since archaeological evidence is very scarce and of arguable origin (Métraux, 1946; Fock, 1961). By contrast, the vast plains of the Chaco were roamed by war-like semi-nomadic hunter-gatherer aborigines, whose fierceness prevented white-man settlements until late XIX century in certain parts of the Argentine Chaco and the first third of this century in Paraguay and Bolivia. Their languages pertained mainly to the Zamucoan, Matacoan, Guaicuruan, Mascoian and Lule-Vilelan language families, rather than Quechua (Métraux, 1946). How is it then that the name 'Chaco' was so widely used for this area since early colonial times in South America?. The jesuit Camaño (1955) provided the most likely and logical explanation: the quechua-speaking indians of Humahuaca (in NW Argentina) used to go hunting in the plains east of their mountainous country; the Spaniards, who came from Peru to NW Argentina to found the oldest cities of that country, must have enquired what lay further to the east, and the answer 'chacu' -and

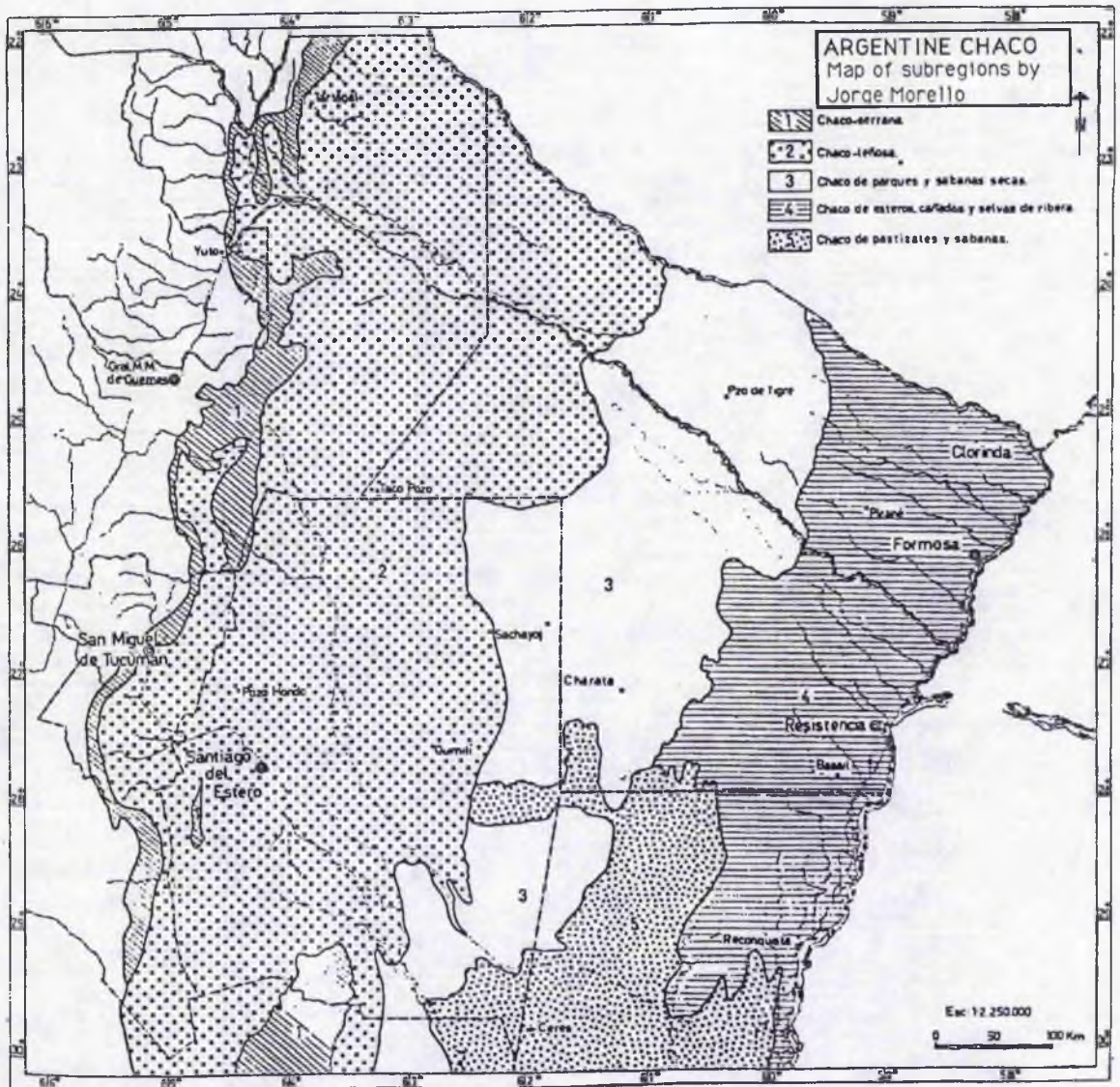


Fig. 2.1: Subregions of the Argentine Chaco. Modified from Morello & Adámoli, 1968.

subsequently by mispronunciation: 'chaco'- was believed to be the name of those lands. When finally the first Spanish colonies were established on the margins of the Paraguay and Paraná rivers, which are the actual eastern borders of the geographical Chaco, the name had already spread throughout the River Plate Dependencies to designate the lands east of the Subandean and Pampean chains, south of the Santiago and Chiquitos ranges in Bolivia, north of the treeless Pampas and west of the rivers Paraná and Paraguay.

This last eastern limit proved most difficult to colonize and it was not until nearly 1880 that the first contingents of immigrants founded Resistencia and Formosa cities on the W margin of the Paraná and Paraguay rivers respectively. This protracted stage of *terra incognita* must have helped cement the concept of the Chaco Geographical Region as a unit, which is a very useful abstraction from the anthropological, economic and administrative point of view (see for example the study by Morello, 1985), but not necessarily so as regards the phytogeography of the continent.

## 2.2 (a)- Geology and geomorphology:

The topography of the Chaco shows an amazing monotony all over the region, with some low-height elevations towards the western limit in Argentina and Bolivia, and also in a sector of the Paraguayan-Bolivian border (Ramella & Spichiger, 1989); the terrain is nearly horizontal, thus provoking the only three rivers crossing the Chaco (all of them alloctonous) to meander, and at the same time to have laterally fluctuating courses<sup>1</sup> within an up to 100 km wide flat valley covered with abandoned ox-bows.

Perhaps the most characteristic feature of the geomorphology of the Chaco-Pampean plains is that they consist of a massive accumulation of Quaternary sediments over the deeply sunk Pre-Cambrian Brazilian Shield. These sediments are the result of the erosion of the at that time recently risen Andes, which were transported æolically to the southern half of the Chaco geosinclinal (therefore called Chaco-Pampean loess or loessic sediments), or æolically but mainly

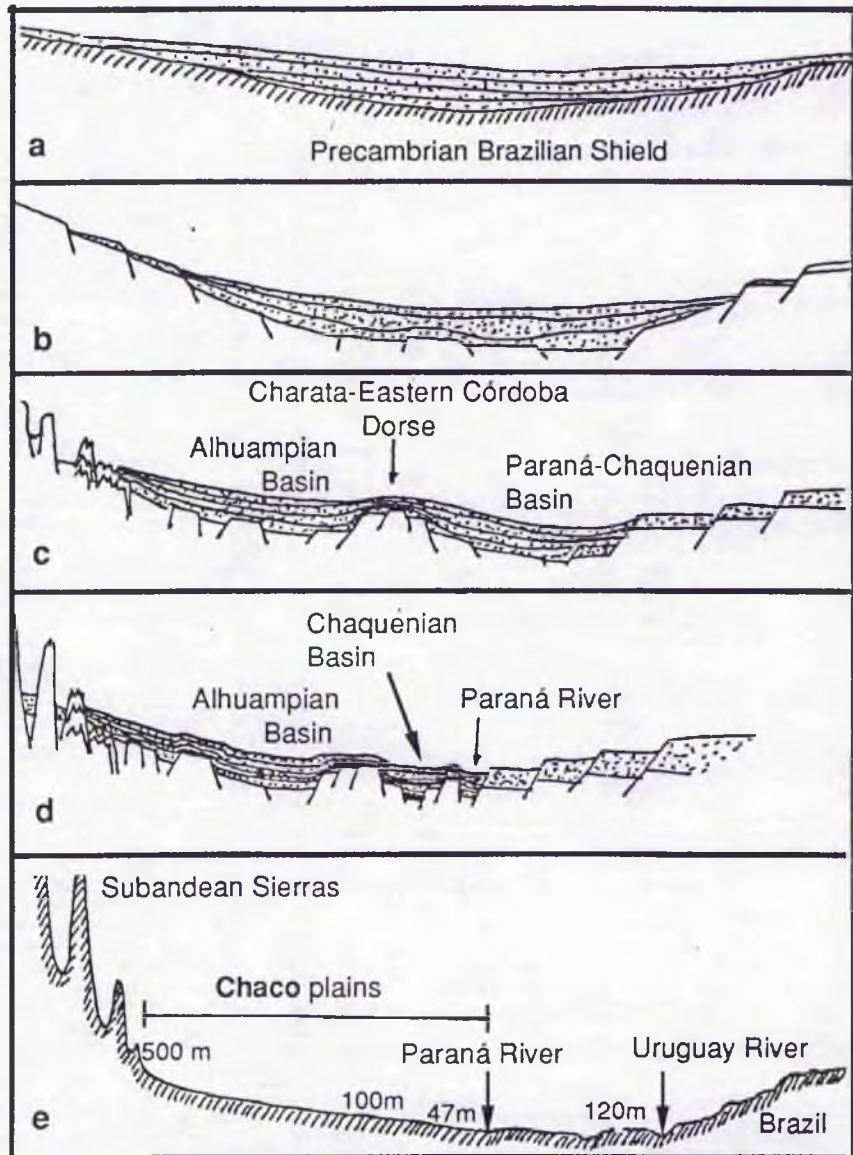
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<sup>1</sup> For example, geomorphologists have detected at least five changes of course of the Salado river (Castellanos, 1968), and its bed fluctuated of position once in this century.

hydrologically to the northern half of the Chaco trough, to form the scarcely known 'Chaco sediments' of the Paraguayan Chaco (Putzer, 1962). These plains must have originated as a vast sedimentary basin in the Palæozoic, extending further east than today over the Pre-Cambrian Shield (Fig. 2.2a). From the beginning it had a tendency to subside (Popolizio et al., 1980a), and the pressure of the successive layers of sediments provoke the crystalline base to fracture in smaller blocks with a general NE-SW direction (Fig. 2.2b). During the Tertiary these blocks moved differentially; the Argentinian Mesopotamia and eastern Paraguay started to rise (Teruggi, 1970), thus putting an abrupt eastern border to the Chaco plains, while in the W the Subandean Sierras were formed as an even more straightforward limit. In the middle of the plains, a line of blocks rose forming what today is known as the Charata-Eastern Córdoba Arc or Dorse (Padula & Mingramm, 1963) (Fig. 2.2c), which divides the area in two geomorphological basins, Alhuampian and Chaquenian. During the Quaternary the modern features of these plains were settled with the deposition of massive loessic sedimentary layers, obliterating most of the previous relief caused by the movements of the crystalline blocks (Fig. 2.2d). The Pampean loess is missing over the north of Argentine Mesopotamia and eastern Paraguay (Teruggi, 1970).

The differential block movements in the same NE-SW direction (Brazilian alignment) spread not only in the Argentine Chaco but also in the Paraguayan, as shown in Putzer's geological map (1962). In NW Paraguay the Brazilian alignment of fractures meets a Caribbean one (NW-SE direction), this allowing for a much deeper fault movement of over 1000 m (Putzer, 1962) which created the tectonic horst of the Cerro León area. This block, basically formed by Lower Devonian and Silurian outcroppings, has risen up to 720 m above sea level (Ramella, in litt.). There are some other isolated hills near the Cerro León area which generally share a common tectonic horst genesis, such as the Cristián, Cabrera, Caimán and San Miguel tableland hills, of which the latter is the highest point within the expanse of the Chaco (Ramella & Spichiger, 1989). Thus, it is clear that the sparse relief basically originated from an underlying horst and graben structure covered by a thick sedimentary layer, and that the Chaco comprises true plains caused by accumulation. The Chaco plains cannot be regarded as peneplains as claimed by Ramella & Spichiger (1989), i.e. extensive piedmonts caused by erosion





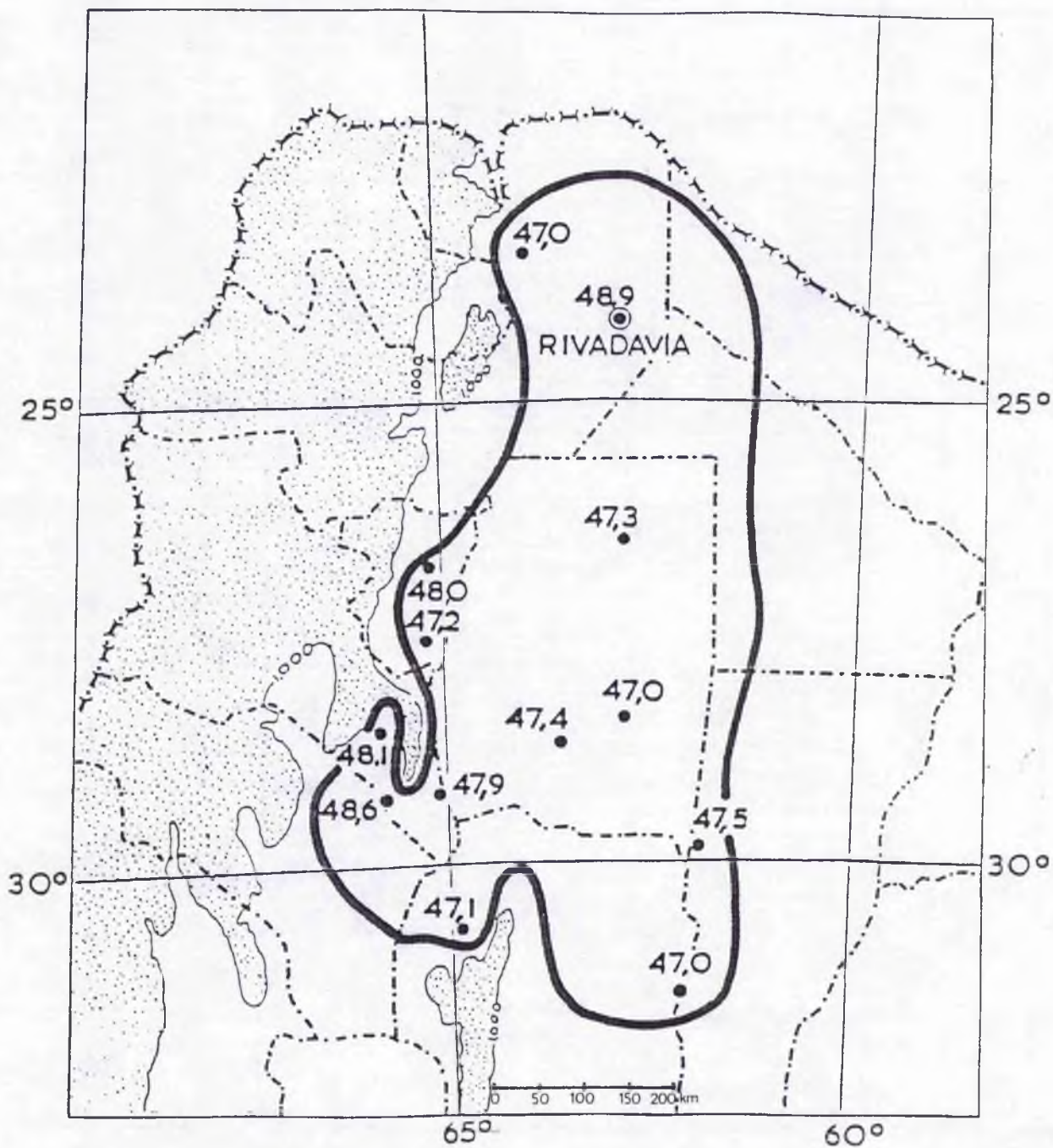
**Fig. 2.2:** Geological origin of the Chaco plains (see explanation in text). Modified from Popolizio et al., 1980a .

and removal of massive amounts of material; there is absolutely no evidence of such a process in the Chaco, where no glacis or inselbergs can be found. The origin of the localized palæodunes fields in W Paraguay and E Bolivia is also debatable; this author believes they can hardly have originated from fluvial transport and accumulation (cf. Ramella & Spichiger, 1989), but rather they must be the remnants of a much drier period probably caused by Pleistocenic climatic fluctuations such as those which formed the palæodunes fields of the middle São Francisco river valley in the Caatingas (Tricart, 1985). Such fluctuations did occur in the northern Chaco where the draining system of a more humid period during the Pleistocene, which left behind the youngest sedimentation to be found, is recognizable from the air (Putzer, 1962).

Popolizio et al. (1980a) divided the Chaco region in four major morphogenetical units, from west to east: a) *piedmont chaco*, in transition with the western mountainous ranges and in the shape of a narrow fringe along them; b) *bajada chaco*, over a huge alluvial apron of extinct rivers and which is under the influence of a semiarid subtropical modelling system; c) *western chaco plains*, coinciding with the slightly elevated Charata dorse; d) *eastern chaco plains*, under a humid, with no dry season, subtropical modelling system on mainly recent alluvial deposits from the Paraguay-Paraná axis. This last unit is the only one with autochthonous rivers, which are still modelling the surface in a dendritic net unique in the Chaco region, and this fact together with the scarce energy of the relief, soils with impeded drainage and higher rainfalls, provoke the unit to undergo the effects of waterlogging, floodings and marsh formation.

## 2.2 (b)- Climate:

The highest absolute temperatures in South America have been registered in the Chaco. Prohaska (1959) referred to the area encompassed by the 47°C isotherm of absolute maxima as the 'South American Pole of Heat' (Fig. 2.3). Nevertheless, this very hot summer with maxima up to 48.9°C is associated with frosts in winter (Galmarini & Raffo del Campo, 1964). In fact, apart from a narrow fringe in the east and parallel to the major rivers, no point within the Chaco geographical region is free from frosts, their average frequency ranging from nearly 0 in the east to 11.3 days or more in the west (Marlange, 1972). Consequently, there is also an east-west gradient with regard to the



**Fig. 2.3:** The 'South American Pole of Heat', according to Prohaska (1959). Modified from Galmarini & Raffo del Campo, 1964.

lowest absolute temperatures, from  $-1.1^{\circ}\text{C}$  in Corrientes to  $-7.2^{\circ}\text{C}$  in Santiago del Estero. In contrast, the mean annual temperature varies in a north-south latitudinal effect from about  $26^{\circ}\text{C}$  in N Paraguay (Fariña Sánchez, 1973; López Segovia et al., 1988) to  $17^{\circ}\text{C}$  or less in the hills of the Sierra Chaco (Ragonese & Castiglioni, 1970).

The map of Fig. 2.4 shows the isolines of precipitation, extracted from Galmarini & Raffo del Campo (1964). Again there is an outstanding E-W gradient from 1267 mm in Formosa city to 514 mm in Rivadavia, and down to about 350 mm in Catamarca or La Rioja in the extreme W and SW of the Chaco. There is a manifest yearly variation in rainfall, with a strong, marked dry season in winter-spring, and a rainy season from October to April; the length of the dry season increases markedly from E to W, with no dry month in Formosa (Papadakis, 1973) to 6 months with negligible rainfall in Rivadavia in the Salta province, or in Catamarca or La Rioja. In the western limit of the area there is a sudden inversion of the rainfall gradient as a result of the cooling of the warm air masses, which cross the plains and lose most of their humidity in the eastern third as they encounter the first heights in the western border of the Chaco (Pampean Sierras in the S, Subandean Sierras in the N). Thus, there is a moderate increase of rainfall in the Pampean Sierras (owing to their relatively low altitude) from about 500 mm in the nearby plains to over 700 mm, and a more dramatic one along the eastern slope of the Subandean Sierras from the province of Tucumán to the north. In this latter case the first low hills to the east, although not high enough to generate orographic rains, benefit from the effect of the mountains to the west and receive up to 800 or 900 mm/year (Sarmiento, 1972). Further away from the plains height has increased from about 500 m to 2000 m or more, and with it rainfall rises from 900 mm up to 1500 or even 2000 mm (Groeber, 1958). Again there is a marked drop in rainfall in the rain-shadow slopes of the subsequent ranges of mountains, resulting in dry west-facing slopes (700 mm down to 300 mm) as opposed to humid east-facing slopes in the same valleys (up to 1500 mm) (Hueck, 1954; Sarmiento, 1972).

Although the general E-W rainfall gradient of the Gran Chaco is a well-known fact, it is not a gradual and steady decrease. In Table 2.1

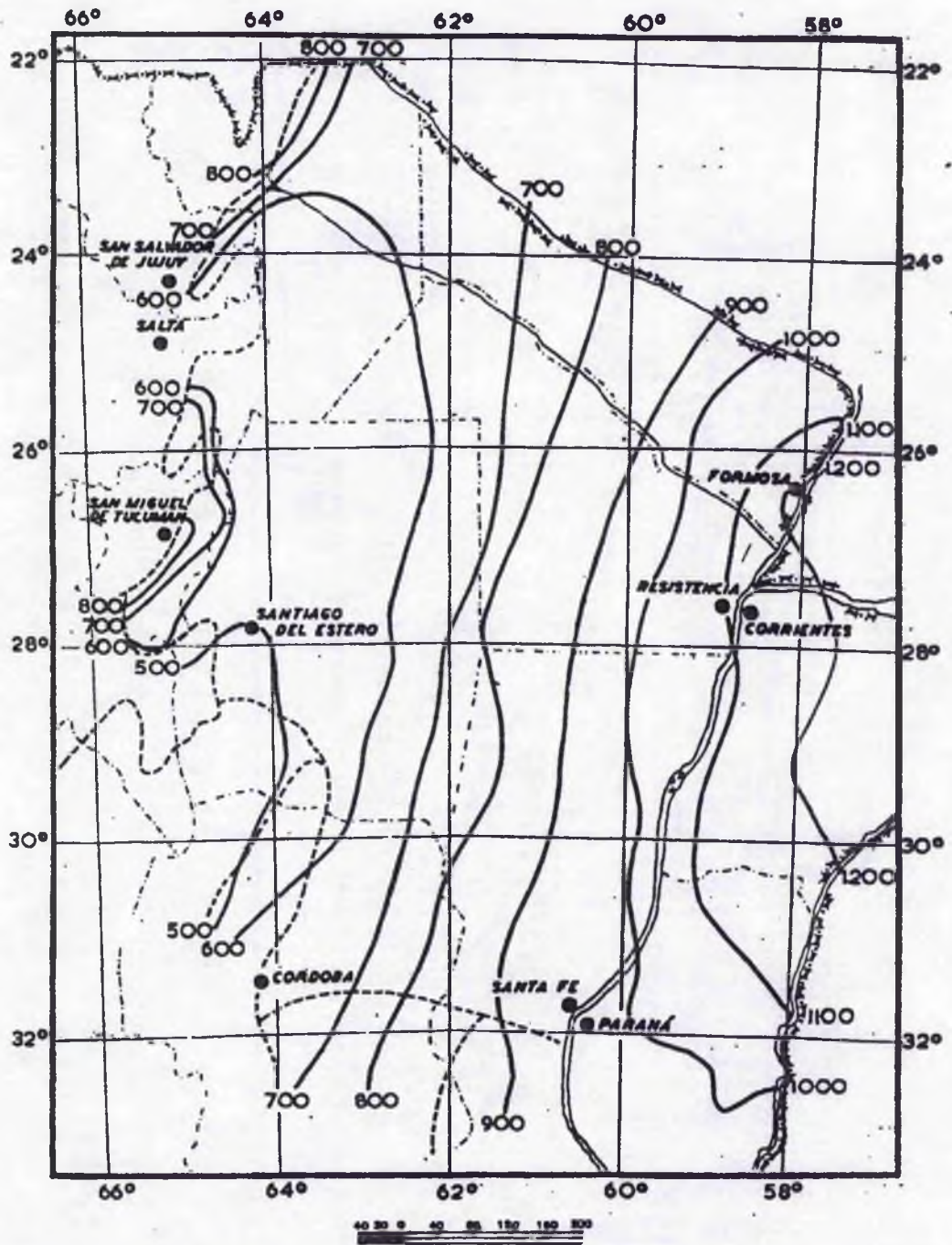


Fig. 2.4: Rainfall isolines for the Argentine Chaco. Modified from Galmarini & Raffo del Campo, 1964.

**TABLE 2.1: Rate of decreasing rainfall (mm/km) in two W-E transects across the Gran Chaco (data from Galmarini & Raffo del Campo, 1964, and Boletta, 1988).**

	WEST				EAST			
	J.V. GONZÁLEZ	RIVADAVIA ING. JUÁREZ	POZO DEL TIGRE	PIRANÉ	FORMOSA			
a) Rainfall (mm/year)	539	514	672	858	1027	1267		
Appr. distance (km)	165.00	107.50	178.75	157.00	100.00			
Decreasing rainfall rate (mm/km)	0.15	-1.47	-1.04	-1.08	-2.40			
b) Rainfall (mm/year)	481	554	580	799	985	1186		
Appr. distance (km)	322.50	142.50	180.00	110.00	100.00			
Decreasing rainfall rate (mm/km)	-0.23	-0.18	-1.21	-1.69	-2.01			

two E-W rainfall transects are shown, with data from Galmarini & Raffo del Campo (1964) and Boletta (1988). In the first case, since the localities are nearly at the same latitude, distances shown are measured on a straight line uniting each pair of localities; in the second case an imaginary line uniting Corrientes with Santiago del Estero was drawn, and distances measured where it intersects with the meridian corresponding to each locality. In both cases the decreasing rainfall rate shows a dramatic fall in the first 100 km of over 2 mm/year for every km to the west, but once deeply within the Chaco, the rate decreases only gradually to reach virtually zero values in the far west of the region.

Potential evapotranspiration decreases southwards from 1150 mm to 900 mm, but increases westwards up to 1200 mm in the centre of western Chaco, to decrease again near the mountainous ranges with very close isolines. A sharp fall in Moisture Index values (*sensu* Box, 1986) from east to west would be expected as a consequence, and this is confirmed by his figures and also by Papadakis' Hydric Index (1973) values across the area. It should be pointed out that the critical MI=1 isoline, the hypothetical boundary between humid and dry climates, when using the Thornthwaite potential evapotranspiration estimate, runs parallel to the meridians and puts most of Eastern Chaco on the humid side (Box, 1986).

### 2.2 (c)- Soils:

The parent materials of the Gran Chaco soils are fine sediments brought in by a æolian or fluvial transportation, or depositions of lacustrine or even Devonian marine incursions sediments. In this context stones and pebbles are of extremely rare occurrence, and rock outcroppings are non-existent. Only a few exceptions occur and always in marginal areas close to the borders and linked to the western mountain ranges. One of the constant features of the soils across the area is their texture, since particles never go beyond 2 mm (Marlange, 1972); this characteristic is not only important because of its mechanical and physical implications, but also because whilst several pedogenetical elements vary from E to W (climate, vegetation), texture remains fairly constant. Thus, the kind of soil present is a direct result of the influence of the prevailing environmental factors, particularly climate.

As a consequence, there is an E-W gradient of climatogenic soil types; according to Bonfils (1970; also Bonfils, in Ragonese & Castiglioni, 1970) well developed Brunizem soils are present in a narrow strip parallel to the river Paraná on high topographic position. Espino et al. (1983) in their description of the soils of northern Santa Fe, and that of Ledesma (1973) for Chaco administrative province, coincide in assigning the most important soils of the eastern area to Brunizem with a clay textural B horizon through illuviation. Further inland, Grumosols and Reddish Chestnuts dominate the landscape, usually with an argillic B horizon, and associated to Planosols and Solonetz together with others of the saline cycle. Towards the centre of the Gran Chaco, Regosolic Chestnuts are common, while in the western third of the region some aridic soils prevail, such as Cinnamon Chestnuts and finally Reddish Browns (Bonfils, 1970), associated with extended Alluvial soils in the NW and massive saline areas in the extreme SW. The Sierra Chaco is generally established on Lithosols in the Pampean Sierras, while in the northern Subandean mountains there are Alluvial soils in the bottoms of dry valleys, Lithosols on dry slopes and Forest Brown on the humid windward slopes (Bonfils, 1970). Vargas Gil & Vorano (1988) classified the Gran Chaco soils according to the 7th Approximation, but this does not alter the E-W gradient; they found typical Hapludols and Argiudols in the extreme east, Argiustols and Haplustols in the central area, and typical Haplustol, aridic Haplustol and aridic Haplustalfs in the west.

Some non-climatogenic soils also occur in the Gran Chaco. The overflowing of rivers, now extinct or severely diminished in their caudal, provided extensive layers of alluvial sediments (Putzer, 1962) to form a series of young and scarcely developed soils such as those in the Alluvial Salta Chaco in eastern Salta province (Adámoli et al., 1972). Alluvial Quaternary deposits also occur in the eastern third of the Formosa province soils. Planosols with a perched water table can be found in depressions all across the Gran Chaco, although hardly perceptible by topographic difference. There are extensive areas with soils of the saline cycle, and due to the arid and semi-arid climate soluble salts are abundant. Thus, Saline, Solonetz and Soloth soils are a common feature in low areas with poor drainage. The abundance of salts provokes an easy dispersion of clay, and the consequent heavy-textured sub-soils are prone to flooding in the rainy season (Beek & Bramaio, 1968).



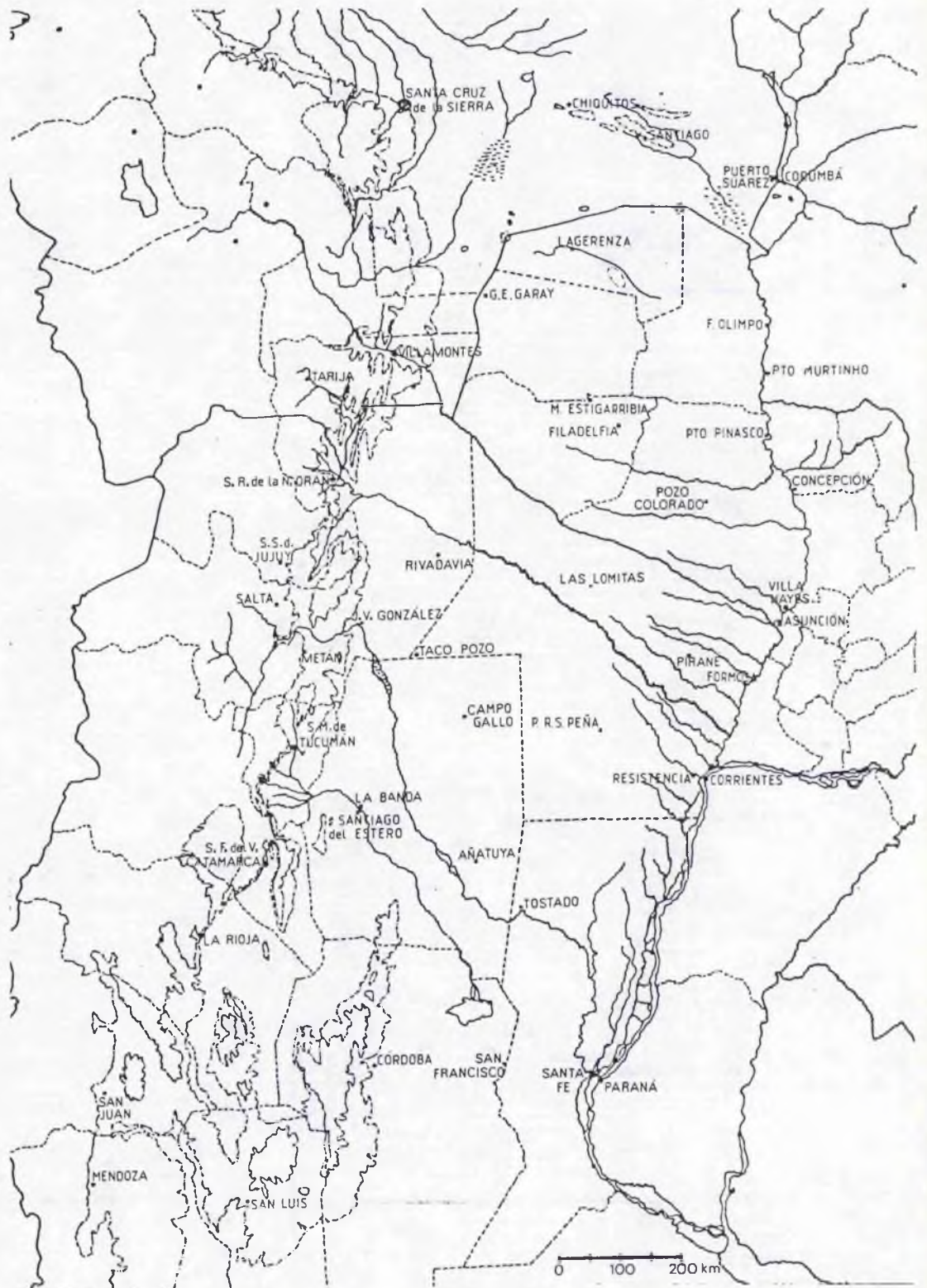
The Gran Chaco soils are poor in organic matter, and the humic horizon is relatively shallow; in the east it can extend up to 20 or 25 cm depth (Espino et al., 1973), but it nearly disappears in the west. Daily maxima temperatures are high even in winter, and this together with environmental dryness and scarcity of protective Graminae facilitates a very quick mineralization of organic residues (Papadakis, 1973). Parent materials and the mainly semiarid climate make mineral deficiencies very improbable, although ant mounds generate very localized sterile spots (Bucher, 1982a). There is usually a calcium carbonate-rich horizon, and nearly all soils give an increasing effervescent reaction to HCl from west to east (Papadakis, 1973). Hardpans of calcium carbonate and silica are frequent in the east of the Chaco. In Papadakis' view, the main set-backs of the soils of the Gran Chaco are poor drainage, salinity and alkalinity, flooding under occasional excessive rainfalls, and the presence of clay textured horizons or even hardpans in places.

### 2.3- Vegetation:

The plant cover of the plains of the Gran Chaco, considering its extension and the several environmental gradients already described, inevitably shows a certain degree of variability, although some general features might remain constant. The analysis will be carried out from east to west so as to follow the major environmental gradients, and it will be mainly focused on the Argentine Gran Chaco, for which there is abundant information coupled with field experience of this author. For the Paraguayan and Bolivian Chaco, and also for the Brazilian sector with allegedly Chaco vegetation, information is scanty and sometimes imprecise, but nevertheless some tentative conclusions can be reached. The geographical range of this study (see Fig. 2.5a & b) extends from the Paraguay and Paraná river valleys in the east to the western mountainous ranges, and from the Santiago and Chiquitos ranges in Bolivia to the peri-steppic Thorn Woodlands (Espinal Periestépico, *sensu* Lewis & Collantes, 1973, and Cabrera, 1976) in the south, which is actually an enormous ecotone-Chaco-Pampa. Morello & Adámoli's (1968) subdivisions of the Gran Chaco will be followed and frequently referred to throughout this chapter, though with more simplified nomenclature. Thus, their 'Chaco de esteros, cañadas y selvas de ribera' along with the 'Chaco de pastizales y sabanas' (see Fig. 2.1)



**Fig. 2.5a:** Political divisions and main geographical features of the Gran Chaco area.



**Fig. 2.5b:** Some critical localities of the Gran Chaco area.

equals what here is called Eastern Chaco; their 'Chaco de parques y sabanas secas' will be referred to as Central Chaco; their 'Chaco leñosa' as Western Chaco; and the 'Chaco serrana' is equivalent to the Sierra Chaco. These equivalents are only used as convenient subdivisional names, but the vegetation or phytogeographical territories ascribed to them by these authors are not necessarily accepted.

In general terms the most peculiar feature of the vegetation of the Chaco consists of the dominance by species of the arboreal genus *Schinopsis*. In the humid, frequently waterlogged eastern plains the predominant species is the simple-leaved *S. balansae*; in the dry and flat plains of central and western Chaco the most important tree is *S. quebracho-colorado*, with imparipinnate, linear-lanceolate, numerous leaflets. In the lower belt of the western Sierras the dominant species is *S. haenkeana*, which closely resembles the former but with ovate leaflets. Their vernacular names - 'quebracho' (from 'quebra-hacha' or axe-breaker) - reflects the hard quality of their tannin-rich wood. Also characteristic are the forests of *Bulnesia sarmientoi* ('palo santo') in western Formosa and eastern Salta, and those dominated by *Aspidosperma quebracho-blanco* ('quebracho blanco') in the plains of eastern Catamarca, La Rioja and San Juan, NW San Luis and W of Córdoba in Argentina (Ragonese & Castiglioni, 1970).

However, forests and woodlands are not the only feature of the Gran Chaco, since savannas are also a very important component of the landscape: *Elionurus muticus* savannas with scattered *Prosopis* spp. trees are common throughout the region; *Spartina argentinensis* savannas, with or without trees, have been extensively studied by Lewis et al. (1990a & b). Palm savannas and palm-tree woodlands of *Copernicia alba* are very important and sometimes dominant in the landscape from the Brazilian Pantanal to NE Santa Fe in Argentina, always on alluvial, seasonally flooded ground under the influence of river systems in the east of the region. Such savannas are not evenly distributed across the Gran Chaco and there is an evident decreasing frequency of savanna physiognomy towards the west, as the subregional names by Morello & Adámoli (1968) clearly show (Fig. 2.1). This is why, as already stated by Morello & Adámoli (1974), it is certainly improper to denominate this region as Chaquenian Park ('Parque Chaqueño'), as employed by Parodi (1945), Cabrera (1953) and Ragonese & Castiglioni

(1970), since although this physiognomy is frequent and in areas dominant, it is not the case for the whole of the Gran Chaco.

A number of woody communities can be found in each sector, some of which are exclusive to it and some others, with minor variants, are roughly the same throughout the three main sectors of the Chaco. In dealing with every sector only the exclusive communities will be described, while the more generalized ones will be dealt with under the heading 'Azonal woody formations'. In Table 2.2 an attempt has been made to fit the main chaquenian woody communities into Beard's (1955) system of vegetation physiognomy, and this is compared with Sarmiento's (1972) nomenclature when available. Since Beard's system was designed for tropical vegetation, the term 'subtropical' should be added before his classes in this table.

### 2.3.1- Gallery Forest:

The islands in the river Paraná, together with the banks of the river Paraguay and their western tributaries, present a peripheral levee ('albardón') above the level of waters except for the flooding season, which is formed by the deposition of coarse materials brought in by the river floods. The vegetation is usually a forest up to 20 m high, which is floristically rich although it is in effect an impoverished version of the Subtropical Rain Forests of Misiones (Argentina), southern Brazil and eastern Paraguay (Cabrera, 1970; Sarmiento, 1972; Klein, 1972; Cabrera, 1976). It comprises up to three tree strata and is rich in lianas, ferns and vascular epiphytes (Ragonese, 1941), and the species not rising above the middle storey are evergreen. This forest is subject to yearly floodings from the nearby rivers and this strongly determines the floristic composition, e.g. as the presence of Lauraceous trees and several other species found only in this kind of community demonstrates (see Ch. 6, Table 6.1 for a typical example). Following the courses of the tributaries such forests may penetrate up to 100 to 150 km into the Gran Chaco plains. Good descriptions of this formation can be found in Burkart (1957a), Franceschi & Lewis' *Forestum Nigrum* (1979), Franceschi et al. (1985) and Eskuche (1986). Morello & Adámoli's (1974, p.108) 'bosque alto o selva de inundación' corresponds to this unit as well.

**TABLE 2.2: Physiognomy classes equivalences for the main woody communities of the Chaco and neighbouring formations.**

	BEARD (1955)	SARMIENTO (1972)
Gallery forest	Semideciduous Seasonal Forest	Deciduous Rain Forest
Selva de Ribera	Semideciduous Seasonal Forest	-----
Austro-Brazilian Transitional Forest	Deciduous Seasonal Forest	Subtropical Deciduous Forest
Quebrachal of <i>Schinopsis balansae</i>	Thorn Woodland	-----
Quebrachal of 3 quebrachos	Deciduous Seasonal Forest/Thorn Woodland	Dry Subtropical Forest
Quebrachal of white quebracho	Thorn Woodland	-----
Quebrachal of 2 quebrachos	Deciduous Seasonal Forest/Thorn Woodland	Dry Subtropical Forest
Palosantales of <i>Bulnesia sarmientoi</i>	Deciduous Seasonal Forest/Thorn Woodland	-----
Arid Chaco Woodland	Thorn Woodland	Dry Subtropical Wood.
South Sierra Chaco	Deciduous Seasonal Forest/Thorn Woodland	Dry Montane Forest
North Sierra Chaco	Deciduous Seasonal Forest/Thorn Woodland	Dry Montane Forest
Algarrobales of <i>Prosopis</i> spp.	Thorn Woodland	-----
Cardonales of <i>Stetsonia coryne</i>	Cactus Scrub	-----
Palmares of <i>Copernicia australis</i>	Seasonal-Swamp Thicket with Palms	-----
Vinalares of <i>Prosopis</i> <i>ruscifolia</i>	Thorn Woodland	-----
'Palo blanco' forest	Deciduous Seasonal Forest	Deciduous Subtropical Forest
'Tipa' and 'Pacará' forest	Deciduous Seasonal Forest	Deciduous Subtropical Forest

### 2.3.2- 'Selva de ribera' (River margin forest), 'Selva' or 'Monte Alto':

This forest can be found side by side with the previous unit but on higher ground, which is never reached even by the extraordinary floods of the Paraná river (Lewis et al., 1987). In the provinces of Chaco and Santa Fe there is a strong erosion scarp 3 m high (Popolizio et al., 1980b) left by an ancient course of the river Paraguay (Popolizio, 1970), and which extends in N-S direction from the cities of Resistencia to Santa Fe and is the effective western limit of the alluvial valley of the river Paraná. It holds an up to 30 m tall forest, locally called 'selva' for its abundance in lianas and epiphytes (Schulz, 1967) and its floristic richness. It is very closely related to the previous unit, with which it is often confused, and most available descriptions have mixed floristic lists (Hauman, 1931; Ragonese, 1941; Hueck, 1972; Sarmiento, 1972; Cabrera, 1976; Reboratti & Neiff, 1986). However, the unique topographical position above the highest possible peaks of floodings, on well developed soils (typical Argiudols, Espino et al., 1983), and the peculiar floristic composition - free from hygrophilous trees such as the Lauraceae, and from inland xerophytic Chaquenian trees - allow for a definitive detachment from the Gallery Forest. To date only Schulz (1967), Morello & Adámoli (1974), and Prado et al. (in press, a) show this forest as a distinct unit; the latter provide not only a floristic list but also a quantitative assessment of this 'bosque subtropical semideciduo' dominated by *Holocalyx balansae*, *Ficus luschnathiana* and *Patagonula americana*. Again this forest is an impoverished version of floristically much richer formations in Brazil (Klein, 1967 & 1972) and Paraguay (Tortorelli, 1967). The floristic composition shown in Table 6.1 is basically the Prado et al. (op. cit.) list, with the addition of those species cited by Morello & Adámoli (1974) which appear further north because of a latitudinal enrichment of this unit.

### 2.3.3- Eastern Chaco Forests (sensu Morello & Adámoli, 1968, see above):

In this area there are two major woody communities which have been repeatedly mistaken for a single one (e.g.: Hauman, 1931; Ragonese, 1941; Hueck, 1959 & 1972; Ragonese & Castiglioni, 1970; Cabrera, 1971 & 1976; Sarmiento, 1972; Marlange, 1972; Cabrera & Willink, 1980; Bucher, 1982a). Although Morello & Adámoli (1974, p. 103) hint at these differences when they refer to the forestal types 'monte alto' and 'monte fuerte', it was not until Lewis & Pire (1981) pointed out their

very distinct topographical position and soil substratum that the matter was settled. These two major subunits are:

(a) Austro-Brazilian Transitional Forest:

This forest corresponds to what Lewis & Pire (1981) denominated 'bosque chaqueño', and the 'monte alto' in Morello & Adámoli (1974). It occupies the highest topographical position in NE Santa Fe, eastern Chaco administrative province and eastern Formosa (Morello et al., 1971), in well developed and intermediate soils (Ledesma, 1973; Espino et al., 1983). Usually two strata can be distinguished, the superior continuous but of variable density. Lianas and epiphytes are frequent but not abundant, and in dense stands shrubs are inconspicuous. The floristic composition suffers an evident N-S temperature gradient, and is much richer in the Chaco and Formosa provinces. The dominant species of this kind of forest are what Hauman (1931) called "elements venus des forets hygrophiles: *Tecoma ipe*, *Patagonula*, *Gleditschia*, quelques Myrtacees...". The simple-leaved 'quebracho' *Schinopsis balansae*, if at all present, is here a foreigner coming from the nearby communities of the next unit, and is usually scarce and in marginal position (Pire, E.F., unpublished data; Lewis, *in litt.*). In Table 6.1 the floristic list is shown, compiled from Lewis and Pire (1981) and the author's field experience for NE Santa Fe; further north in Argentina several other very important species are added to this community, such as *Astronium balansae*, *Diplokeleba floribunda*, *Ceiba speciosa* (Morello et al., 1971; Morello & Adámoli, 1974), or even *Pithecellobium scalare* and others (Cabrera, 1976).

(b) 'Quebrachal' (quebracho woodland) of *Schinopsis balansae*:

Also called 'monte fuerte' in Morello & Adámoli (1974), and 'quebrachal' in Lewis & Pire (1981). This unit is always found at a lower topographical position than the previous one, on heavy-textured soils of the saline cycle, such as typical Natracualf with over 15% of Na<sup>++</sup> in the exchangeable ion complex (Espino et al., 1983). Furthermore, the ground is usually waterlogged in the rainy season because of the strongly argilic subsoil, local microrelief and consequent impeded drainage. Durland (1924) pointed out the close relationship between the Quebrachal and underground water, since it had been consistently established that water originating from subterranean sources within a belt or patch of quebracho-forest is invariably brackish, while beyond the limits of this



community it is invariably fresh (obviously out of the range of sodium-rich soils). Thus the dominant hygrophilous tree species of the Austro Brazilian forest are excluded from this kind of substratum and the forest is dominated by *Schinopsis balansae* ('quebracho colorado chaqueño'), from which this community derives its name. Two arboreal strata can be distinguished, the higher generally composed of *Schinopsis*, *Aspidosperma* and *Caesalpinia* spp., and the lower by Mimosoideae, *Schinus* and *Celtis* spp.. Often the lower stratum comprises only a dense population of young *S. balansae* treelets. The broken canopy allows a shrubby layer which is far more conspicuous than in the previous unit, and Cactaceae are a common feature. In slightly higher areas where the quebracho can generate a dense, continuous canopy, massive spiny Bromeliaceae populations predominate. Lianas and vines are extremely scarce, but the abundance of lichens and epiphytic *Tillandsia* is a typical feature of this formation. The flora listed in Table 6.1 for this forest is a compilation from Lewis & Pire (1981) and the author's field experience.

#### 2.3.4- Central Chaco Forests:

Essentially this sector is transitional to both the Eastern and Western ones; it does not possess a floristic individuality that could characterize its vegetation. However, from an ecological point of view some of the communities to be found here are unique, or nearly so, to this sector, such as the case of the 'quebrachal of three quebrachos' unit. It is in the Central Chaco where the *Elionurus muticus* savannas are more conspicuous and have provided most of the agricultural land. These savannas are mainly determined here by heavy-textured soils with a perched water table (Beek & Bramao, 1968; Bucher, 1982a), whereas in Eastern Chaco they are determined either by strong salinity or by flooding tolerance.

##### (a) 'Quebrachal' of three 'quebrachos':

This unit, treated in detail by Lewis & Pire (1981), is also called 'Bosque Mixto' (Mixed Forest) in Ragonese & Castiglioni (1970). It has been briefly described in Ragonese (1941), Sarmiento (1972), Morello & Adámoli (1974) and Bucher (1982a). This unit is characterized by the shared dominance of *Schinopsis quebracho-colorado*, *Schinopsis balansae* and *Aspidosperma quebracho-blanco*. This is the only area within the Chaco in which the three species occur together in the same

community. This forest, with its definitely more xerophilous character than those in the east, consists of two continuous and dense arboreal strata (Lewis & Pire, 1981), the higher comprising the three dominants plus generally *Ziziphus mistol*, *Caesalpinia paraguariensis* and sometimes *Sideroxylon obtusifolium*. There is a conspicuous shrub layer, while the herbaceous layer is very variable in importance or absent. The floristic composition of this unit for NW Santa Fe (Lewis & Pire, 1981; also Ragonese, 1941, and personal field experience) is shown in Table 6.1.

(b) 'Quebrachal' of white 'quebracho':

Described in Lewis & Pire (1981) and D'Angelo et al. (1987) and also in Morello et al. (1971). Mainly towards the south-east of the sector, but also in localized areas elsewhere within the Central Chaco, the *Schinopsis* spp. disappear and *Aspidosperma quebracho-blanco* takes over dominance. This unit is somewhat lower, with variable density of the arboreal layer; there is a scattered emergent stratum of *A. quebracho-blanco*, from 5 to 8 m high in the south to 8 to 16 m high in the north. The bulk of the forest is in the second stratum, 4 to 5 m high in the south and up to 8 m in northern areas. In the Formosa province this community can be found on slightly elevated areas above the position of the 'vinales' (see) on less alkaline loamy soils (Morello et al., 1971). The floristic composition shown in Table 6.1 has been compiled from Lewis & Pire (1981) and Morello et al. (1971).

### 2.3.5- Western Chaco Forests:

In this part of the region environmental factors such as rainfall are more uniform (Table 2.1), and consequently the vegetation is more homogeneous. Western Chaco is the driest, most continental sector, with the highest maxima and lowest minima in both absolute and average temperature values, longest frost period, and its vegetation shows the most pronounced xeromorphy. Cactaceae are very abundant here, and amongst them the arborescent habit is particularly conspicuous: *Stetsonia coryne*, *Opuntia quimilo*, *Cereus validus*, *Quiabentia pflanzii*, *Pereskia sacharosa*. Lianas and epiphytes are generally extremely rare. There are a number of anthropogenic communities (Morello & Saravia Toledo, 1959a & b), because of both the higher fragility of these semiarid ecosystems and older european colonization. A few endemic genera (*Lophocarpinia*, *Mimoziganthus*,

*Stenodrepanum* , *Setiechinopsis* ) are present as well as numerous endemic species (Ragonese & Castiglioni, 1970) and there is also an important intrusion of species coming from the Monte phytogeographical province (Morello, 1958).

(a) 'Quebrachal' of two 'quebrachos':

This unit of Adámoli et al. (1972) it is also known as 'quebrachal of quebracho-colorado' (Ragonese & Castiglioni, 1970), plain 'quebrachal' by Morello & Adámoli (1968), forests of quebracho colorado and quebracho blanco in Cabrera (1971, 1976), 'quebrachaie' in Marlange (1972). Also described briefly in Castellanos (1958), Hueck (1959, 1972), Sarmiento (1972), Bucher (1982a), and extensively in Morello & Saravia Toledo (1959a & b) and Morello & Adámoli (1974). It consists of a medium-tall forest, 16-18 m high, with a second arboreal stratum 12 m high, and it is the most widespread vegetation unit in this sector. The area dominated by this kind of forest coincides roughly with Ragonese & Castiglioni (1970) 'Santiaguénian District' in their Western Chaco Park, excluding the subdistrict 'Santiaguénian Park' which corresponds to the Central Chaco. It also matches well with the 'Woody Chaco' of Morello & Adámoli (1968). There are other minor communities within the range of this forest, such as the 'iscayantales' of *Mimoziganthus carinatus* and also communities of *Tabebuia nodosa* in depressed localities, which will not be dealt with here. The floristic composition, compiled from Morello & Adámoli (1968) and Adámoli et al. (1972) and the author's experience in the area, is shown in Table 6.1.

(b) 'Palosantales' of *Bulnesia sarmientoi* :

Studied by Morello & Adámoli (1968, 1974), Ragonese & Castiglioni (1970), Hueck (1972), Adámoli et al. (1972), and as 'forests of quebracho colorado and palo santo' in Cabrera, 1971 & 1976. The dominant species, up to 20 m high, is often accompanied by *Schinopsis quebracho-colorado* as a subdominant (Castellanos, 1958) unless the community is on clayish, heavy-textured soils with very impeded drainage and temporary anaerobiosis (Adámoli et al., 1972). The area covered by this unit, with or without the quebracho colorado, is what Ragonese & Castiglioni called the 'Matacoan District', to which some exclusive species pertain: *Jatropha matacensis* , *Lophocarpinia aculeatifolia* . The floristic composition shown in Table 6.1 is taken from Morello et al. (1971), and Adámoli et al. (1972).

## (c) Arid Chaco Woodland:

Also called 'Quebrachales' of *Aspidosperma quebracho-blanco* in Ragonese & Castiglioni (1970) and Sayago (1969). This community appears everywhere within Western Chaco, particularly as a result of overgrazing pressure and selective felling (Morello & Saravia Toledo, 1959a & b), but in the SW of this area it is particularly dominant due to the disappearance here of *Schinopsis quebracho-colorado*. The latter sector corresponds to the 'Llanos District' of Ragonese & Castiglioni (1970) and also to the Arid Chaco Woodland of Sarmiento (1972). Some authors have proposed that this district should be referred to the Monte province on account of the high number of Monte intruders, but both Ragonese (1951) and Morello (1958) have demonstrated the propriety of keeping it within the Chaco. This formation shows an open and scattered arboreal stratum comprising isolated individuals of *Aspidosperma quebracho-blanco*, accompanied by mainly Chaco elements but also some Monte species, as shown by Sayago (1969, p.159) floristic list (Table 6.1).

**2.3.6- Sierra Chaco:**

## (a) South Sierra Chaco (Pampean Sierra Chaco):

In the western fringe of the region the vegetation covering the mountainous ranges of the Pampean Sierras has been considered to be of undoubted chaquenian lineage and physiognomy, despite a number of endemic species in the dominant and subsidiary taxa. The Pampean Sierra Chaco received detailed study by Sayago (1969) and Luti et al. (1979), but further analysis or mapping can be found in Morello & Adámoli (1968), Ragonese & Castiglioni (1970), Cabrera (1971, 1976), Marlange (1972), Sarmiento (1972), Bucher (1982a) and Vargas Gil & Vorano (1988). However, it was inexplicably overlooked by Hueck (1959, 1972) and Hueck & Seibert (1981) although these authors do recognize a very similar formation further north in the Subandean Sierras. Lewis, J.P. (unpublished data) distinguishes three basically different kinds of woody associations within the Pampean Sierra Chaco: a) piedmont Sierra forest, mainly comprising *Prosopis* spp.; b) 'quebrachal' of *Schinopsis haenkeana* in middle-slope; c) 'mollar' of *Lithraea ternifolia* on the slopes above the quebrachal and below the shrublands of *Flourensia* or *Heterothalamus* spp., and also in the south of this sector where *S. haenkeana* disappears (Lewis & Pire, 1981). The floristic list of

what Sayago (1969) qualified as the most typical Sierra Chaco forest is included in Table 6.1.

(b) North Sierra Chaco (Subandean Sierra Chaco):

A rather more contentious issue is raised by the entity referred to as the Subandean Sierra Chaco. Some authors have apparently merged this unit with the so-called Transitional Forest (Morello & Adámoli, 1968; Ragonese & Castiglioni, 1970), whereas others (Hueck, 1959 & 1972; Cabrera, 1971 & 1976; Marlange, 1972; Adámoli et al., 1972; Sarmiento, 1972) have separated them, a treatment favoured here since floristic composition clearly links the Subandean to the Pampean Sierra Chaco (cf. Marlange, 1972, list for the Lomas de Olmedo area in Table 6.1). Because it only occupies a small area and interdigitates with the several neighbouring phytogeographical provinces, this forest has been generally omitted from vegetation maps with the exception of Vervoorst's detailed regional map in Hawkes & Hjerting (1969, p. 38).

### 2.3.7- Azonal woody formations of the Chaco:

(a) 'Algarrobales' - *Prosopis* spp. communities:

These thorn woodlands, also called 'raleras' (Morello & Adámoli, 1974), are found throughout the Chaco proper in low lying areas. In E Chaco, if the topographic gradient is followed down from the *Schinopsis balansae* 'quebrachales' towards a high water table, the first species to disappear is *S. balansae*, followed by *Caesalpinia paraguariensis* and most of the accompanying species of the 'quebrachal', until the arboreal stratum is reduced to mainly *Prosopis nigra* or *P. alba* dominated stands. These 'algarrobales' are common around seasonal swamps or small, somewhat undefined streams; the soil is regularly flooded in the rainy season mostly by overflow from the adjacent water courses. When the flooding recedes, the salinization process of soils is resumed, resulting generally in typical Natracualf or Natracuol (Espino et al., 1983). The arboreal stratum may be very simple: *P. nigra*, *Geoffroea decorticans*, *Aspidosperma quebracho-blanco* and *Acacia caven*, and is continuous and often dense and just over 3 m high (Lewis & Pire, 1981). There is no well defined shrub layer, and during the dry season the herbaceous layer has very low coverage or is absent altogether. Further north in the Formosa province (Morello et al., 1971) the 'algarrobales' show a much richer composition as shown in Table 6.1.

(b) 'Cardonales' of *Stetsonia coryne* :

This kind of low-height formation is scarce in Eastern Chaco (Lewis & Pire, 1981), but much more frequent in Western Chaco (Sayago, 1969). It is dominated by candelabra-like individuals of the monotypic Cactaceous genus *Stetsonia*, endemic to the Chaco, and usually 60% or more of the strongly saline soil is bare ground or it is covered only by mosses and *Selaginella sellowii*. The stands are very poor in the east, but a much richer western one is listed in Table 6.1 from Sayago (1969). Similar communities are described by Adámoli et al. (1972), and *sub* 'peladares' by Ramella & Spichiger (1989) for Paraguay.

(c) 'Palmares' of *Copernicia alba* :

These palm groves and savannas usually comprise a nearly monospecific open arboreal layer of very variable density, 8 to 10 m high, of this fan-leaved palm-tree. They are always found in low lying position close to or within marshes, on seasonally flooded alkaline soils (Ragonese, 1941; Ragonese & Castiglioni, 1970). The herbaceous layer is dominated by *Spartina argentinensis*, though sometimes *Paspalum* spp. might replace it (Lewis & Pire, 1981). Additional information can be found in Markley (1955), Hueck (1959, 1972) and Dahlgren & Glassman (1961); references for Paraguay in Fiebrig (1933), Rojas & Carabia (1945), Tortorelli (1967), Esser (1982), Spichiger & Ramella (1989) and Ramella & Spichiger (1989). Citations of this community in the Bolivian Chaco in Werding (1976), and for Brazil in Veloso (1947), Prance & Schaller (1982) and Ratter et al. (1988b). The more complete floristic lists of these 'palmares' available to date refer to the Argentine Chaco, such as those in Cabrera (1976) and Lewis & Pire (1981) for the Eastern Chaco shown in Table 6.1, together with the author's field experience; the 'palmares' in Western Chaco show a somewhat different composition (Morello & Saravia Toledo, 1959a; Cabrera, 1971, 1976; Adámoli et al., 1972), and it is also provided in Table 6.1.

(d) 'Vinalares' of *Prosopis ruscifolia* :

In Central and Western Chaco the areas under the influence of the only three rivers running across the Gran Chaco are ecologically very unstable; the lack of energy of these flat plains generates a wide divagation of the water courses, and subsequently creates new open spaces to be colonized, especially alkaline swamps in dessication (such as

drying-out abandoned ox-bows). *Prosopis ruscifolia* is particularly adapted to this kind of environment and successfully colonizes large expanses of land, even forming virtually monospecific communities with no herbaceous layer and where the shrub stratum is the only one to add some variability. There is a host of different facies for these woodlands according to relative degrees of flooding, salinity or anthropogenic influence, as studied proficiently and extensively by Morello et al. (1971). In Table 6.1 the floristic composition of a typical 'vinalar' is provided.

### **2.3.8- Subandean Piedmont Forests** (usually known as Transitional Forests):

These forests occupy a narrow strip between the dry forests of Western Chaco and the more humid Lower Montane Forest (Sarmiento, 1972) or 'Distrito de las Selvas Montanas' (Cabrera, 1976), extending in a meridional fashion from the area of Santa Cruz de la Sierra in Bolivia to slightly south of the limit Tucumán-Catamarca provinces in NW Argentina. Their very peculiar position as a wedge between two major phytogeographical units (the Chaco and Yungas provinces, *sensu* Cabrera, 1976), at an intermediate altitude (350 to 500 m in Cabrera, 1976, or 450 to 900 m in Meyer, 1963), and also with intermediate rainfall figures (from 700 to 1000 mm) of monsoonian character (Vervoorst, 1982), allows for a particular kind of forest to develop with its own floristic identity. According to Sarmiento (1972) this formation has the highest proportion of deciduous species (79 %) of all the subtropical seasonal forests. They are located in the piedmont area of the Subandean Mountains in SW Bolivia and NW Argentina (hence their name), but their southernmost extension is actually placed in the northern extreme of the Sierras Pampeanas in S Tucumán and E Catamarca.

Towards the east and down the topographic gradient these forests intermingle with Sierra or Western Chaco, whereas to the west and uphill they receive some elements from the Yungas forests. Some authors have regarded the Transitional Forests as having more in common with the Chaco area than with the Yungas (Hueck, 1959 & 1972; Morello & Adámoli, 1968; Ragonese & Castiglioni, 1970; Marlange, 1972; Hueck & Seibert, 1981; Vargas Gil & Vorano, 1988). However, leaving aside the negligible ecotonal areas with Chaco proper, their floristic composition clearly puts them within the Yungas or Tucumanian-Bolivian Forests province (Hauman, 1931; Meyer, 1963; Cabrera, 1971,

1976). Correa Luna (1955) describes a locality in which Piedmont Forest occurs side by side with Chaco scrubland, but their elements do not intermix at all: at this site there is a relatively dry valley, the lower plains of which are covered by *Acacia* spp., *Prosopis* spp., *Geoffroea decorticans*, *Celtis spinosa*, *Opuntia* sp. and *Cereus* sp., while small elevations within the range of this valley hold *Anadenanthera colubrina* var. *cebil*, *Pterogyne nitens*, *Ceiba chodatii*, all species which can also appear in the tall humid forests on the nearby mountains bordering the valley. Species of the genera *Schinopsis*, *Caesalpinia*, *Cercidium* do not appear in the valley, since they belong to less elevated grounds (i.e. the Chaco plains).

There are two major types of forests within this unit, ordered in N-S direction by a temperature gradient, and separated by a gap dividing the mountainous ranges (Vervoorst, in Hawkes & Hjerting, 1969, p.38) which allows the intrusion of Chaco communities into the inner dry valleys (e.g. the Lerma valley):

(a) 'Palo blanco' forest:

This unit takes its name from its most conspicuous dominant, the elegant Rubiaceae tree *Calycophyllum multiflorum*. Also known as 'Übergangswalder' in Kanter, 1936; 'Forest with *Calycophyllum multiflorum*' in Hueck, 1954, 1959 & 1972; 'High Mesophytic Forest' in Coro, 1956; 'Palo blanco and Palo amarillo' forest in Cabrera, 1971 & 1976; 'Paloblancal' in Sarmiento, 1972; 'Bosque Húmedo Templado' in Unzueta, 1975 (p. 218). It was briefly studied by Frenguelli & Cabrera (1938), Meyer (1944), Adámoli et al. (1972) and Marlange (1972), and mapped by Hueck (1954), Vervoorst (in Hawkes & Hjerting, op.cit.), Unzueta (1975), Hueck & Seibert (1981), and Vargas Gil & Vorano (1988). Unfortunately, and despite the apparent wealth of references, this forest is one of the least known vegetation units in Argentina, a fact also pointed out by Unzueta (1975, p.223) for Bolivia. Placed on good agricultural soils, and located along the corridor of the early Spanish colonization, it was cleared or well-logged before any settlement was established in, for example, neighbouring Chaco forests. The present day information on this forest is therefore extremely scanty and patchy, and although some relictual stands seem to remain in NW Argentina and in Bolivia, a thorough phytosociological study has never been carried out.



In NW Argentina this unit reaches 30 m high, with white straight boles up to 1 m diameter mainly of 'palo blanco' (*Calycophyllum multiflorum*) and 'palo amarillo' (*Phyllostylon rhamnoides*). A shrub layer of about 2 m high makes transit very difficult, together with abundant lianas, vines and epiphytes (Cabrera, 1976), which are completely absent from the nearby dry Chaco forests. The floristic list of Table 6.1 has been compiled from Meyer (1944), Coro (1956), Adámoli et al. (1972), and Cabrera (1976).

(b) 'Tipa' and 'Pacará' forest:

This is a latitudinally impoverished version of the previous unit, deprived of the two major dominants ('palo blanco' and 'palo amarillo'). It underwent a complete destruction by human activity, as pointed out by Hauman in 1931, and nowadays sugar cane fields and citrus orchards are found instead. Paradoxically the 'tipa' (*Tipuana tipu*) and 'pacará' (*Enterolobium contortisiliquum*) forest is somewhat better known than the previous unit, with brief descriptions to be found in Hauman (1931), Hueck (1954, 1959, 1972), Meyer (1963), Digilio & Legname (1966) and Cabrera (1971, 1976). A complete phytosociological survey of a stand, itself transitional between these two subunits, was performed by Brown et al (1985) *sub* 'selva de quina y cebil'. Its floristic composition is shown in Table 6.1, compiled from some of the aforementioned references.

### 2.3.9- The Brazilian Chaco problem:

A number of phytogeographical accounts and vegetation maps of South America depict a narrow wedge of so-called Chaco vegetation, entering into Brazil in SW Mato Grosso do Sul state as a continuation of the main area in Argentina, Paraguay and Bolivia (Fig. 1.1). The alleged presence of Chaco forests in that area has been reported by diverse authors, e.g. Hueck (1955, 1959, 1972), Morello & Adámoli (1968), Ragonese & Castiglioni (1970), Cabrera & Willink (1980), Hueck & Seibert (1981), Bucher (1982a), Prance & Schaller (1982), Adámoli (1982), Eiten (1983), Ratter (1984), Allem & Valls (1987), and Ratter et al. (1988b). The first phytogeographer to report 'bosques chaquenhos' within Brazil was Hueck (1955), and he included a map showing the extent of the Chaco intrusion in Mato Grosso, which has been followed by all subsequent workers. However, Prado et al. (in press, b) carried out a survey in the spur of Chaco in Brazil in 1989, on the basis of which they segregated the

vegetation into five major woody communities: a) *Diplokeleba -Tabebuia - Capparis* scrubland; b) *Schinopsis balansae* parkland; c) *Aspidosperma - Mimosa* scrubland; d) Calcareous woodland; e) Chaquenian forest at Porto Murtinho (see Table 6.1 for their floristic composition).

The latter community is the only one they accept as truly chaquenian, with about 70% of Chaco elements s.s. between both dominant and accompanying species. The first three communities are regarded as transitional, since they comprise only a minority of chaquenian elements together with cerrado and semideciduous forest species. Finally, the *Schinopsis brasiliensis* -dominated calcareous woodlands are absolutely non-chaquenian, both in physiognomy and floristic composition, and some of its elements can be found elsewhere in South America in formations such as the Caatingas in NE Brazil, the Yungas of Bolivia and Argentina (particularly in the so-called Transitional forests), and the subtropical forests on both banks of the rivers Paraguay and Paraná (Prado et al., in press, b). No trace was found in the studied area of *Schinopsis quebracho-colorado*, although this should be a very frequent and dominant tree according to Hueck (1955), and these authors conclude that a case of mistaken identity with *S. brasiliensis* misled Hueck. Thus, the extent of the Chaco ingression into Brazil, which is a meeting place for three different floristic stocks, is dramatically diminished, now restricted to a reduced area around Porto Murtinho, far less than previously thought and hardly mappable on a continental scale.



**Plate 2.1:** Some aspects of the Chaco vegetation. **Top:** scrub dominated by Mimosoideae in Quimilí, Santiago del Estero, Arg. **Center:** *Elionurus muticus* savanna in NW Santa Fe, Arg. **Bottom:** *Schinopsis quebracho-colorado* forest in Quimilí.

### 3. THE CAATINGAS VEGETATION

The Caatingas province in NE Brazil extends from 2° 54' S to 17° 21' S (ca. 850,000 km<sup>2</sup>), and includes the states of Ceará, Rio Grande do Norte, most of Paraíba and Pernambuco, SE Piauí, W Alagoas and Sergipe, north and central Bahia, and a wedge extending into Minas Gerais following the São Francisco river together with an outpost in the dry valley of Middle Jequitinhonha river (Fig. 1.1). Fernando de Noronha island should also be included (Andrade-Lima, 1981). The name 'caatinga' is of Tupí-Guaraní amerindian origin and is usually taken to mean 'white forest'<sup>1</sup>, which certainly well characterizes the aspect of the vegetation in the dry season, when all leaves have been shed and only the bright white trunks of trees and shrubs are left in a desiccated landscape. Martius referred to the Caatingas as *Hamadryades* or the descriptive phrases '*silva horrida*' or '*silva aestu aphylla*', the latter ('the forest leafless in summer') following local custom in treating the rainy season of the Caatingas as 'winter', although it actually coincides with the summer solstice.

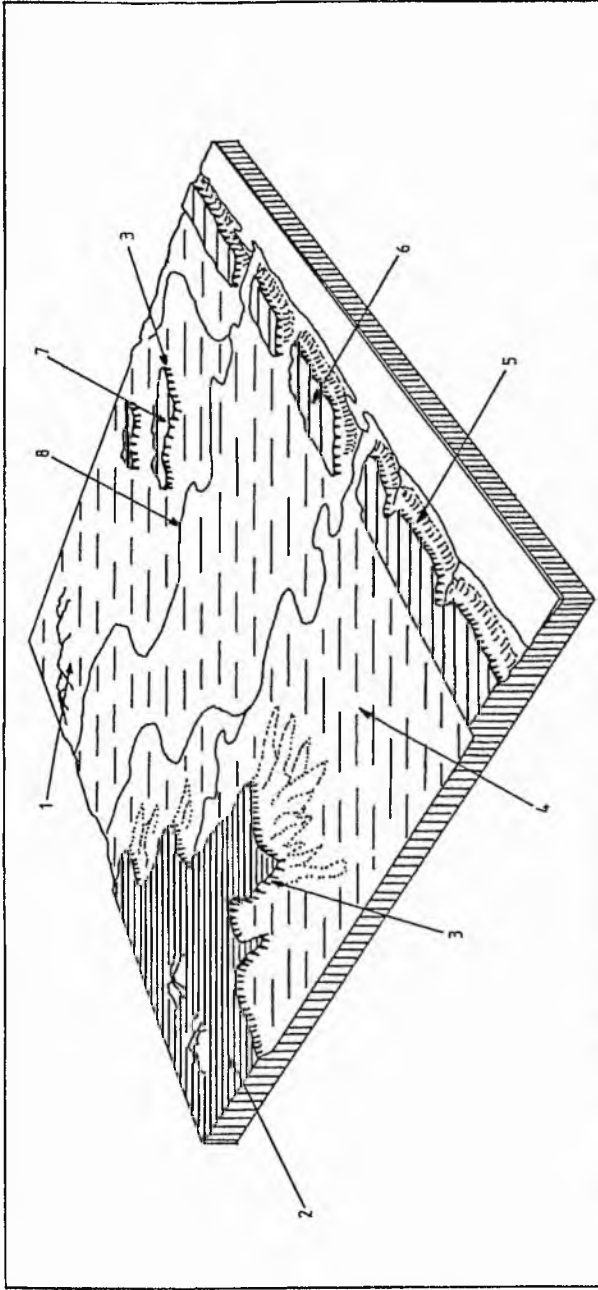
Unfortunately, the name 'caatinga' has also been widely used for the geographical region of NE Brazil, and this has given rise to some confusion, as with the similar use of the word 'Chaco' (Castellanos, 1960). The concept of the Caatinga Region includes areas such as the Chapada do Araripe, with cerrado vegetation, or the wetter sectors of the 'brejos' of Pernambuco, with rain or cloud forests, and excludes areas which, although floristically part of the Caatingas vegetation, are not considered to be in the geographical region, such as the dry valley of the Jequitinhonha river in Minas Gerais or certain parts of the Rio Grande basin in W Bahia. It should also be emphasized that the phytogeographical concept of the Caatingas used here does not include Amazon Caatingas, which are a floristically unrelated kind of white-trunked forests restricted to extremely dystrophic white sands in the Amazon region. Following Andrade-Lima (1966a) it is accepted that the province should be called 'the Caatingas', in plural, since it includes several different physiognomies of vegetation and numerous facies,

<sup>1</sup> The Tupí-Guaraní etymology consists of the particles *ca'a*, plant or forest; *ú*, white (derived from *morotí*, white); and the suffix *'ngá* (from *angá*), resembling, near to (Peralta & Osuna, 1952). Thus, "the whitish forest".

which are generally referred to as 'caatinga' plus either a vernacular or technical epithet (e.g. arboreal caatinga).

### 3.1- Geology and geomorphology of the Caatingas:

In the Brazilian northeast most of the Caatingas vegetation areas are located on intertableland depressions (Ab' Sáber, 1974, *sub* 'depressões interplanálticas'), but some localized exceptions occur, such as the low 'chapada' (tableland) of Raso da Catarina (Bahia), the Borborema range in Paraíba, or the Apodi plateau in Rio Grande do Norte where Caatingas vegetation is found not only in the depressions but also on the highlands (Andrade-Lima, 1981). In the main, however, this province extends over undulated pediplains (Andrade & Lins, 1965, p.21), dissected from Cretaceous or Tertiary sediments covering the underlying Pre-Cambrian Brazilian Shield (Cole, 1960). A massive process of pediplanation took place during the late Tertiary and lower Quaternary (Ab' Sáber, 1974) to uncover the present-day surface of Pre-Cambrian crystalline rocks (gneiss, granites and schists), and leaving only isolated relics of the younger surfaces scattered throughout the Caatingas. These remnants are referred to as inselbergs (such as those in Quixadá - Ceará, and Patos - Paraíba), 'serras', or 'chapadas', in order of decreasing erosion. Thus, the 'chapadas' usually still show the complete features of the original Tertiary sedimentary sandstone surfaces, whilst the 'serras' indicate a more advanced stage of the process of pediplanation and the inselbergs are the last remains yet to be eroded away. In general their vegetation varies accordingly, with cerrado vegetation on top of the Tablelands (such as the Chapada de Araripe and the coastal 'taboleiros'), semideciduous or evergreen wet forests on top of the 'serras' (such as the 'brejos' of Pernambuco; see Andrade-Lima, 1964b, and Andrade & Lins, 1964), and dry forests or arboreal caatinga formations on the slopes and on the inselbergs (Fig. 3.1, modified from Cole, 1960). There are also some sedimentary areas within the Caatingas, such as those in Rio Grande do Norte - coastal areas and the river Mossoró basin (Andrade-Lima, 1964c), and in Bahia the Raso da Catarina and sectors under the influence of the São Francisco river.



**Fig. 3.1:** Relationship between vegetation and geomorphology in NE Brazil (redrawn from Cole, 1960). 1: caatinga forest on slopes of serras; 2: cerrados on Sul-Americana surface; 3: caatinga scrub or dry forest on escarpment slopes; 4: caatinga scrub on Paraguaçu surface; 5: rainforest covering dissected terrain of coastal zone; 6: cerrado on coastal taboleiros; 7: cerrado on remnants of Velhas surface; 8: forests following stream courses.

As a result of this genesis of the Caatingas substratum the soils are stony and shallow, with a scarcely decomposed bedrock at about 1 m deep, and very frequent massive rock outcroppings (Tricart, 1961; Ab' Sáber, 1974). The slightly undulated, hilly country so characteristic of the 'sertão', has originated in the process of pediplanation following two main types of erosive processes (Tricart, 1961): millimetric exfoliation, peculiar to this province and only some millimetres deep which results in abundant sand taken away by run-off waters to the foot of the pediments, fashioning the inclined plains typical of the topography of the semi-arid NE Brazil; and metric exfoliation, about 1 m deep and exploring fissures parallel to the surface, yielding large boulders found at the foot of inselbergs and crystalline mounds.

The morphogenetical action of run-off water takes three main forms in the Caatingas (Tricart, 1961): a) in crystalline hills with abundant naked rock there is an immediate quick drainage of rainfall, with scarcely any mechanical effect but mostly chemical corrosion; b) diffuse drainage along the pediments, the run-off water carrying away the finest particles (clay, silt, fine sand) and leaving behind coarse sand, gravel and stones to conform the characteristic extensive detrital pavements ; c) concentration of run-off waters downstream of the inclined plains, where they join to cut small valleys with temporary drainage. The hydrography of the region consists of seasonal intermittent watercourses with exorheic drainage (Ab' Sáber, 1974); in drier years the rivers in the affected sectors become sporadic or ephemeral. Such rivers flow during the rainy season, but gradually disappear subsequently, and during this annual terminal phase the rivers seem to receive a residual feeding from the, at the time, full water table; no sooner have the rains ceased than a hydrological inversion takes place, this phenomenon being responsible for the disappearance of the watercourses: the river feeds back to the water table and dries away until the next rainy season.

It has been postulated that during the Quaternary the Caatingas did not undergo the marked climatic changes which affected other areas of Brazil (Cailleux & Tricart, 1959). The only evidence of a Pleistocenic fluctuation has been provided by certain localized layers of rough pebbles which seem to be the product of a more torrential regime.

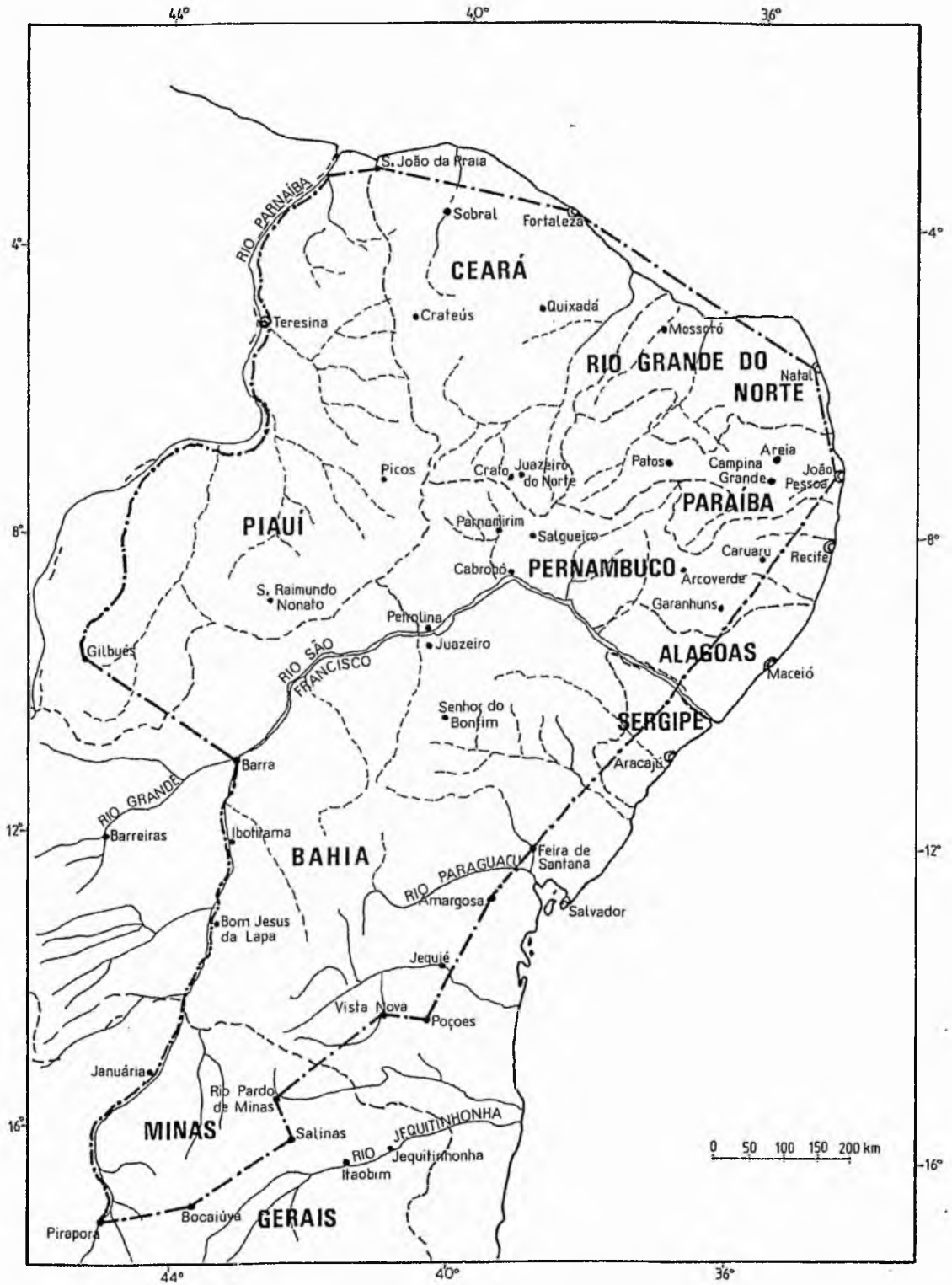
However, evidence accumulated recently indicates that NE Brazil had an even drier climate during certain periods of the Quaternary, originating the palæodune fields of Xique-Xique, Bahia (Ab' Sáber, 1977a; Tricart, 1985). These æolian formations must have originated when the aloctonous São Francisco river, the only major perennial river to cross the Caatingas, dried up in its middle course (probably close to the locality of Barra, Bahia) and the sandy and loamy alluvial sediments previously spread in the area were shaped into dunes by mainly easterly winds (Tricart, 1985). It is supposed that the middle São Francisco and its tributaries are presently at a climatic limit of exorheism, and that any serious and permanent fall in precipitation will result in endorheic conditions (Tricart, 1985) with subsequent increase in salinity.

### 3.2- Climate:

The semiarid Caatingas, compared to other Brazilian formations, hold most of the extreme values amongst the meteorological parameters: highest solar radiation, lowest cloudiness, highest annual average temperature, lowest percentages of relative humidity, highest potential evapotranspiration, and above all the lowest and most irregular precipitations, limited in most of the area to a very short period of the year (Reis, 1976). Catastrophic phenomena are very frequent, namely droughts and floodings, which have undoubtedly shaped the peculiar plant and animal life of the Caatingas. However, it is the scarcity or complete absence of rainfall in some years which mostly characterizes the region, rather than the rare local occurrence of double or even triple level of precipitation (Nimer, 1972). In an attempt to coordinate the study of the cyclic droughts successive laws have been passed by the Brazilian government to delimit the so-called 'Polygon of Droughts' (Polígono das Secas), which now roughly coincides with the phytogeographical province of the Caatingas (Fig. 3.2).

The semiarid nature of this area results mainly from the predominance of stable air masses pushed from the SE quadrant by the Trade Winds, which have their origin in the the action of the South Atlantic Anticyclone. The entire eastern coastal Brazil consists of a narrow strip of lowlands behind which there is a range of mountains extending from Rio Grande do Norte to Rio Grande do Sul: the Serra do Mar. When the water-vapour laden Atlantic Equatorial air masses are

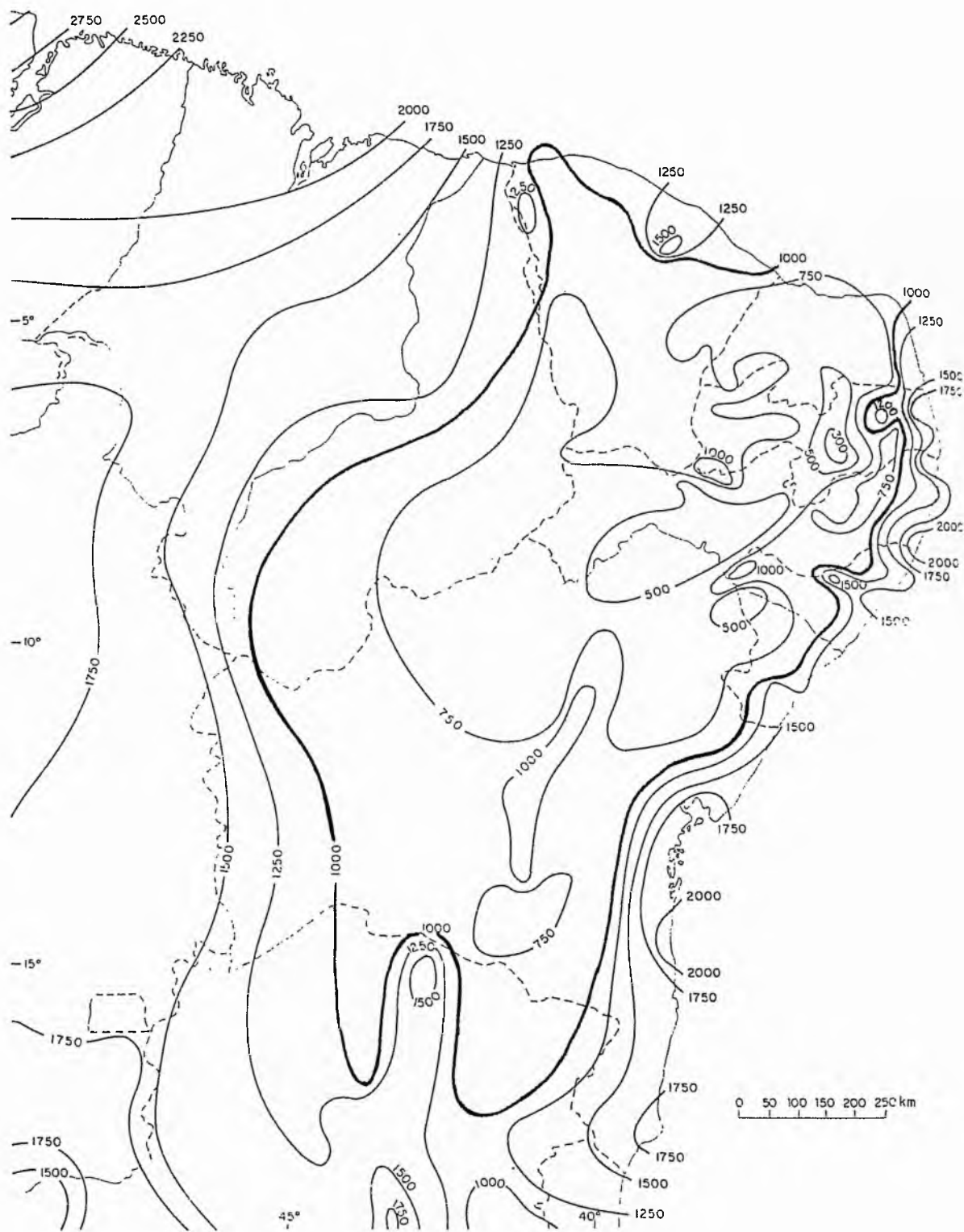




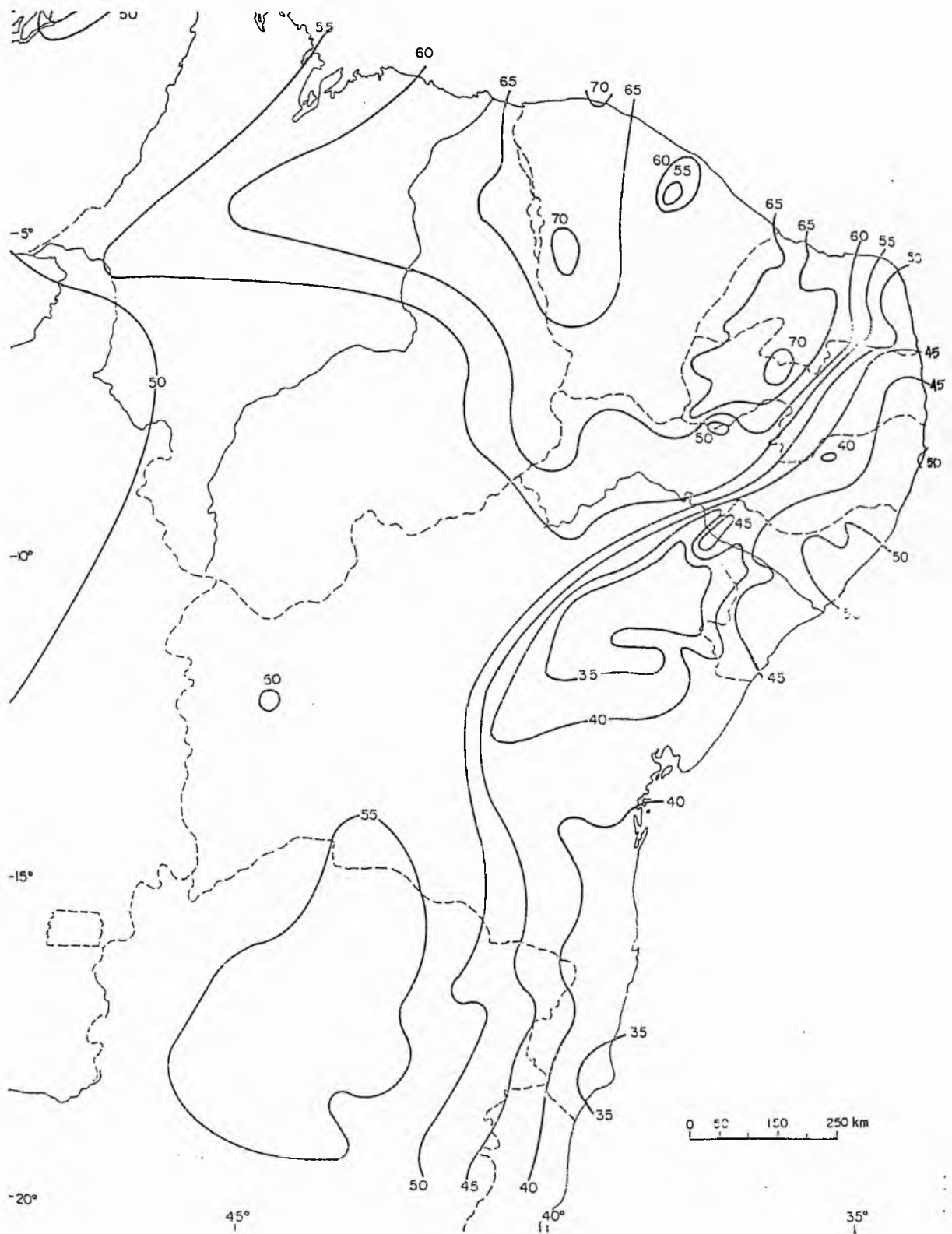
**Fig. 3.2:** The 'Polygon of Droughts' of NE Brazil. Redrawn from Andrade-Lima, 1981.

carried by the Trade Winds against the coastal ranges in NE Brazil, they are adiabatically cooled and precipitate annually *ca.* 2000 mm of rainfall. This is the area of the Coastal Atlantic rainforests, where the Atlantic Equatorial System loses most of its humidity, while on the rain-shadow of the mountain ranges the Caatingas lie under the effect of dry, stable air masses (Andrade & Lins, 1965). It is only when the latter encounter some of the few elevations left behind by the pediplanation process that the 'brejos' phenomenon takes place as humid islands within a semiarid region (Andrade-Lima, 1964b; Andrade & Lins, 1964), since again the air mass is raised and cooled, and deposits there its remaining water. The low pressure zone known as Intertropical Convergence or Intertropical Front, where Trade Winds of both hemispheres meet, lies roughly parallel to the Equator at about 10° N. During summer this line of encounter moves south of the Equator, bringing high instability to the weather of the northern half of the Caatingas from February to April, which is the rainy season for most of NE Brazil. The Continental Equatorial humid mass originates over Amazonia, producing there very heavy convective showers, and it can reach W Caatingas from November to January particularly when allied to the southward displacement of the Intertropical Convergence. Thus, the rainy season follows a sequence from November to January in the west and southwest, to February to April in the north and northeast, depending on the penetrations of two unstable humid masses coming from the north and west, and on their ability to displace a stable, dry mass brought in by the Trade Winds. Catastrophic droughts happen when the former are unable to reach the Caatingas because of the latter (Andrade & Lins, 1965; Reis, 1976).

It has been shown elsewhere (Nimer, 1972; Reis, 1976; Andrade-Lima, 1981) that the generally accepted phytogeographical concept of the Caatingas coincides roughly with the 1000 mm rainfall isohyets (Fig. 3.3). About 50 % of the area receives less than 750 mm, while certain localized sectors have under 500 mm, such as the Raso da Catarina, together with much of central Pernambuco and central Paraíba (Fig. 3.3). However, it is not the total amount of yearly rainfall that matters most, but rather the yearly distribution and deviation of the mode. Figure 3.4 shows that nearly all of the area under study suffers a concentration of 50 to 70 % of rainfall in three consecutive months, thus constituting a very strong seasonal climate. Throughout the area the



**Fig. 3.3:** Rainfall isolines for NE Brazil (1000 mm isohyet highlighted).  
Modified from Nimer, 1972.



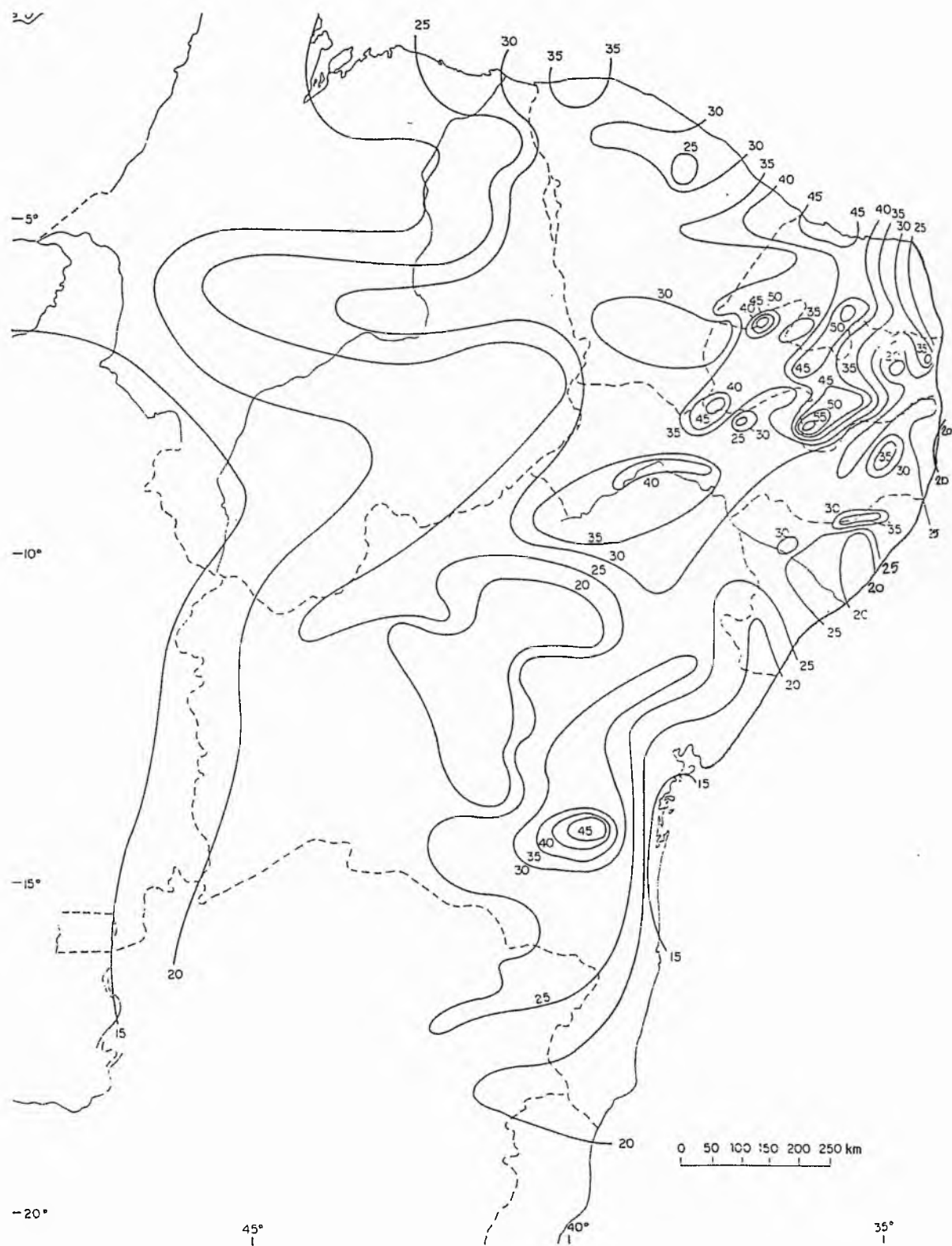
**Fig. 3.4:** Percentage of rainfall concentration in three consecutive months in NE Brazil. Modified from Nimer, 1972.

length of the dry season is very variable, ranging from two to three months in wet 'brejos', through six to nine months in most of the region, and up to 10-11 months in Raso da Catarina (Nimer, 1972). In general the dry period increases from the periphery to the center of the 'sertão' (Nimer, 1972; Nishizawa, 1976). The most characteristic feature of this climate is the extreme irregularity of rainfall from year to year such that the average yearly deviation expressed as a percentage ranges from 20 - >50 % (Fig. 3.5). Furthermore, those sectors with higher rainfall deviations are linked in general to those with a lower yearly total, with higher concentration in three months and consequent longer dry period (Nimer, 1972). However, since this deviation is an average figure, it does not show how marked is the irregularity. Thus, in Table 3.1, rainfall figures for Sobral, Ceará, during the period 1934-52 show an extraordinary range from 363 to 1348 mm (data from Guerra, 1955).

No frosts have ever been registered in the Caatingas, and the lowest temperatures (4°C) within the region occur as an effect of altitude in some 'serras' (Fig. 3.6). On the other hand, the average absolute maxima are rarely over 40°C (Fig. 3.7), and they are mainly restricted to the driest sectors (lower São Francisco river, and the Jequitinhonha river valley in Minas Gerais), whilst in wetter areas outwith the Caatingas such as Pará or Goiás states temperatures over 40 or 42°C are far more frequent (Nimer, 1972). However, very high mean annual temperatures are another characteristic feature of the 'sertão' (Reis, 1976), with values ranging between 26 and 28°C (Nimer, 1972), although all areas over 250 m of altitude have lower mean temperatures (20 - 22°C).

### 3.3- Soils:

In Section 3.1 the morphogenetical factors which give rise to the present soils of the Caatingas were explained with regard to parent material (crystalline Pre-Cambrian rocks and localized sedimentary sectors). The rock surfaces that must generate the subsequent soils under weathering action are alkaline, but rainfall water produces a dissolution of the bases which are leached away and then an acidic microenvironment is created. The formation of clays starts in weathering rock, but the prevailing pH (due to the presence or absence of bases) will determine its nature; in acidic environment kaolinite is formed, while montmorillonite will predominate if rainfall is insufficient



**Fig. 3.5:** Percentage of average yearly rainfall deviation in NE Brazil. Modified from Nimer, 1972.

TABLE 3.1: Rainfall data for Sobral, Ceará (Brazil), during the period 1934-1952. Modified from Guerra, 1955.

YEAR	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
1934	71.7	258.8	325.8	284.3	120.7	75.5	0.1	-	4.0	-	10.4	51.6	1202.9
1935	37.1	266.8	204.9	313.3	143.1	84.9	3.6	-	-	-	-	1.7	1105.4
1936	20.4	97.4	67.6	66.1	92.6	22.5	-	-	-	0.1	-	-	366.7
1937	43.1	119.4	165.2	180.5	117.9	70.4	45.7	-	14.8	8.2	-	-	765.2
1938	30.1	65.4	416.8	237.0	104.3	2.5	5.5	-	-	1.0	1.0	-	863.6
1939	12.0	356.0	205.3	131.2	83.6	50.7	6.6	-	-	27.5	7.5	-	880.4
1940	94.0	93.1	286.4	353.3	99.6	66.6	7.4	-	-	7.5	2.0	17.3	1027.2
1941	-	84.9	241.6	165.8	63.8	9.2	21.2	-	-	-	-	-	586.5
1942	12.8	172.7	175.4	74.0	11.5	-	-	-	-	-	-	40.5	486.9
1943	42.9	16.6	288.3	140.1	59.4	16.8	2.4	-	13.5	-	-	56.7	636.7
1944	38.9	7.3	229.2	249.5	192.3	-	-	-	-	-	-	42.7	759.9
1945	120.6	451.1	329.1	243.1	138.8	40.0	18.6	-	-	-	-	6.3	1348.2
1946	98.2	192.2	270.6	198.1	15.8	39.1	-	-	-	-	4.0	23.5	841.5
1947	22.1	159.1	273.9	227.5	95.4	4.5	-	-	-	-	21.5	70.2	874.2
1948	52.7	89.0	147.7	152.4	61.4	15.6	9.7	-	-	-	-	-	528.5
1949	?	?	?	174.1	135.2	17.0	-	?	?	?	?	?	?
1950	88.5	78.8	282.4	278.0	176.0	2.3	10.5	-	-	-	-	-	916.5
1951	30.9	5.5	10.4	132.0	24.9	27.3	-	-	-	-	-	132.0	363.0
1952	12.9	81.7	244.6	179.3	157.6	19.5	-	-	-	-	-	11.2	706.8



**Fig. 3.6:** Annual absolute minima of temperature in NE Brazil. Modified from Nimer, 1972.





**Fig. 3.7:** Annual absolute maxima of temperature in NE Brazil. Modified from Nimer, 1972.

for salt leaching. According to Tricart (1972, p. 33) "here is a sure criterion to delimit the humid tropics from the semiarid zone. In the caatinga regions of Brazil [...] films of salt accumulate between the crystalline hills, indicating an insufficiency of salt leaching. Kaolinite cannot form in such circumstances." Thus the predominant clay to be found is montmorillonite, responsible for a particular kind of soils, Grumosols or Vertisols, which are very common in the interfluvial platforms across the Caatingas pediplane. Indeed, Vertisols have been regarded as the climatogenic soils of this area (Ab' Sáber, 1974 & 1977a).

Perhaps the commonest soil class are the Non-Calciic Browns (Beek & Bramaio, 1968; Bautista, 1986), frequently ranging from Vertic with intermediate features to Vertisol (Figueiredo Gomes, 1981), with a textural B horizon and characteristic stones and boulders in surface. Given the nature of the region, Entisols and particularly Lithosols are very abundant, derived by weathering of parent rocks. Extensive rock outcroppings are regionally called 'lajedos', which act ecologically as desertic environments and where only succulent plants are to be found (generally *Pilosocereus gounellei* and *Encholirium* spp.). Pediments covered by a more or less continuous layer of stones (Desertic Pavements) are also frequent. Incipient soils can be found under the stone layer of some Lithosols, and pockets with thin Vertisols or moderately deep alkaline soils are frequent (Ab' Sáber, 1974) in the intermingling of soils resulting from the different erosive phases (Beek & Bramaio, 1968). Some Solonetz with high concentration of clay and sodium in the B horizon occur in localized areas of Ceará and Bahia (Ab' Sáber, 1974), and in Rio Grande do Norte in more extended areas on the Mossoró river valley (Figueiredo, 1987). Also very restricted areas locally called 'salgados' (brackish) can occur, where intermittent rivers fail to reach a major river. However, it should be emphasized that it is only the exorheic character of the Caatingas drainage that prevents halomorphic soils from being a much more prominent feature of the region (Ab' Sáber, 1974 & 1977a). Also noteworthy are the presence of rather isolated areas with red soils (Dark Red Latosols, in Bautista, 1986) with a prismatic B horizon, which are mainly located in the highest areas of the intertablelands depressions (Ab' Sáber, 1974) and which represent the remnants of what has been called the 'sertão old surface' which has escaped complete pediplanation. Such red soils, also reported by Tricart

(1961), are apparently true palaeoferralitic soils, and are found in western Pernambuco, Alagoas, and Rio Grande do Norte, where they are covered by dense arboreal caatinga. The existence of these soils within a semiarid region is regarded as evidence for more humid climates in the Upper Pleistocene than those of the present-day, and they could have supported dry or even wet tropical forests (Ab' Sáber, 1974). Other important classes of soils reported from the Caatingas are the poorly studied calcimorphic soils in Ceará, Bahia and particularly Rio Grande do Norte (Andrade-Lima, 1964c; Ab' Sáber, 1974), alluvial and some hydromorphic soils related to watercourses (Ab' Sáber, 1974; Figueiredo Gomes, 1981; Figueiredo, 1983), and the deep sedimentary sandy soils usually known as Areias Quartzosas in Brazil (Quarztsamments, 7<sup>th</sup> Appr.) which occur in the Cipó series in Pernambuco and Raso da Catarina, Bahia (Andrade-Lima, 1981).

#### 3.4- Vegetation of the Caatingas<sup>1</sup>:

The Caatingas can be characterized as woodlands, both forests and scrublands, comprising mainly low, deciduous trees and shrubs, many of which present spines or thorns, microphyllly and some xerophytic features. Cactaceae and Bromeliaceae are abundant whilst lianas are very scarce, and a few evergreen species (*Ziziphus joazeiro*, *Capparis yco*, *Copernicia cerifera*, *Maytenus rigida*, *Licania rigida*) also occur. The herbaceous layer is ephemeral and dominated by therophytes of the families Malvaceae, Portulacaceae and Graminae. Although succulency is found mainly in Cactaceae and Bromeliaceae, water storage organs are typical in some other cases (i.e. *Spondias tuberosa*, *Cavanillesia arboorea*, *Ceiba glaziovii*, *Jacaratia* sp., *Manihot* spp., *Luetzelburgia auriculata*).

Two terms closely linked with Caatingas and their phytogeographical concept are 'agreste' and 'sertão', and a brief discussion of these is necessary to clarify the subsequent analysis. Agreste is the name applied to a narrow strip of vegetation extending between the Serra do Mar ranges in the east, where rain forests thrive, and the drier hinterlands to the west. It has an elongated shape with a general north-south direction, and it can be found from Rio Grande do Norte to central Bahia, where it is replaced in this transitional position by

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<sup>1</sup> A more detailed analysis of caatinga floristic elements is given in Sect. 4.2.

the so-called 'mata de cipó'. The agreste enjoys a better rainfall regime (up to 1000 mm/year), and it is less subject to catastrophic droughts, since it benefits from the residual humidity of the SE winds. Its vegetation shares most of its features and species with the vast semiarid expansions to the west: deciduousness, thorny plants, abundant cacti and bromeliads on stony ground, generalized microphyllly, and the more characteristic woody and succulent species in the agreste all occur in the rest of the Caatingas, such as *Schinopsis brasiliensis*, *Pilosocereus gounellei*, *Aspidosperma pyrifolium*, *Cereus jamacaru*, *Caesalpinia pyramidalis*, *Tabebuia impetiginosa*, *T. caraiba*, *Commiphora leptophloeos*, *Cnidocolus phyllacanthus*, *Mimosa* spp. (Andrade-Lima, 1954, 1960, 1970, 1973). Thus, as Andrade-Lima demonstrated, the agreste should be regarded as part of the Caatingas, as a hipoxerophilous variant of the communities to be found to the west.<sup>2</sup>

The term 'sertão' is very much widely used in Brazil, from São Paulo state to the Northeast with the rather vague meaning of uncultivated place or zone, short of resources, removed from major populations and civilization (Egler, 1951). The English words such as hinterland, backlands or bush are used in a similar way. More debatable is the connotation of the word sertão in NE Brazil. Luetzelburg (1922-23) claimed that the driest and resourceless parts of the Caatingas were called sertão, while the rest was considered caatinga proper, particularly the areas where *Cereus jamacaru*, a cactus used as fodder, could be found. Egler (1951) was opposed to the use of the term sertão because of its vagueness, and proposed to separate agreste from caatinga proper, but as noted above this division has been shown to be inadequate. However, Vasconcelos (1941) and Andrade-Lima (1954, 1960, 1970) considered that the Caatingas should be simply divided into agreste and sertão, that is the transitional eastern sector on one side and the dry hinterlands on the other. This criterion is followed by the present author.

In SE Piauí there is a complex ecotone where the Caatingas meet Cerrados vegetation and varying communities can occur. There exist several degrees of transition between these major formations, i.e.

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<sup>2</sup> The name 'agreste' has also been applied to the very different cerrado vegetation on top of the Chapada do Araripe, Ceará.

(a) semideciduous cerrado, with some few caatinga elements, (b) the 'carrasco' or 'catanduva', with about equal proportion of cerrado and caatinga elements but also with some exclusive elements, and (c) typical caatinga with sparse cerrado elements (Eiten, 1972; Andrade-Lima, 1978). It is notable, however, that in this area the cerrado vegetation is largely confined to sedimentary sectors with sandy soils, while the Caatingas tend to appear in sectors affected by diabasic rock outcroppings with much more fertile soils (Andrade-Lima, 1978; Emperaire, 1983), even though the rainfall regime is the same at *ca.* 1000 mm/year.

There have been several attempts to classify the vegetation of the world according to its physiognomy (Schimper, 1903; Drude, 1913; Trochain, 1957; Ellenberg & Mueller-Dombois, 1967). A number of authors have also devised hierarchical physiognomic classifications of vegetation at a continental (Beard, 1944 & 1955; Smith & Johnston, 1945; Eiten, 1974) or Brazilian level (Castellanos, 1960; Rizzini, 1963; Veloso & Góes Filho, 1982; Eiten, 1983). No attempt is made here to analyse these systems, since the emphasis of this study is on the floristic links of the Caatingas, but probably Eiten (1974 & 1983) provides the most detailed and useful survey of the different structural types of the Caatingas vegetation. At the other extreme, it is very difficult to accept the use of the word steppe ('estepe') to denominate this formation as employed by Radambrasil (Veloso & Góes Filho, 1982), taken on board from the Yangambi Agreement (Trochain, 1957). The Russian and Siberian steppes are grasslands, sometimes with scattered low shrubs, which undergo a severe winter with frozen soil, and its use for the Caatingas has already been challenged by Kuhlmann (1974). Once again, however, this is a purely geographic term and its use for vegetation physiognomy has been rejected (Tanfiljew, 1905; Cain & Castro, 1959, p. 48).

The physiognomy of the Caatingas vegetation is very variable, depending on the rainfall regime and soil type, ranging from a tall, dry forest up to 15-20 m high, e.g. the 'arboreal caatinga' (the true caatinga of the Tupí indians, according to Andrade-Lima) found scattered from Bahia (Andrade-Lima, 1975) and Minas Gerais (Magalhães, 1961) to Rio Grande do Norte (Andrade-Lima, 1964c) on somewhat better soils and in more humid localities, to rock outcroppings with scattered and sparse low shrubs, cacti and bromeliads in crevices. Intermediate

physiognomic forms are numerous but they can be reduced to a few generalized types, such as 'open arboreal caatinga with an open shrub layer', 'shrubby-arboreal caatinga with a closed shrub layer', 'closed thorn scrub with scattered overtopping low trees' – which is perhaps the most common kind of present-day caatinga community (Eiten, 1974 & 1983), 'closed thorn scrub', 'open shrubby caatinga' (common in areas with extended shallow soils), 'scrub savanna with shortgrass layer' ('seridó'; Andrade-Lima, 1966a; Eiten, 1983), and '*Copernicia* palm groves' along intermittent rivers mainly in NW Caatingas province.

Another group of authors have tried to analyse and identify the different units of vegetation in the Caatingas, following floristic-physiognomic criteria but with most of the weight on the floristic composition of the communities. A landmark effort in this sense was that by Luetzelburg (1922-23) in his 'Estudo Botânico do Nordeste', a work based on the author's extensive travels throughout the Caatingas over a 10 year period. His classification, although interspersed with taxonomical and conceptual mistakes (Andrade-Lima, 1954), can still be seen as the framework for the overview by Andrade-Lima (1981). Luetzelburg divided the Caatingas roughly into two classes: 1) shrubby or scrub caatinga ('caatinga arbustiva'), and 2) arboreal caatinga or caatinga forest ('caatinga arbórea'), which he then subdivided in several groups:

#### Class 1: Scrub Caatinga

- 1.1- *Euphorbia* - *Croton* - *Caesalpinia* caatinga
- 1.2- *Mimosa* - *Caesalpinia* caatinga
- 1.3- *Spondias* - *Caesalpinia* - *Cnidoscolus* caatinga
- 1.4- *Cereus* - *Mimosa* - *Spondias* - *Bromelia* caatinga
- 1.5- *Combretum* - *Aspidosperma* - *Caesalpinia* caatinga
- 1.6- *Jatropha* - *Cnidoscolus* - *Mimosa* caatinga
- 1.7- *Chorisia* - *Mimosa* - *Manihot* caatinga
- 1.8- Caatinga-carrascal or 'caatinga suja' [literally: dirty caatinga]
- 1.9- Caatinga serrana (mountain caatinga)

#### Class 2: Arboreal Caatinga

- 2.1- *Aspidosperma* - *Schinopsis* (sub *Melanoxylon*) - *Piptadenia* caatinga

2.2- *Chorisia - Piptadenia - Spondias* caatinga2.3- *Cocos coronata - Copernicia cerifera - Cocos comosa* (sub *Mimosa*) caatinga

Some of these units have been recognized or slightly modified by Andrade-Lima (1981), such as groups 1.3 or 2.1 and 2.2. In group 2.1 *Melanoxylon* is in fact *Schinopsis*, one of the common mistakes in this work, while *Mimosa* in group 2.3 must be a compilation error for *Cocos* (= *Syagrus*) *comosa*, the catolé palm, which occasionally occurs in Caatingas (Glassman, 1987). Group 1.8 is clearly what is known as 'carrasco' or 'catanduva' (Andrade-Lima, 1978; Emperaire, 1983; Oliveira et al., 1988), a transitional type of vegetation with the Cerrados in SE Piauí which, whilst it includes species of caatinga, is floristically, physiognomically and phenologically (semideciduous) closer to cerrado vegetation, and it is not accepted here as part of the Caatingas. The term 'suja' alludes to the fact that these communities have mixed elements of the Cerrados formation. Group 1.9 refers to low or dwarfed scrubby vegetation on inselbergs and dry sierras, mainly on rock outcroppings, but not to arboreal caatinga which can occur on less dry slopes nor to the wet 'brejos' which occur in the east of the Caatingas and are floristically excluded from the province. Hueck (1972) criticised Luetzelburg's classification, and presented it in his own work "only for historical reasons", but in fact his strictures are rather insubstantial, and he simply succeeded in having Luetzelburg's mistakes perpetuated and compounded, including the most obvious errors such as the misidentification of *Schinopsis* for *Melanoxylon*.

Rizzini (1963), in his floristic-phytosociological study of Brazilian vegetation, concluded that the Caatingas should be treated as a subprovince of what he called the 'Atlantic Province', on account of what he regarded as the very close floristics links between the Caatingas and the coastal forests. Thus, Rizzini's 'Northeastern Subprovince' includes:

- 1- Agreste sector: deciduous xerophilous forests;
- 2- Sertão sector: thorny and succulent scrub, which also involves three internal districts, 2.1: *Copernicia cerifera* palm consociations; 2.2: higromontane rain forests ('brejos'); 2.3: xeromontane savannas and woodlands on sedimentary surfaces ('agreste' of Araripe);

3- Seridó sector: semiarid scattered scrub and succulent scrub;

4- Fernando de Noronha Island: agreste type of woody vegetation, with a six months long dry season.

Rizzini (1963) grouped together disparate kinds of vegetation which have little in common with the Caatingas as accepted by most authors, either floristically or physiognomically, such as the cerrado vegetation of the Chapada do Araripe and coastal taboleiros, and the rain- and cloudforests of the 'brejos'.

Veloso (1964) also presented a vegetation map of the Northeast, but he divided the region into subregions (which he called physiognomical areas) based on geographical criteria. The result is inadequate for the phytogeographical synthesis which was intended since, although most of the Caatingas are grouped together, several facies are separated into different so-called 'subregions', e.g. the agreste is fragmented and sometimes confused with cerrado vegetation but never associated to the Caatingas. For the bulk of the Caatingas, denominated Semiarid Vegetation of Eastern Northeast, from which Veloso correctly detached the Serra do Araripe cerrado, the vegetation of the pediplains was classified as follows:

a- 'caatinga formation'<sup>3</sup>: predominantly deciduous thorny vegetation. This was further subdivided into three subclasses based on their physiographic position on the terrain (instead of their floristics): (a.1) sandy tablelands caatinga, with dense shrubby vegetation interspersed with trees; (a.2) caatinga of the depressions, shrubby with occasional trees; (a.3) caatinga on inselbergs and arid depressions, with vegetation in scattered clumps and spiny succulents.

b- 'forest formation': deciduous, thorny, arboreal vegetation interspersed with evergreen trees. This evidently refers to arboreal caatinga, as described by Andrade-Lima (1981), but the presence of evergreen trees cannot possibly be used to characterize it since they occur throughout the Caatingas (e.g. *Ziziphus joazeiro*).

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<sup>3</sup> Veloso (1964) misused the term "formation", which is a physiognomic vegetation unit with similar structure and a characteristic essential habitat, and it is independent of the flora (Beard, 1944, 1955). A "caatinga formation" would be possible only if it had a physiognomy exclusive to it, which is certainly not the case. The Caatingas can easily fit into Beard's (op.cit.) "thorn woodland", and so does the Chaco. At the other extreme, "forest formation" is too ambiguous.



TABLE 3.2: Main units of vegetation and community types of the Caatingas (modified from Andrade-Lima, 1981)

UNIT	VEGETATION TYPE	PHYSIOGNOMY & LOCATION	SUBSTRATUM
I	<i>Tabebuia-Anadenanthera-Astronium-Cavanillesia-Schinopsis</i>	Tall caatinga forest; N Minas Gerais & S central Bahia	limestone Bambuí or Pre-Cambrian crystalline rocks
II	<i>Astronium-Schinopsis-Caesalpinia</i>	Median caatinga forest; most of the centre of the province	mainly Pre-Cambrian crystalline rocks
II	<i>Caesalpinia-Spondias-Commiphora-Aspidosperma</i>	Median caatinga forest; drier area than preceding	mainly Pre-Cambrian crystalline rocks
II	<i>Mimosa-Syagrus-Spondias-Cereus</i>	Low caatinga forest; N central Bahia	mainly P.Cambrian crystalline rocks
III	<i>Pilosocereus-Poeppigia-Dalbergia-Piptadenia</i>	Low caatinga forest; sandy soils from the Cipó series	Cipó series sandstone rocks
II	<i>Cnidocolus-Commiphora-Caesalpinia</i>	Open arboreal caatinga; SW Ceará and medium dry areas with loose, acid soils	mainly P.Cambrian crystalline rocks
IV	<i>Caesalpinia-Aspidosperma-Jatropha</i>	Shrubby caatinga; drier areas in the São Francisco valley	mainly P.Cambrian crystalline rocks
IV	<i>Caesalpinia-Aspidosperma</i>	Open shrubby caatinga; Cariris Velhos, Paraíba	mainly P.Cambrian crystalline rocks
IV	<i>Mimosa-Caesalpinia-Aristida</i>	Open shrubby caatinga (seridó); Rio Grande do Norte & Paraíba	mainly P.Cambrian crystalline rocks
IV	<i>Aspidosperma-Pilosocereus</i>	Open shrubby caatinga; Cabaceiras, Paraíba	mainly P.Cambrian crystalline rocks
V	<i>Calliandra-Pilosocereus</i>	Open shrubby caatinga; small, restricted scattered areas with gravelly soils	mainly P.Cambrian metamorphic rocks
VI	<i>Copernicia-Geoffroea-Licania</i>	Fringe caatinga forest; river valleys of Ceará, Piauí & Rio Grande do Norte	mainly alluvial soils
II	<i>Auremma-Mimosa-Luetzelburgia-Thiloa</i>	Median caatinga forest; W Rio Grande do Norte & central Ceará	mainly P.Cambrian crystalline rocks

Schnell (1966) also proposed a simplified classification of the Caatingas, with (1) dense dry forests with some swollen-trunk tree species, (2) dense scrub with large Cactaceae, (3) open scrub with a 'steppic' character, and (4) diffuse caatinga with spaced bushes in the driest areas. Hayashi & Numata (1976) attempted to classify the Caatingas on the basis of life forms, but this study was too reduced in geographical scope to be of value.

The most coherent and comprehensive work on this vegetation is that by Andrade-Lima (1981). This overview, which treats the Caatingas as a Dominium (a chorionomic unit equivalent to the more widely used Province unit, Takhtajan, 1986), builds on Luetzelburg's substantial pioneer reports, but is also the result of Andrade-Lima's numerous previous studies which dealt with particular areas of the Caatingas as a whole, and especially with the vegetation of the state of Pernambuco (Andrade-Lima, 1953, 1954, 1960, 1961, 1964b, 1964c, 1966a, 1966c, 1967b, 1970, 1971, 1973, 1975, 1977, & 1978). Essentially, Andrade-Lima's concept of the Caatingas, which was basically a floristic conception of the province without losing contact with the physiognomy and ecology of the vegetation, is the one followed here.

Table 3.2, modified from Andrade-Lima (1981), shows in a condensed manner the main units of vegetation and community types for the Caatingas, which includes a new vegetation type proposed here. A brief discussion on the units follows:

UNIT I: Veg. Type 1, Tall Caatinga Forest. It is entirely agreed that this is a member of the province; although the physiognomy of this community is very distinct to that of other vegetation types within the Caatingas, the clear-cut leafless period and above all the floristic composition firmly link this forest-type to the province. Genera and species dominant here are common throughout the Caatingas, and sometimes they will appear only in caatinga areas (e.g. *Commiphora leptophloeos*). Certainly some alien mesophytic species are also to be found in this type of forest, but they are always only minor members of the community. See also Magalhães (1961), Andrade-Lima (1971, 1975, 1977), Magalhães & Ferreira (1976, *apud* Andrade-Lima, 1981), Ratter et al. (1978). In

Ceará a kind of mid-slope Mata Seca (dry forest) or mesophilous forest has been described by Figueiredo (1984) which lack the swollen-trunk Bombacaceae but in all other respects seems to be arboreal caatinga with some mesophilous elements. Out of 16 species mentioned by this author, 10 are members of caatinga forests and an eleventh is very occasionally found (*Syagrus comosa*). In E and SE Bahia the 'mata de cipó' (lianas forest) seems to comprise a wide transition between the coastal rainforests and the inner Caatingas, and consists of different types of dry deciduous forests and subhumid semideciduous forests. At least some facies of them contain typical species of caatinga (Andrade-Lima, 1971). There is very little knowledge about this formation, a fact also remarked by Bégué (1967 & 1968), but some short but accurate descriptions (Andrade-Lima, 1966a, 1971; see also Noblick, *in litt.*, in Plowman, 1987) allow for the inclusion of at least some of the dry forests as arboreal caatinga.

UNIT II: Veg. Types 2, 3, 4 & 6 (for veg. type 13, see below), typical Median Caatinga Forest, with variable density in the tree layer, 7-15 m tall. Very widespread and common unit of vegetation throughout NE Brazil, probably with a multitude of facies of which Andrade-Lima commented on four. Several of the dominant species in Unit I also appear as scattered elements in these kind of communities, such as *Anadenanthera colubrina* var. *cebil*, *Commiphora leptophloeos*, *Astronium urundeuva*, *Schinopsis brasiliensis*, and *Amburana cearensis*. Most of Andrade-Lima's papers carry at least one description of this vegetation type; also in Figueiredo Gomes (1981), Figueiredo (1983 & 1987), Figueiredo & Fernandes (1985), Carvalho (1986).

UNIT III: Veg. Type 5, Low Caatinga Forest. A very distinct unit, described in somewhat more detail in Egler (1951) and Andrade-Lima (1960, 1970). Very restricted in area to the sandy soils in south-central Pernambuco (Moxotó tableland) and northern Bahia (Raso da Catarina), and characterized by the species *Pilosocereus piahuiensis*, *Poeppigia procera*, *Dalbergia cearensis*, *Pilosocereus tuberculatus*. The palm *Syagrus coronata* ('ouricouri') can also occur here in fairly big populations, but

although Egler and Andrade-Lima (*op. cit.*) mentioned the species previously, the latter author failed to include it in his overview (Andrade-Lima, 1981).

UNIT IV: Veg. Types 7, 8, 9 & 10, Dense or Open Shrubby Caatinga.

This is the most widespread vegetation type nowadays, and it is still a contentious matter as to what extent it is entirely natural or man-induced. Although the influence of man in the area has been marked, to consider this unit as a completely secondary vegetation would seem to grossly underestimate the homeostatic ability of these ecosystems. On the contrary, Carvalho (1986) for instance found stability as the main feature of the Caatingas of western Pernambuco for the period 1955-1983, together with a moderate expansion of agriculture, despite the probably heavy human pressure in the intervening years. Furthermore, it is a striking coincidence that this Unit IV corresponds geographically to the driest areas within the province, such as the São Francisco valley (type nº 7), the 'seridó' (type nº 9), or the vegetation of the Cariris Velhos, Paraíba (types nº 8 & 10, in the Borborema Plateau), with the lowest rainfall record of the Caatingas (Cabaceiras: 252.4 mm/year; Figueiredo Gomes, 1981). Moreover, there is a direct correlation between rainfall, soil depth, and soil permeability to height and density of the community (Sampaio et al., 1981), which would allow one to predict the vegetation type to be found in one area. This unit consists typically of scattered trees of species such as *Amburana cearensis*, *Spondias tuberosa*, *Aspidosperma pyrifolium*, in a shrubby matrix of *Caesalpinia* spp., *Mimosa* spp., *Jatropha* spp., and *Acacia* spp.. More information on this unit is available in Vasconcelos (1941), Egler (1951), most of Andrade-Lima's papers, Anon. (1980), Figueiredo Gomes (1981), Figueiredo (1987).

UNIT V: Veg. Type 11, Low Open Shrubby Caatinga. Very restricted in surface and area, on shallow sandy or gravelly soil under a long dry period (8-9 months). Dominated by *Pilosocereus gounellei*, *Calliandra depauperata* and *Melocactus bahiensis*, the unusual small height of this community (0.70-1 m) seems to be caused by grazing (Andrade-Lima, 1981). Only reported in the literature by

Andrade-Lima (*op. cit.*), its status is doubtful to the present author who visited one small stand of this community in Ceará. It seems very probable it is simply the result of heavy overgrazing and therefore of indirect anthropic influence, but further research is necessary.

UNIT VI: Veg. Type 12, fringe forest along watercourses mainly in Piauí, Ceará and Rio Grande do Norte. Physiognomy dominated by the palm *Copernicia cerifera* ('carnaúba'), accompanied by *Licania rigida*, *Geoffroea striata*, *Sideroxylon obtusifolium*, *Erythrina velutina*, *Ziziphus joazeiro*, *Capparis yco*. The dominant palm-tree species, the Chrysobalanaceous tree *Licania rigida* and perhaps *Capparis yco* are not only endemic to the Caatingas but also to this limited environment, where there is relatively constant supply of water from the water-table during droughts, and it is flooded in the rainy season. The very slow dessication of heavy alluvial soils causes salinization, a rather rare phenomenon in the Caatingas. Descriptions of this vegetation type can be found in Andrade-Lima (1954, 1964c, 1978), Emperaire (1983), Figueiredo (1987).

UNIT II: Veg. Type 13, Median Caatinga Forest. This comprises a new addition to Andrade-Lima's classification which is proposed here. The existence of such a unit was indicated by Andrade-Lima (1981) who commented: "In the states of Rio Grande do Norte and Ceará, this unit (II) presents a facies (which may be an independent unit of its own to be recognized after further studies) in which *Auxemma oncocalyx* is one of the dominant species". During field work in Ceará the present author had the opportunity to visit several stands of this community, and can confirm that it should constitute a separate entity since it shows a distinct subset of species which are largely restricted to this vegetation type: *Auxemma oncocalyx*, *Mimosa caesalpinifolia* ('sabiá'), and in piedmont-areas *Luetzelburgia auriculata* ('pau mocó') (Lima, 1982), and, less consistently, *Thiloa glaucocarpa*. The community is sometimes dominated by other widespread species such as *Astronium urundeuva*, *Anadenanthera colubrina* var. *cebil*,

*Aspidosperma pyrifolium* , *Caesalpinia pyramidalis*, which share the canopy with *Auxemma oncocalyx* .



**Plate 3.1:** The caatinga vegetation at Parnamirim, Pernambuco, Brazil. Top: 'angico' and 'jamacaru' predominate in open shrubland. Center: shrubby caatinga with sparse *Commiphora leptophloeos*. Bottom: the 'umbú', *Spondias tuberosa*.

#### 4. WOODY AND SUCCULENT SPECIES FLORISTIC LISTS

To evaluate the floristic links between the Chaco and the Caatingas vis-à-vis the rest of seasonal forests and woodlands of South America basic floristic lists of both provinces were needed. These have been built up based on the following sources:

- a- Exsiccata obtained on loan from diverse Herbaria (G, GH, A, E), plus visits to K, BM, E, UB, UEC, IPA, EAC and UNR.
- b- Exhaustive checks on taxonomic literature and verification of identity of those species cited in floristic lists and phytogeographical accounts.
- c- Field experience of the present author.

In general all species cited in the following tables have been reported in at least two reliable floristic studies or phytogeographical accounts, whereas the sole mention of a taxon in monographic treatments is taken as enough evidence of its occurrence in the area under study.



#### 4.1- Woody and succulent species of the Chaco s.s. :

In the floristic list of Chaco s.s. woody and succulent species, those indicated with an asterisk (\*) correspond to taxa known to occur only in the Sierra Chaco within the scope of the Chaco as here understood (see Ch.2). The taxa indicated with a capital m letter (M) are regarded as Monte intruders into the Chaco, in no way typical chaquenian species. In the 'Main Synonym' column the names between brackets (...) are common identification mistakes or binomials wrongly applied to the entities shown in the 'Species Name' column, not to be treated as taxonomic synonyms. In the 'References' column, h.s. stands for 'herbarium specimens' in those cases in which exsiccata have been taken by the present author as evidence of the alleged presence of the species in the area.

Fly N°	Gen N°	Sp N°	SPECIES NAME	MAIN SYNONYM	VERNACULAR NAME	REFERENCES
1			ACHATOCARPACEAE			
	1	1	<i>Achatocarpus praecox</i> Gris.	<i>A. nigricans</i> Triana	palo de tinta, palo mataco, ruma caspi, tala negro	378, 315, 9, 135, 281, 67
2			ANACARDIACEAE			
*	2	2	<i>Lithraea ternifolia</i> (Gillies)Barkley	<i>L. gilliesii</i> Gris.	molle blanco, molle de beber, chichita, etc.	378, 47, 136, 281
	3	3	<i>Schinopsis balansae</i> Engler	<i>Quebrachia morongii</i> Britton	quebracho colorado chaqueño, q. c. correntino, q. chaq., urunday	378, 304, 97, 67
		4	<i>Schinopsis cornuta</i> Loes.		soto negro	304

*	5	<i>Schinopsis haenkeana</i> Engler	<i>S. marginata</i> Engler; <i>S. lorentzii</i> var. <i>marginata</i> (Eng.)Cabr.	horco quebracho, q. colorado del cerro, q. serrano, q. cordobés	378,136, 304, 281
	6	<i>Schinopsis heterophylla</i> Rag. & Cast.		quebracho colorado mestizo	378, 323
	7	<i>Schinopsis quebracho-colorado</i> (Schlecht.) Barkley & Meyer	<i>S. lorentzii</i> (Gris.) Engler	quebracho, q.macho, q.coronillo, q.colorado, q.col.santiagueño	378,109,315, 413, 304,97, 281, 67
	4	<i>Schinus bumelioides</i> I.M.Johnston	<i>S. myrtifolius</i> Cabr.	molle, m.blanco, m.colorado, m. negro, m.chico, moradillo	45, 315, 281
	9	<i>Schinus fasciculatus</i> (Gris.)Johnst.	<i>S. polygamus</i> f. <i>fasciculatus</i> Cabrera	molle, m.blanco, m.colorado, m. santiagueño,trementina, etc.	378, 45, 7, 281, 67
		var. <i>arenicola</i> (Haum.) Barkley	<i>S. p. f. arenicola</i> Cabr.	molle, m.blanco, m.de incienso	45, 315
*	10	<i>Schinus molle</i> L. var. <i>areira</i> (L.)DC.	<i>S. areira</i> L.	aguaribay, molle	378, 45, 97
	11	<i>Schinus piliferus</i> I.M.Johnston var. <i>boliviensis</i> (Barkl.)Barkley		molle, m.blanco, m.criollo, etc.	45, 97
*	12	<i>Schinus praecox</i> (Gris.)Speg.	<i>Duvaua praecox</i> Gris.	chirimolle, molle, m.de incienso	45, 315
3		APOCYNACEAE		molle de curtir, moradillo	45, 281
	5	<i>Aspidosperma quebracho-blanco</i> Schlechtendal	<i>A. quebrachoideum</i> Rojas Acosta	quebracho blanco, q.morotí, cacha-cacha, q.branco	378, 315, 136, 97, 281,286
	14	<i>Aspidosperma triternatum</i> Rojas Acosta	<i>A. chakensis</i> Speg., A. <i>horko-kebracho</i> Speg.	quebracho negro, q.blanco chico, q.blanco lagunero	378, 315, 136,286
	6	<i>Vallesia glabra</i> (Cav.)Link.	<i>Rawolfia glabra</i> Cav.	ancoche, engorde, teta de gata	315,136,97,281
4		ARECACEAE			

7	16	<i>Copernicia alba</i> Morong	<i>C. australis</i> Becc.	carandá, caranday, c.-hú (palma negra), c.-morotí (p.blanca), c.-puitá (p.colorada)	378,93,109,315, 379,9
8	17	<i>Trithrinax biflabellata</i> Barb. Rodr.		carandillo, palma	134,97,354,67
	18	<i>Trithrinax campestris</i> (Burm.) Drude & Gris.		palma, palmera, carandilla, caranday	136,97,354,281
5		ASCLEPIADACEAE			
9	19	<i>Marsdenia castillonii</i> Lillo ex Meyer		mandioca, yuca, batata d. monte	38
6		ASTERACEAE			
*	10	<i>Baccharis articulata</i> (Lam.) Pearson		carqueja, carquejilla	281, 91
*	21	<i>Baccharis flabellata</i> Hook. & Arn.			413, 281, 91
*	22	<i>Baccharis myrtilloides</i> Grisebach			281, 91
	23	<i>Baccharis notosergha</i> Grisebach		carqueja	413, 7, 97
	24	<i>Baccharis salicifolia</i> (R. & P.) Pers.		suncho, chilca, chilca blanca	93,315,413,97
11	25	<i>Cyclolepis genistoides</i> Gill. ex Don		palo azul, matorro	315,379,9,281
*	12	<i>Eupatorium buniifolium</i> Hook. & Arn.		romerito	97,281,91
*	27	<i>Eupatorium viscidum</i> Hook. & Arn.			134,413,281
*	13	<i>Flourensia campestris</i> Gris.		chilca	134,413,281
*	29	<i>Flourensia oolepis</i> Baker		chilca	281
*	14	<i>Heterothalamus alienus</i> OK.		romerillo	413,379,97,281
	15	<i>Hyalis lancifolia</i> Baker			97
*	16	<i>Ophryosporus axilliflorus</i> Hieron.			97

* 17	33	<i>Proustia ilicifolia</i> Hook. & Arn.	<i>P. pungens</i> Poepp.	altepe, huanil, sachá rosa, rosa del monte, chilca de Castillo	134, 281
18	34	<i>Tessaria absinthioides</i> (H. & A.) Cabr.		chilca, suncho, s. negro	93, 413, 9
	35	<i>Tessaria dodoneaeifolia</i> (H. & A.) Cabr.		chilca negra, suncho negro	378, 93, 315, 379, 314, 9
	36	<i>Tessaria integrifolia</i> Ruiz & Pavón		palo bobo, aliso	93, 9, 97
7		BERBERIDACEAE			
* 19	37	<i>Berberis hieronymi</i> Schn.			340, 281, 91
	38	<i>Berberis ruscifolia</i> Lam.		quebrachillo/a, sachá uva, uvilla, palo azul, talilla	340, h.s.
8		BIGNONIACEAE			
20	39	<i>Dolichandra cynanchoides</i> Cham.	<i>Macfadyena cynanchoides</i> (Cham.) Morong	sachá-huasca, teyú-igsipó, malagraik-laachí	416, 164, 413, 281
21	40	<i>Mansoa truncata</i> Sprague	<i>Petastoma truncatum</i> (Sprague) Hassler		416, 134, 164
22	41	<i>Pithecoctenium cynanchoides</i> DC.	<i>P. clematideum</i> (Gris.) Gris.	chacha, trompetilla de Venus, peine de mono, caí-quiguá, etc.	416, 134, 164, 413, 281, 67
23	42	<i>Tabebuia nodosa</i> (Grisebach) Grisebach	<i>Tecoma nodosa</i> Gris.; <i>Bignonia morongii</i> Brt.	torataí, tororotay, palo cruz, uññaj, Martín Gil, labón	416, 134, 378, 315, 164, 413, 281, 67
9		BOMBACACEAE			

24	43	<i>Ceiba chodatii</i> (Hassler) Gibbs & Semir comb. ined.	<i>Chorisia insignis</i> Kth.	palo borracho, yuchán, painero, algodonero, etc.	134,378,109,315, 9,97,67, Gibbs (pers.comm.)
10		BORAGINACEAE			
25	44	<i>Cortesia cuneifolia</i> Cav.		campa	413,97,281,64
11		BROMELIACEAE			
26	45	<i>Bromelia hieronymi</i> Mez		chaguar blanco, cardo vid	315,9,97,281, 159, 67
	46	<i>Bromelia serra</i> Grisebach		chaguar, cardo gancho	109,315,9,67
	47	<i>Bromelia urbaniana</i> (Mez)L.B.Smith	<i>Deinacanthon</i> <i>urbanianum</i> (Mez)Mez	chaguar salado, chaguarillo	109,315,9, 281
*	27	<i>Deuterocohnia longipetala</i> (Baker)Mez		chaguar	432, 281
	28	<i>Dyckia ferox</i> Mez		chaguar	432
	50	<i>Dyckia floribunda</i> Grisebach	<i>D. chaguar</i> Castell.	chaguar	9, 432, 281
	51	<i>Dyckia ragonesei</i> Castellanos		chaguar	432
	52	<i>Dyckia tweediei</i> Mez		chaguar	432
*	29	<i>Puya spathacea</i> (Gris.)Mez		chaguar del burro, chagual	432, 281
12		BUDDLEJACEAE			
	30	<i>Buddleja brasiliensis</i> Jacq. ex Spreng.		palo blanco	134,413,281
*	55	<i>Buddleja cordobensis</i> Grisebach		palo blanco	413,379,281,91
*	56	<i>Buddleja mendozensis</i> Benth.		palo blanco, salvilora	134,413,281
	57	<i>Buddleja stachyoides</i> Cham.& Schlecht.			134,413

13		CACTACEAE					
*	31	<i>Acanthocalycium violaceum</i> (Werd.) Backeberg					238, 281
	32	<i>Castellanosia caineana</i> Cárđ.					159
	33	<i>Cereus æthiops</i> Haworth			víbora		76, 281, 67
	61	<i>Cereus comarapanus</i> Cárđ.					159
	62	<i>Cereus validus</i> Haworth					76, 378, 93, 109, 315, 9, 281, 67, 159
	34	<i>Cleistocactus baumannii</i> (Lem.)Lemaire				<i>C. forbesii</i> Otto	76, 378, 315, 413, 238, 281, 159, 240
	64	<i>Cleistocactus bruneispinus</i> Backeberg				<i>C. flavispinus</i> (K.Sch.) Back.; <i>Cereus</i> <i>baumannii</i> Lem.	
	65	<i>Cleistocactus smaragdiflorus</i> (Web.)Br. & Rose				<i>Cereus smaragdiflorus</i> Weber	159
	35	<i>Echinopsis chacoana</i> Schütz					76, 109, 315, 9, 240
	67	<i>Echinopsis leucantha</i> (Gillies)Walper					159
	68	<i>Echinopsis minuana</i> Spegazzini				<i>E. melanopotamica</i> Spg	76, 93, 281, 157
	69	<i>Echinopsis schaferi</i> Br. & Rose					76, 314
	36	<i>Eriocereus bonplandii</i> (Parm.)Ricc.					76, 109, 314
	71	<i>Eriocereus guelichii</i> (Speg.)Berg				<i>Harrisia bonplandii</i> (Parm.)Br. & Rose	76, 109, 315, 9, 159
						<i>Harrisia g.</i> (Sp.)B. & R.	76, 378, 97, 159

	72	<i>Eriocereus martinii</i> (Lab.)Ricc.	<i>Harrisia martinii</i> (Lab.)Br. & Rose		76,378,314,97, 159
	73	<i>Eriocereus pomanensis</i> (Web.) ?	<i>Harrisia pomanensis</i> (Web.) Br. & Rose	ulúa	76,109,315,9, 281,67
	74	<i>Eriocereus tortuosus</i> (Forb.)Ricc.	<i>Harrisia t.</i> (Forb.)B.&R.		76,159
*	37	<i>Gymnocalycium capillensis</i> Hosseus			281
M	76	<i>Gymnocalycium delactii</i> (K.Sch.)Hoss.			281
	77	<i>Gymnocalycium friedrichii</i> (Werd.)Paz. var. <i>moserianum</i> Paz. var. <i>albiflorum</i> Paz.			159
	78	<i>Gymnocalycium megatae</i> Y. Ito			159
	79	<i>Gymnocalycium mihanovichii</i> (Fric & Gürke) Br. & Rose	<i>Echinocactus mihanovichii</i> Fr & Gür		76,159
*	80	<i>Gymnocalycium multiflorum</i> (Hooker) Br. & Rose	<i>Echinocactus multiflorus</i> Hooker		76, 379
	81	<i>Gymnocalycium pflanzii</i> (Vaup.)Werd.			159
	82	<i>Gymnocalycium ragonesei</i> Castellanos			93,379,281
38	83	<i>Monvillea cavendishii</i> (Monv.)Br. & Rose	<i>Cereus cav.</i> Monv.; <i>M. partoniana</i> (Mon.)Bor.		76,378,109,315, 288,159
	84	<i>Monvillea spegazzinii</i> (Weber)Br. & Rose	<i>Cereus sp.</i> g. Weber; <i>C. anisitsii</i> K.Sch.		76,378,109,315, 159
39	85	<i>Opuntia aurantiaca</i> Lindley			76, 159





44	101	<i>Stetsonia coryne</i> (Salm-Dyck) Br. & Rose	<i>Cereus coryne</i> Salm-Dyck	cardón	76,378,93,109, 315,238,281,159
*	45	<i>Trichocereus andalgensis</i> (Web.)Hos.	<i>Cereus andalg. Weber</i>		239
*M	103	<i>Trichocereus candicans</i> (Gill.)Br. & R.	<i>Cereus candicans</i> Gill.		76,239,281
	104	<i>Trichocereus lamprochlorus</i> (Lem.) Br. & Rose	<i>Cereus lamprochlorus</i> Lemaire		76,239
	105	<i>Trichocereus spachianus</i> (Lem.)Ricc.	<i>T.santiaguensis</i> (Sp.)Bk		76,239
M	106	<i>Trichocereus terscheckii</i> (Parm.)Br.&R.	<i>Cereus terscheckii</i> Pm.	cardón grande, siski? <sup>1</sup> , cholo? <sup>1</sup>	76,315 <sup>1</sup> ,9 <sup>1</sup> ,239
*	107	<i>Trichocereus thelegonus</i> (Web.)Br.&R.	<i>Cereus thelegonus</i> Web	cola de león	76,239
14		CAPPARIDACEAE			
	46	<i>Capparis atamisquea</i> O. Kuntze	<i>Atamisquea emarginata</i> Miers	atamisquei/e, matagusanos, mata negra,leña hedionda	378,197,315,9, 281, 97
	109	<i>Capparis retusa</i> Grisebach var. <i>retusa</i> var. <i>velutina</i> Hauman	<i>C. cynophallophora</i> L. var. <i>retusa</i> (Gris.)OK	sacha poroto, ibirá-pororó, ababán	378,197,109,315, 9,67
	110	<i>Capparis salicifolia</i> Grisebach		sacha sandía, sandía hedionda, sandía de cabra	197 378,197,109,315, 97,67
	111	<i>Capparis speciosa</i> Grisebach	<i>C. pruinosa</i> Griseb.	sacha limón, s. naranjo, palo / bola verde, naranjillo, payaguá naranjo, meloncillo, amarguillo	378,197,109,315, 97,67

<sup>1</sup> Both 315 and 9 cited in fact *T. lamprochlorus* for E Salta (Argentina) and as an arboreal cactus, under the vernacular names "siski" or "cholo", but this species is not arboreal nor it is known to occur in that area (see Kiesling, 1978). Probably they must have referred to the candelabra-like *T. terscheckii* (Parm.) Br. & Rose.

	112	<i>Capparis tweediana</i> Eichler			sacha membrillo, mboy-curé-caá yerba de la comadreja, cayampa, meloncillo, sacha coca	378,197,109,315, 97,67
15		CARICACEAE				
	47	<i>Jacaratia corumbensis</i> Kuntze		<i>J. hassleriana</i> Chod.	yacón, Akol-yacón, cipoy	104,308,379,43
16		CELASTRACEAE				
	48	<i>Maytenus spinosa</i> (Gris.) Lour. & O'Don.		<i>Moya spinosa</i> Gris.	abreboca, sacha mistol, molle negra, piquillín negro, p. de loro	378,315,413,97, 281,67
*		<i>Maytenus viscifolia</i> Grisebach			tapia, palta, asperillo, chasqui yuyo, mucamo	134,308,136,413, 281
	116	<i>Maytenus vitis-idaea</i> Grisebach			coique-yuyo, carne gorda, sal de indio, palta, yuquí-guaycurú	378,315,413,9, 281
17		CHENOPODIACEAE				
	49	<i>Allenrolfea patagonica</i> (Moq.) OK.			jume colorado	93,413,379,281
	118	<i>Allenrolfea vaginata</i> (Gris.) OK.			jume, jume negro, jume blanco	378,93,315,413, 379,9,281
	50	<i>Atriplex argentina</i> Spegazzini			cachiyuyo	93,97,281,321
	120	<i>Atriplex cordobensis</i> Gaud. & Stuck.			cachiyuyo	413,379,321
	121	<i>Atriplex eximia</i> Soriano				321
	122	<i>Atriplex lampa</i> (Moquin) Dietrich			cachiyuyo, zampa	9,97,281,321
	123	<i>Atriplex spegazzinii</i> Soriano ex Mülg.			cachiyuyo verde, cach. cresco	321
	51	<i>Heterostachys olivaceus</i> Spegazzini			jumecillo	413, 281

	125	<i>Heterostachys ritteriana</i> (Moq.) Ung. Stern		jumecillo	93,413,379,97, 281,157
	52	<i>Holmbergia tweediei</i> (Moq.) Speg.			93,413,314,97
	53	<i>Salicornia ambigua</i> Mich.		verdolaga salada	413,281
	54	<i>Suaeda divaricata</i> Moq.		jume, vidriera	93,315,413,9, 97,281
18		CONVOLVULACEAE			
	55	<i>Ipomoea hieronymi</i> (OK.) O'Donell			413
	130	<i>Ipomoea stueckertii</i> O'Donell			413,379,281
19		ERYTHROXYLACEAE			
	56	<i>Erythroxylum microphyllum</i> St.-Hil.		tetita de gato	314, h.s.
20		EUPHORBIACEAE			
	57	<i>Acalypha communis</i> Müll. Arg.		albaquilla, hortensia angosta	413,281,67, h.s.
*	133	<i>Acalypha poiretti</i> Spreng.			413,281
	58	<i>Croton bonplandianum</i> Baill.		tupucharó	413,64
	135	<i>Croton parvifolius</i> Müll. Arg.			281
	59	[ <i>Euphorbia</i> spp.] <sup>2</sup>			441
	60	<i>Jatropha chacoana</i> Fernández Casas			167,179
	137	<i>Jatropha excisa</i> Grisebach		higuera del zorro, piñón, sacha higuera, higuerrilla, treinta y tres, higuerón, comida del zorro	134,109,308,413, 9,281,159

<sup>2</sup> No woody species are known for the Chaco, where there occur about 12 herbaceous *Euphorbia* species (Subils, 1977)

	138	<i>Jatropha flavovirens</i> Pax & K.Hoffm.				159
	139	<i>Jatropha grossidentata</i> Pax & K.Hoffm.			piñón	109,379,9
	140	<i>Jatropha hieronymi</i> O.Ktze			piñón, sachá higuera	134,308,256
	141	<i>Jatropha macrocarpa</i> Grisebach			piñón, sachá higuera, ortigón bravo macho	134,308,315,9, 159, 256
	142	<i>Jatropha matacensis</i> Castellanos				109,379
	61	<i>Julocroton subpannosus</i> Müll. Arg.				413,281
	62	<i>Sapium hæmatospermum</i> Müll. Arg.			lecherón, curupí	315,413,281
*	63	<i>Sebastiania klotzschiana</i> (M.A.)M.Arg.			blanquillo, amarillo	134,281
*	64	<i>Stillingia bodenbenderi</i> (OK.)McVaugh			lechilla	379,281
21		FABACEAE				
		CAESALPINIOIDEAE				
	65	<i>Bauhinia argentinensis</i> Burkart var. <i>argentinensis</i>			pata de vaca, pata de buey, ilta'á, wayka amnek	84,178
	66	<i>Caesalpinia gilliesii</i> Wall. ex Hook.			lagaña de perro, barba de chivo, piscala, espiga de amor, mal de ojos, disciplina de monja, etc.	134,378,84,413, 281
*M	149	<i>Caesalpinia mimosifolia</i> Grisebach			pishcalilla	134,84,413
	150	<i>Caesalpinia paraguariensis</i> (D.Parodi) Burkart			guayacán, guayacán negro, ibirá- berá	378,84,315,379, 9,97,67
	151	<i>Caesalpinia stuckertii</i> Hassler			guaycurú, huay-curú, hai-curú	134,84,379

67	152	<i>Cercidium praecox</i> (R. & Pav.) Harms	<i>C. australe</i> Johnston	brea, chañar brea	378,84,315,379, 9,97,281
68	153	<i>Lophocarpinia aculeatifolia</i> (Burkart) Burkart	<i>Cenostigma ? aculeatifolia</i> Burkart	brea del bordo	84,86,379
69	154	<i>Parkinsonia aculeata</i> L.		cina-cina	84,315,97
70	155	<i>Senna acanthoclada</i> (Gris.) Irwin & Barneby	<i>Cassia acanthoclada</i> Gris.		84,413, 379,73, 281
M	156	<i>Senna aphylla</i> (Cav.) Irwin & Barneby	<i>Cassia aphylla</i> Cav.	pichana, pichanilla, retamilla, cabello de indio, escoba dura	134,378,84,109, 315,413,379,73
	157	<i>Senna chacöensis</i> (Bravo) Irwin & Barneby	<i>Cassia chacöensis</i> Br.; <i>C. rigida</i> (Hier.) Burk. var. <i>robusta</i> Burkart	palo mataco, timoyuyo, retama, matorral, timo, barba de tigre	84,315,413,73, 281
	158	<i>Senna chloroclada</i> (Harms) Irwin & Barneby	<i>Cassia chloroclada</i> Harms	sacha-alfa, iauham iaamit [lengua]	84,315,379,9, 74
	159	<i>Senna morongii</i> (Britton) Irwin & Barneby	<i>Cassia morongii</i> Brit.; <i>C. rojasiana</i> Hassler	sen, pito, p. canuto, algarrobo de los caranchos	84,109,413,281, 74
	160	<i>Senna occidentalis</i> (L.) Irwin & Barneby	<i>Cassia occidentalis</i> L.	café cimarrón, café de Bonpland, taperibá, fedegoso	84,109,413,281, 74
	161	<i>Senna spiniflora</i> (Burk.)Irw. & Barneby	<i>Cassia spiniflora</i> Burk.		84,73
	71	<i>Stenodrepanum bergii</i> Harms			84,413,379,281
M	72	<i>Zuccagnia punctata</i> Cavanilles MIMOSOIDEAE		pus-pus, jarilla macho, j. pispito	84,379

73	164	<i>Acacia aroma</i> Gill. ex Hook. & Arn.	<i>A. moniliformis</i> Gris.	tusca, aromita, aroma negro, espinillo Santa Fe	378,84,315,9, 97,281,117,67
	165	<i>Acacia atramentaria</i> Benth.	<i>Prosopis astringens</i> Gill.	espinillo negro, e.bravo, e.fuerte, aroma negro, garabato negro, etc	84,413,281,117
	166	<i>Acacia bonariensis</i> Gill. ex Hook. & Arn.		ñapindá, yuquerí, y. morotí, uña de gato, garabato, g. blanco, etc	84,97,117
	167	<i>Acacia caven</i> (Mol.) Mol. var. <i>caven</i> var. <i>dehiscens</i> Burk. ex Cialdella	<i>A. cavenia</i> (Mol.) H&A.	churqui, aromita, espinillo, e. de bañado, e. Santa Fe, e. flojo, cavén, aroma criollo	378,315,9,117 379,117 117
	168	<i>Acacia curvifructa</i> Burkart		churqui, tusca gorda	84,117,67
	169	<i>Acacia furcatispina</i> Burkart	<i>A. furcata</i> Gill. ex Hook. & Arn.	teatín, brea, tintitaco, garabato negro, g. macho, g. rubio, etc.	378,84,315,9, 97,281,117
	170	<i>Acacia macracantha</i> Humb. & Bonp. ex Willdenow		tusca, jarro	84,315,379,9, 97,117
	171	<i>Acacia praecox</i> Grisebach	<i>A. hassleri</i> Chodat	garabato, g.negro, yuquerí negro	378,84,315,117
	172	<i>Acacia tucumanensis</i> Grisebach	<i>A. riparia</i> auct.	garabato, g. negro, g. blanco	84,315,97,117
*	173	<i>Acacia visco</i> Lor. ex Grisebach	<i>A. polyphylla</i> Clos	visco, v.negro, arca, viste, viscote	84,379,97,117
74	174	<i>Desmanthus brevipes</i> B.L.Turner	<i>D. chacoënsis</i> Burkart		84,87
75	175	<i>Mimosa argentinensis</i> Burkart		vergonzosa	84
	176	<i>Mimosa detinens</i> Benth.		singui, s. blanco, teatín, garabato, g. blanco	378,84,315,413, 9,97,281,67
	177	<i>Mimosa farinosa</i> Grisebach		singui, shingue, tusca blanca	84,315,413,9

76	178	<i>Mimozyanthus carinatus</i> (Gris.) Burkart	<i>Mimosa carinata</i> Gris.	isecayante, lata, diamante	134,378,84,315, 413,9,97,281
77	179	<i>Prosopis</i> <sup>3</sup> <i>abbreviata</i> Benthham		algarrobillo espinoso	134,379,88
	180	<i>Prosopis affinis</i> Sprengel	<i>P. algarobilla</i> Gris.; <i>P. nandubey</i> Lor.ex Gris.	ñandubay, algarrobillo, ibopé-morotí, espinillo	413,97,88
	181	<i>Prosopis alba</i> Grisebach var. <i>alba</i>	<i>P. atacamensis</i> Philip.	algarrobo blanco, árbol, á.blanco, ibopé-pará	378,315,379,9, 97,88,281,67
			<i>P. panta</i> (Gris.)Hieron.	alg. panta, a.impanta, cama tala	134,413,88
*	182	<i>Prosopis campestris</i> Grisebach		algarrobito/illo, alpataco chico	134,413,88,281
M	183	<i>Prosopis chilensis</i> (Mol.) Stuntz emend. Burkart var. <i>chilensis</i>	<i>Ceratonia chilensis</i> Molina	algarrobo, a. blanco, a. chileno, árbol blanco	134,315,413,88, 281
	184	<i>Prosopis elata</i> (Burkart) Burkart	<i>P. campestris</i> Gris. var. <i>elata</i> Burkart	algarrobito, huaschillo, guajchillo, quiscataco	315,413,88,281, 67
	185	<i>Prosopis fiebrigii</i> Harms			88
	186	<i>Prosopis hassleri</i> Harms var. <i>hassleri</i> var. <i>nigroides</i> Burkart		algarrobo paraguay, ibopé-hú	134,88,67
*	187	<i>Prosopis humilis</i> Gill. ex Hook. & Arn.		algarrobo amarillo	88
	188	<i>Prosopis kuntzei</i> Harms	<i>P. barbatigradis</i> Stuck.; <i>P. casadensis</i> Penzig	algarrobilla, barba de tigre palo mataco, jacarandá, barba de tigre, itín, carandá, lanza-lanza	134,413,88,281 378,315,413,379, 97,88,281,67

3 A number of natural hybrids between some of the Chaco species of *Prosopis* have been studied by Palacios & Bravo (1981): *P. ruscifolia* x *P. nigra*, *P. ruscifolia* x *P. alba*, *P. ruscifolia* x *P. hassleri*, *P. hassleri* x *P. alba*, *P. hassleri* x *P. fiebrigii*, *P. hassleri* x *P. nigra*, *P. alba* x *P. nigra*, *P. alba* x *P. fiebrigii*, *P. hassleri* x *P. fiebrigii* x *P. alba*.

	189	<i>Prosopis nigra</i> (Grisebach) Hieronymus var. <i>nigra</i> var. <i>ragonesei</i> Burkart var. <i>longispina</i> Burkart	<i>P. dulcis</i> Kunth var. <i>australis</i> Benth	algarrobo negro, yura-tacu, árbol negro, ibopé-hú algarrobo amarillo algarrobillo	378,315,379,9 97,88,281,67 413,88 88
	190	<i>Prosopis pugionata</i> Burkart		algarrobo de las salinas, alpataco	413,379,88,281
	191	<i>Prosopis reptans</i> Benth. var. <i>reptans</i>		mastuerzo, retortuño, retortón	93,413,97,88
	192	<i>Prosopis rojasiana</i> Burkart	<i>P. striata</i> sensu Fiebrig		88
	193	<i>Prosopis ruscifolia</i> Grisebach		vinal, visnal, ibopé-morotí, quilín, algarrobo blanco	378,315,379,315, 97,88,281
	194	<i>Prosopis sericantha</i> Gill. ex Hook. & Arn.		barba de tigre, albardón, temoj, retama, huaschilla, timo-yuyo	315,315,413,379, 9,88,281
M	195	<i>Prosopis torquata</i> (Cav. ex Lagasca) DC.	<i>P. adesmioides</i> Gris.	quenti, tintitaco, schinqui, tusca, lata, ischilín, quintitacu, etc.	378,315,413,97, 88,281
	196	<i>Prosopis vinalillo</i> Stuckert		vinalillo, quilín, algarrobo santiagueño	378,315,413,9, 97,88
		PAPILIONOIDEAE			
*	78	<i>Apurimacia dolichocarpa</i> (Gris.) Burk.	<i>Tephrosia dolich.</i> Gris.		84,379,281
*	79	<i>Collaea argentina</i> Gris.			84,91
	80	<i>Coursetia hassleri</i> Chodat 4	<i>C. guaranitica</i> Chod.; <i>Cracca corumbae</i> Hoeh		281,84,253, Lavin, in litt.

4 Usually known in the Argentine literature as *Benthamantha glabrescens* (Benth.) Burkart (a combination never legitimately published by Burkart, and in any case superfluous to *B. glabrescens* (Benth.) Alefeld) or *Cracca glabrescens* (Benth.) Benth., all of which are at present synonyms of *C.*



81	200	<i>Geoffroea decorticans</i> (Hook. & Arn.) Burkart	<i>Gourleia decorticans</i> Gill. ex Hook. & Arn.	chañar	378,83,315,379, 9,97,281,67
* 82	201	<i>Psoralea higuera</i> Gill.	<i>P. higuera</i> Gris.	higuera	84,91
* M 83	202	<i>Ramoinoa giroloae</i> Spegazzini		chica	84,379
* 84	203	<i>Sophora linearifolia</i> Grisebach			84,379,281
22		FLACOURTIACEAE			
* 85	204	<i>Banara umbraticola</i> Arechav.			413,281
23		LAMIACEAE			
* 86	205	<i>Minthostachys mollis</i> Berg		peperina, poleo	134,97,64
* 87	206	<i>Minthostachys verticillata</i> (Gris.) Epling		peperina	281,453
24		LOBELIACEAE			
* 87	207	<i>Siphocampylus foliosus</i> Grisebach			281,91
25		LYTHRACEAE			
88	208	<i>Heimia salicifolia</i> (Kunth) Link		quiebra arado	413,9,97,281
26		MALPIGHIACEAE			
* 89	209	<i>Cordoba argentea</i> (Gris.) Niedenzu			336,329,413,281
90	210	<i>Janusia guaranitica</i> (St.-Hil.) Juss.		mariposa, loconte chico	336,329,413,67
* 91	211	<i>Mionandra camareoides</i> Grisebach			336
M 92	212	<i>Tricomaria usillo</i> (Gill.) Hook. & Arn.		usillo, surf pelado	336,329,413,281

*caribaea* (Jacq.) Lavin var. *ochroleuca* (Jacq.) Lavin (Lavin, 1988) which reaches neither Argentina nor the Chaco. In Lavin's view (*in litt.*) Fig. 72 in Burkart (1952, p.262) is definitely *C. hassleri* Chod., and in all likelihood this is the taxon generally misidentified for *B. glabrescens* (see Adámoli et al., 1972; Luti et al., 1979).

27		MALVACEAE				
93	213	<i>Abutilon virgatum</i> (Cav.) Sw.				413,7,281
94	214	<i>Pavonia argentina</i> Gürk.				413
95	215	<i>Sida argentina</i> K.Schum.				315,413,281
	216	<i>Sida dictyocarpa</i> Grisebach				109,315,9,67
	217	<i>Sida spinosa</i> L.				315,281,67, h.s.
96	218	<i>Sphaeralcea bonariensis</i> (Cav.) Gris.			malvisco	109,315,67
	219	<i>Sphaeralcea miniata</i> (Cav.) Spach.				97
97	220	<i>Wissadula densiflora</i> R.E.Fries				315,413,281,67
28		MENISPERMACEAE				
98	221	<i>Cissampelos pareira</i> L. var. <i>gardneri</i> Diels			zarza, caá-pebá, pareira brava, mbaracayá-nambí	134,109,64,228
99	222	<i>Odontocarya asarifolia</i> Barneby				39
	223	<i>Odontocarya thamnoides</i> (DC.) Miers			uva del monte	134,64,228
29		MYRTACEAE				
*	100	<i>Myrcianthes cisplatensis</i> (Camb.) Berg.		<i>Eugenia cispl.</i> Camb.	mato, vil-vil, güili, sachá mato	136,413,281
30		NYCTAGINACEAE				
	101	<i>Bougainvillea campanulata</i> Heimerl.			palo amarillo, guáncar, espuela de gallo, coronillo	134,315,9,451, 67,452
	226	<i>Bougainvillea infesta</i> Grisebach			duraznillo	134,315,452,97
	227	<i>Bougainvillea praecox</i> Grisebach			duraznillo	134,315,452,97
M	228	<i>Bougainvillea spinosa</i> (Cav.) Heimerl.				134,413,452

*M	229	<i>Bougainvillea stipitata</i> Grisebach			alfiler/illo, taludo, guáncar falso, talafalsa, coronillo blanco	134,413,451,281,452
31		OLACACEAE				
102	230	<i>Ximena americana</i> L.		<i>Amyris</i> ? <i>arborescens</i> P. Browne	albaricoque, albarillo del campo, pata, p. del monte, albaria, etc.	134,378,109,413,281,64,428,67
32		OLEACEAE				
103	231	<i>Menodora integrifolia</i> (Cham. & Schlech.) Steyerl.				413,97,281,64,228,67
33		POLYGALACEAE				
*	104	<i>Monnina dictyocarpa</i> Grisebach				413,228
34		POLYGONACEAE				
105	233	<i>Ruprechtia apetala</i> Weddell		<i>R. corylifolia</i> Gris.; <i>R. mollis</i> Wedd.; <i>R. boliviensis</i> Herzog	manzano del campo, higuérón /illa, h. macho/hembra, sachá manzana, duraznillo, d. blanco	378,119,315,120,413,379,9,97,281,67
	234	<i>Ruprechtia triflora</i> Grisebach		<i>Triptaris triflora</i> (Gris.) O. Kuntze	duraznillo colorado, d. blanco, choroqui, guaimí-piré	378,109,119,315,120,379,9,67
35		PORTULACACEAE				
106	235	<i>Amphipetalum paraguayense</i> Bacig. <sup>5</sup>			initsakás [Manjuy I]	41
107	236	<i>Grahamia bracteata</i> Gill. ex Hook. & Arn.			vinagrillo	134,93,413,97,281,157

5 This is a herbaceous plant, though with a thick, fleshy root, included here because this recently described genus (*Bacigalupo*, 1988) is endemic to the Chaco.

36		RANUNCULACEAE						
	108	<i>Clematis montevidensis</i> Spreng.	<i>C. hilarii</i> Spreng.		loconte, bejuco, centella, barba de viejo, zarza, cabello de indio, etc.	134,413,314,281,453,67		
37		RHAMNACEAE						
*M	109	<i>Colletia spinosissima</i> Gmel.	<i>C. horrida</i> Wildenow; <i>C. spinosa</i> Lam.		tola, crucero/fillo, chacay, barba de tigre, brusquilla, espino negro	134,155,413,97,281		
*	110	<i>Condalia buxifolia</i> Reissek			piquillín grande, p. negro, p. de la sierra, orta	134,155,136,64		
	240	<i>Condalia microphylla</i> Cav.	<i>C. lineata</i> A.Gray		piquillín, p. rubio	155,378,315,413,97,281,64		
*	241	<i>Condalia montana</i> Castellanos			piquillín de la sierra, p. negro	155,413,281		
	111	<i>Scutia buxifolia</i> Reissek	<i>Adolia bux.</i> (Reiss.)OK.		coronillo	155,378,234,97		
	112	<i>Ziziphus mistol</i> Grisebach			mistol	155,378,315,413,9,97,281,67		
38		ROSACEAE						
*	113	<i>Kageneckia lanceolata</i> Ruiz & Pavón			sacha durazno, d. de la sierra	134,413,281,256		
39		RUTACEAE						
*	114	<i>Fagara coco</i> (Gill.) Engler	<i>Zanthoxylum coco</i> Gill.		coco, coc(h)ucho, sauco hediondo	378,156,413,379		
40		SANTALACEAE						
	115	<i>Acanthosyrus falcata</i> (Mart. & Eichler) Grisebach			sacha pera, saucillo, sombra de toro hembra	378,109,315,150,97		

116	247	<i>Jodina rhombifolia</i> Hook. & Arn.	<i>J. ruscifolia</i> H. & Arn.;	sombra de toro, quebracho flojo,	378,315,136,413,
41		SAPINDACEAE	<i>J. cuneifolia</i> Miers	peje, chuán, quinchilín	150,97,281
117	248	<i>Allophylus edulis</i> (St.-Hil.) Radlk.	<i>Schmidelia edulis</i> St.-Hil.	chalchal, koku, picazú-rembiú,	134,378,136,9,
118	249	<i>Urvillea uniloba</i> Radlk.		coquy, comida de paloma, etc.	7,64
42		SAPOTACEAE			413,7
119	250	<i>Sideroxylon obtusifolium</i> (Roem. & Schult.) Pennington subsp. <i>obtusifolium</i>	<i>Bumelia obtusifolia</i> Roem. & Schult.; <i>B. sartorum</i> Martius	guaraniná, molle blanco, m. del monte, m.crespo, m.negro, ibirániná, horco-molle, chiri-molle	134,378,136,109, 413,314,7,97,281, 67,351
43		SCROPHULARIACEAE			
*M	251	<i>Monttea schickendantzii</i> Hieron.		tintillo, olivillo	134,281
44		SIMARUBACEAE			
121	252	<i>Castela coccinea</i> Grisebach		meloncillo, molle negro, mistol del zorro, quillai, sacha-melón	378,109,315,413, 9,97,281,67
45		SOLANACEAE			
122	253	<i>Capsicum chacoense</i> A.T. Hunziker		ají silvestre	314,281
123	254	<i>Cestrum parquii</i> L'Héritier		duraznillo negro	281
124	255	<i>Grabowskia duplicata</i> Arnott		burro micuna, pata, matorral	315,413,314,97, 281,67
	256	<i>Grabowskia obtusa</i> Arnott		burro micuna, matorral, uña de tigre, chil, albaricoque	134,109,315,314

125	257	<i>Lycium americanum</i> Jacquin			chile, chili, yuquyrá menor	314,60
	258	<i>Lycium athium</i> Bernardello				60
	259	<i>Lycium cestroides</i> Schlechtendal		<i>Acnistus cestroides</i> (Schlech.) Miers	comida devbora, ischivil, chile/i, tala churqui, chivil, talilla, etc.	413,281,60
M	260	<i>Lycium chilense</i> Miers ex Bertero <b>var. chilense</b>		<i>L. scoparium</i> Miers; <i>L. hunzikeri</i> Barkley	yaoyín, yauyín, coralillo	413,60
M		<b>var. confertifolium</b> (Miers) Barkley		<i>L. melanopotamicum</i> Niederlein		60
M		<b>var. filifolium</b> (Miers) Bernardello		<i>L. filifolium</i> G. ex Ms.	yauyín, frutita de la vbora	60
	261	<i>Lycium ciliatum</i> Schlechtendal		<i>L. argentinum</i> Hieron.	chivil, comida de vbora, c. burro	315,413,60
	262	<i>Lycium cuneatum</i> Dammer		<i>L.c. var. rojasii</i> Barkl.	tala, t.negro, penkoshit, etc.	60
	263	<i>Lycium elongatum</i> Miers		<i>L. confertum</i> Miers	comida de mula, pinchagua	281,60
	264	<i>Lycium infaustum</i> Miers		<i>L. tweedianum</i> Gris.	pela surí, chil, tomatillo	413,281,60
	265	<i>Lycium morongii</i> Britton		<i>L.m. var. indutum</i> Hler	pie de calva, yuá, keesiték	60
	266	<i>Lycium nodosum</i> Miers			chiguil, yuá chico, fecijciuk	60
M	267	<i>Lycium tenuispinosum</i> Miers <b>var. tenuispinosum</b>		<i>L. pubescens</i> Miers; <i>L. spinulosum</i> Miers	pela surí, piquillín de las vboras, yauyín espinudo	413,281,60
M		<b>var. friesii</b> (Dammer) Hitchcock		<i>L. venturii</i> Hitchcock	comida de mula, pinchagua	60
126	268	<i>Solanum argentinum</i> Bitt. & Lillo			cabrayuyo, c. negro, afata, hediódilla del monte	315,9,281,67
	269	<i>Solanum chroniotrichum</i> Morton			cabrayuyo	h.s.
	270	<i>Solanum diflorum</i> Vell.				h.s.

	271	<i>Solanum glaucophyllum</i> Desf.	<i>S. malacoxylon</i> Sendt.	duraznillo, d. blanco, varilla	314,9,97
127	272	<i>Vassobia breviflora</i> (Sendtner) Hunziker	<i>Acnistus brev.</i> Sendt.; <i>A. parviflorus</i> Gris.	candelilla, chalchal de gallina, yuá, ischivil, palo negro, etc.	314,229, h.s.
46		STERCULIACEAE			
128	273	<i>Ayenia acalyphifolia</i> Grisebach			128
*	274	<i>Ayenia cordobensis</i> (Hieron.) Hieron.			128,281
	275	<i>Ayenia eliae</i> Cristóbal			128,67
	276	<i>Ayenia lingulata</i> Grisebach			128
	277	<i>Ayenia o'donellii</i> Cristóbal			315,128,67
47		ULMACEAE			
129	278	<i>Celtis pallida</i> Torrey subsp. <i>pallida</i>	<i>C. spinosa</i> Spr. var. <i>pallida</i> (Torr.) Johnston		405,281
		subsp. <i>sericea</i> (Romanc.) Rom. & Mart.	<i>C. sericea</i> Romanczuk; [ <i>C. chichape</i> (Wedd) Miq.]	tala negra, t. chica, t. churqui, t. pispa	315,413,97,405
	279	<i>Celtis spinosa</i> Sprengel		tala	378,97,405
	280	<i>Celtis tala</i> Gill. ex Planchon	<i>C. sellowiana</i> Miquel	tala	315,413,97,405
48		VERBENACEAE			
*M	130	<i>Aloysia catamarcensis</i> Mold.		salvia blanca	68
	282	<i>Aloysia gratissima</i> (Gill. & Hook.) Tronc var. <i>gratissima</i>	<i>A. lycioides</i> Cham.; <i>Lippia lycioides</i> (Cham.) Steud.	azahar del campo, palo de ángel, poleo del campo, p. chaqueño, niño- rupá chico, cedrón d. monte	134,314,97,281, 68,64,453,67
		var. <i>angustifolia</i> (Tronc.) Botta			68

		<i>var. chacoensis</i> (Mold.) Botta	<i>A. chacoensis</i> Mold.		68
		<i>var. schulziana</i> (Mold.) Botta			68
	283	<i>Aloysia polystachia</i> (Gris.) Mold.	<i>Lippia polystachia</i> Gris	poleo real/de Castilla, té de burro	68,453
*	284	<i>Aloysia scorodonioides</i> (Kunth) Cham. <i>var. scorodonioides</i>			68,67
	131	<i>Lippia integrifolia</i> (Gris.) Hieron.	<i>L. turbinata</i> Gris. <i>var. integrifolia</i> Gris.	poleo, manzanillo, té de inca	134,413,379,281, 453
	286	<i>Lippia salsa</i> Grisebach		yerba del ciervo	413,281,157, h.s.
	287	<i>Lippia turbinata</i> Grisebach		poleo, té del país	413,7,281
M	132	<i>Xeroaloyisia ovatifolia</i> (Mold.) Tronc.	<i>Aloysia ovatifolia</i> Mold.		458,281
49		ZYGOPHYLLACEAE			
	133	<i>Bulnesia bonariensis</i> Grisebach		guacle, jaboncillo, laca, gluaca, guacho/a, palo flojo	134,378,315,413, 97,281,343,67
	290	<i>Bulnesia foliosa</i> Grisebach		palo jabón, jaboncillo, retamo de salinas, r. hojudo	315,413,97,343, 230
M	291	<i>Bulnesia retama</i> (Gill. ex H. & A.) Gris.	<i>B. macrocarpa</i> Phil.	retamo, retama	413,379,281,343
	292	<i>Bulnesia sarmientoi</i> Lorentz ex Gris.	<i>B. gancedoi</i> Rojas	palo santo, hok [Matacol], guayacán (Bolivia)	134,378,109,315, 9,97,230,343
M	293	<i>Bulnesia schickendantzii</i> Hieron.		rodajillo	379,343
M	134	<i>Larrea cuneifolia</i> Cav.		jarilla pispa, j.crespa, j.macho, j. del campo	134,378,413,379, 281



M	295	<i>Larrea divaricata</i> Cav.		jarilla, j.hembra, j. del cerro	134,378,315,413, 7,281
M	135	<i>Plectrocarpa tetracantha</i> Gill. ex Hook. & Arn.		rodajillo	413,97,281,157
	136	<i>Porlieria microphylla</i> (Baill.) Desc., O'Don. & Lourt.		cucharero, palo cuchara, chucupí, guayacán, chucupí	378,315,413,9, 97,281,67

#### 4.2- Woody and succulent species of the Caatingas :

In the floristic list of woody and succulent species of the Caatingas, those indicated with an asterisk (\*) correspond to the more characteristic taxa known to occur in the region, based mainly in Andrade-Lima's works (1954,1960,1970,1981). In the 'Main Synonym' column the names between brackets (...) are common identification mistakes or binomials wrongly applied to the entities shown in the 'Species Name' column, not to be treated as taxonomic synonyms. In the 'References' column, h.s. stands for 'herbarium specimens' in those cases in which exsiccata have been taken by the present author as evidence of the alleged presence of the species in the area.

Fly	Gen	Sp	SPECIES NAME	MAIN SYNONYM	VERNACULAR NAME	REFERENCES
Nº	Nº	Nº				
1			ANACARDIACEAE			
	1	1	<i>Astronium concinnum</i> Schott	<i>A. macrocalyx</i> Engler	itapicurú vermelho, i.ferreiro, guaribú, aroeira do Mucury	48,51
*		2	<i>Astronium urundeuva</i> (Fr.All.) Engler		aroeira	17,18,29,31,33,168, 170,153,400,180, 51,106,173, 337,36
	2	3	<i>Loxopterigium gardneri</i> Engler	<i>Apterokarpos gardneri</i> (Engl.) Rizzini	aroeira-mole	46,396,397,51
*	3	4	<i>Schinopsis brasiliensis</i> Engler var. <i>brasiliensis</i>		brauna, baraúna	17,18,29,31,32,168, 34,170,400,180,51, 174,106, 337,36
			var. <i>glabra</i> Engler	<i>S. glabra</i> (En.)B.&Mey.	brauna, baraúna, b. do norte	304

* 4	5	<i>Spondias tuberosa</i> Arruda		imbuzeiro, imbú, umbú, umbuzeiro	12,17,18,28,29,397, 168,170,153,400, 200,51,106, 337,36
2		ANNONACEAE			
5	6	<i>Annona spinescens</i> Mart.		araticum-de-espinho	280,208,34?,51, 106?
	7	<i>Annona vepertorum</i> Mart.		bruteiro	280,208,34?,51, 106?
6	8	<i>Rolliniopsis leptopetala</i> (Fries) Safford			208,180
3		APOCYNACEAE			
7	9	<i>Allamanda blanchetii</i> A.DC.		pente-de-mocó, quatro-patacas, sete-patacas, sete-patacas roxa	32?,153?,180,36
	10	<i>Allamanda martii</i> Müll. Arg.			36
	11	<i>Allamanda puberula</i> DC. var. <i>puberula</i> var. <i>glabrata</i> Müll. Arg.		sete-patacas, sete-p. amarela	397,208,153?,36
	12	<i>Allamanda cnotherifolia</i> Pohl			208
8	13	<i>Aspidosperma cuspa</i> (Kunth) Blake		pereiro, p. branco, p. amargo/so	397,208
	14	<i>Aspidosperma discolor</i> A.DC.		pau-pereiro, peroba, caranaúba	397,153,174,286
*	15	<i>Aspidosperma polyneuron</i> Müll. Arg.		amargoso, palo rosa	286
	16	<i>Aspidosperma pyrifolium</i> Mart.		pereiro, pau-pereiro	51,286
				<i>A. refractum</i> Mart.; <i>A.</i> <i>populifolium</i> A.DC.	17,18,33,168,170, 400,180,51,106, 173,337,286,212, 36

	17	<i>Aspidosperma riedelii</i> Müll. Arg. subsp. <i>oliganthum</i> (Wood.) Marc.-Ferr.	<i>A. oliganthum</i> Woodson		286
	9	<i>Rauwolfia pauciflora</i> DC.			208
	10	<i>Skytanthus hancorniaefolius</i> Mart.			32,208
4		ARALIACEAE			
	11	<i>Pentapanax warmingianus</i> (Marchal) Harms	<i>Coemansia w.</i> March.; <i>Coudenbergia w.</i> Marc.	tingui-bravo, salbugueirão	35,51
5		ARECACEAE			
*	12	<i>Copernicia cerifera</i> (Arr.Cam.) Mart.	<i>C. prunifera</i> (Miller) H.E. Moore	carnaúba, carnaubeira	17,18,34,153,51, 173,36
	13	<i>Syagrus comosa</i> (Mart.) Mart.		catolé	280,195
*	23	<i>Syagrus coronata</i> (Mart.) Becc.		ouricuri, licuri	280,18,34,51,195
	24	<i>Syagrus microphylla</i> Burret			195
	25	<i>Syagrus oleracea</i> (Mart.) Becc.		catolé, coco catolé	180,106,195,36
	26	<i>Syagrus vagans</i> (Bondar) Hawkes		ariri, licurioba	195
	27	<i>Syagrus wedermannii</i> Burret		coco da vassoura	195
	28	<i>Syagrus x matafome</i> (Bondar) Glassm.		matafome, coco matafome	51,195
6		ASTERACEAE			
	14	<i>Blanchetia heterotricha</i> DC.			208
	15	<i>Dasyphyllum candolleum</i> (Gardner) Cabrera	<i>Flotovia candolleana</i> Gardner		94
	16	<i>Eremanthus martii</i> Baker		chico-Rodrigo	280,208,153

17	32	<i>Ldgasea mollis</i> Cav.				440,208
18	33	<i>Pectis decumbens</i> (Gard.) Sch.Bip.				52
	34	<i>Pectis elongata</i> Kunth			cuminho-bravo, alecrim, etc.	52
	35	<i>Pectis linifolia</i> L. var. <i>linifolia</i>				52
19	36	<i>Telmatophila scolymastrum</i> Mart. ex Baker			carrapicho-de-lagoa	36
	37	<i>Wunderlichia crulsiana</i> Taub.				280
7		BIGNONIACEAE				
21	38	<i>Anemopaegma velutinum</i> Mart. ex DC.				208, h.s.
22	39	<i>Arrabidea chica</i> (Humb.& Bonpl.) Verl.			cipó preta da serra	337
	40	<i>Arrabidea corallina</i> (Jacq.) Sandwith		<i>Bignonia</i> cor. Jacq.; A. <i>rhodantha</i> Bur.& Sch.	cipó açoita cavalo	337
23	41	<i>Cuspidaria argentea</i> (Wawra) Sandw.				208
24	42	<i>Godmania dardanoi</i> (J.C.Gomes) Gentry		<i>Xeroteca dardanoi</i> J.C.Gomes	umbigo-de-viúva, chifre-de-carneiro	28,397,188,35,51, 36
25	43	<i>Jacaranda irwinii</i> A.H. Gentry				306
	44	<i>Jacaranda jasminoides</i> (Thunb.) Sand.				208,306
26	45	<i>Pyrostegia venusta</i> (Ker.) Miers				280,337
*	27	<i>Tabebuia aurea</i> (Manso) ? [Gentry, in litt.]		<i>T. caraiba</i> (Mart.) Bur.	craibeira, caraibeira, paratudo	17,18,28,168,170, 400,51,106,36

*	47	<i>Tabebuia impetiginosa</i> (Mart. ex DC.) Standley	<i>T. avellaneda</i> Lorentz ex Griseb.; <i>T. ipe</i> (Mart. ex Schum.) Standley	pau d'arco roxo	31,32,34,153,180,51,173,337
	48	<i>Tabebuia roseo-alba</i> (Ridley) Sandwith		paudarquinho	32, Proença (pers. comm.)
	49	<i>Tabebuia spongiosa</i> Rizzini		sete-cascas, cascudo	397,153,180,106,36
8		BOMBACACEAE			
*	28	<i>Cavanillesia arborea</i> Schum.		barriguda, b. lisa, embaré, imbaré	283,31,32,168,34,51,360,36
*	29	<i>Ceiba glaziovii</i> (Kuntze) Schum.	<i>Chorisia gl.</i> (K.) Sant.; [Ceiba erianthos Sch.]	barriguda	17,283,31,168,34,180?,51,360,36
	30	<i>Eriotheca parvifolia</i> (Mart. & Zucc.) Robyns	<i>Bombax parvifolium</i> Mart. & Zucc.	embiratanha?	399,22?,173,337?
*	31	<i>Pseudobombax simplicifolium</i> Robyns		embiratanha, imbiratanha, imbiracu, imbirucu, imburucu	399,29?,397,32,170,153,51,106,36
9		BORAGINACEAE			
	32	<i>Auxemma glazioviana</i> Taub.		pau-branco, folha larga	22,397,51,173
*	33	<i>Auxemma oncocalyx</i> (Fr. All.) Taub.		pau-branco, frei-jorge	22,33,34,51,173,36
	36	<i>Cordia curassavica</i> (J.) Roem. & Schult.			445
	37	<i>Cordia dardani</i> Taroda			445
	38	<i>Cordia globosa</i> (Jacq.) Kunth		moleque-duro branco/pequeno	180,445,106,282
	39	<i>Cordia insignis</i> Cham.		folha larga	397,32,180,51,446

*	60	<i>Cordia leucocephala</i> Moricand			moleque-duro, m.-d. preto, m.-d. grande, negro-duro	17,33,168,34,170, 153,171,180,200, 445,106,337,36, 282
*	61	<i>Cordia trichotoma</i> (Vell.) Arrab. ex Steud.		[complex with <i>C. alliodora</i> (R.&P.) Oken]	freijorge, claraiba, freijó, cabo-de-machado	138,32,153,193, 174,51,173,446, 337
	34	<i>Patagonula bahiensis</i> Moricand			mulambá	397,208,51, h.s.
	35	<i>Tournefortia rubicunda</i> Salzm. ex DC.				208
10		BROMELIACEAE				
	36	<i>Aechmea aquilega</i> (Salisbury) Gris. var. <i>chrysocoma</i> (Baker) L.B. Smith		<i>A. chrysocoma</i> Baker; <i>Hohenbergia</i> c. Baker	croatá	432
	65	<i>Aechmea eurycorymbus</i> Harms				432
	66	<i>Aechmea lingulata</i> (L.) Baker var. <i>lingulata</i>		<i>Hohenbergia odora</i> (Mq)Bak; <i>Bromelia</i> l. L.	gravatá	432
	37	<i>Billbergia porteana</i> Brongniart ex Beer				280,432,400
*	38	<i>Bromelia laciniosa</i> Mart. ex Schult.			macambira, macambira-de-cachorro	17,18,26,168,170, 153,200,106,36
	39	<i>Cottendorfia florida</i> Schultes f.				280,432
	40	<i>Dyckia dissitiflora</i> Schultes				432
	71	<i>Dyckia limae</i> L.B. Smith				432
	72	<i>Dyckia pernambucana</i> L.B. Smith				432
*	41	<i>Encholirium spectabile</i> Mart. ex Schult.			macambira-de-boi, m.-de-lajedo (lajeiro), m.-de-flecha/pedra	138,26,32,432,212, 36

	42		74	<i>Hohenbergia caatingae</i> Ule			gravatá	26,34,200
*	43		75	<i>Neoglaziovia variegata</i> Mez			caroá, crauá	17,18,26,32,168, 170,153,200,180, 106
	44		76	<i>Pitcairnia flammea</i> Lindl. var. <i>floccosa</i> L.B. Smith		<i>P. muscosa</i> Mart. ex Schult. f.		280,432
11				BURSERACEAE				
*	45		77	<i>Commiphora leptophloeos</i> (Mart.) Gillet		<i>Bursera leptophloeos</i> Mart.	imburana, imburana vermelha, imburana de cambão, imburana de espinho	17,18,22,29,31,397, 32,33,194,168,34, 29,153,51
12				CACTACEAE				
	46		78	<i>Acanthocereus ? albicaulis</i> Br. & Rose				280,24,90
			79	<i>Acanthocereus brasiliensis</i> Br. & Rose				76,90
	47		80	<i>Arrojadoa penicillata</i> (Gürke)Br.& Rose			rabo de raposa	36
			81	<i>Arrojadoa rhodantha</i> (Gürke)Br.& Rose			rabo de raposa, rabo de onça	280,24,90,400,106
	48		82	<i>Austrocephalocereus dybowskii</i> (Gosselin) Backeberg		<i>Cephalocereus</i> <i>dybowskii</i> (Goss.)Br&R	cabeça branca, cabeça-de-velho, mandacarú de penacho	76,36
			83	<i>Austrocephalocereus purpureus</i> (Gürke) Backeberg		<i>Cephalocereus purpureus</i> Gürke	mandacarú falso	76,32
	49		84	<i>Brasiliopuntia bahiensis</i> (Britt. & Rose) Berger		<i>Opuntia bahiensis</i> Br.& Rose	palminha, quipá, rumbeba, mumbeca, mumbeba	280,17,24,90,28, 168



* 50	<i>Cereus jamacaru</i> P.DC. non SD. ex Pfeiffer		mandacari, cardeiro	17,18,29,31,168, 170,153,180,51, 106,173,337,36
51	<i>Discocactus bahiensis</i> Britt. & Rose			76,90
52	<i>Discocactus placentiformis</i> (Leh.) Sch.			76,90
53	<i>Discocactus zehntneri</i> Britt. & Rose			76,90
54	<i>Eriocereus adscendens</i> (Gürke) Berger	<i>Harrisia adscendens</i> (Gürke) Britt. & Rose	rabo de raposa, chegue-pra-lá	280,17,24,90,168, 180,106,36
55	<i>Espostoa ulei</i> (Gürke) Buxbaum	<i>Facheiroa ulei</i> (Gür.) Wer. <i>F. pubiflora</i> Br&R	facheiro	90,71
* 56	<i>Leocereus bahiensis</i> Britt. & Rose		rabo de raposa	76
57	<i>Melocactus bahiensis</i> Britt. & Rose		coroa-de-frade, croa-de-frade, cabeça-de-frade	76,280,17,24,168, 34,170,153,106
58	<i>Melocactus horridus</i> Werdermann		coroa-de-frade	24,259
59	<i>Melocactus oreas</i> Miquel		coroa-de-frade, croa-de-frade	76,24,36
60	<i>Melocactus zehntneri</i> (Br. & Rose) Back.		coroa-de-frade	76,280,24,32
61	<i>Micranthocereus polyanthus</i> (Wer)Back			90
* 62	<i>Opuntia inamoena</i> K.Schum.		quipá, quipá liso	280,17,18,24,168, 170,153,106,36
63	<i>Opuntia palmadora</i> Britt. & Rose		palmtoria, p. brava, quipá, palminha	280,24,168,34,170, 106,36
64	<i>Pereskia aureiflora</i> Ritter		facho, ora pro nobis da mata	260

	100	<i>Pereskia bahiensis</i> Gürke			quiabento, inh(i)abento, flor de cêra, espinha de Sto Antônio	76,260,36
	101	<i>Pereskia stenantha</i> Ritter			quiabento, flor de cêra, espinha de Santo Antônio	260
59	102	<i>Pilosocereus catiingicola</i> (Gür.)B. & Row.				76
	103	<i>Pilosocereus chrysostele</i> (Vaup.) Byl. & Rowl.		<i>Pilocereus c.</i> (Vp.)Werd	facheiro da serra	280,24
	104	<i>Pilosocereus glaucescens</i> (Lab.) Byl. & Rowl.			facheiro, facheiro azul	76,400,180,106,36
*	105	<i>Pilosocereus gounellei</i> (Web.) Byl. & Rowl.		<i>Pilocereus gounellei</i> Web.; <i>Cereus gounellei</i> K.Sch.	xique-xique, alastrado	280,17,18,24,168,34,170,153,400,180,106,337,36
*	106	<i>Pilosocereus piauiensis</i> (Gürke) Byl. & Rowl.		<i>Pilocereus p.</i> (Gür.) Wer.; <i>Cephalocereus p.</i> (Gürke.) Br. & Rose	facheiro	280,24,33,168,34,170?,400,51,36
*	107	<i>Pilosocereus tuberculatus</i> (Werd.)Byl. & Rowl.		<i>Pilocereus tuberculatus</i> Werd.	caxacubri	17,18,24,34,400
	108	<i>Pilosocereus zehntneri</i> (Br. & R.)Byl. & Rowl.		<i>Cephalocereus zehntneri</i> Br. & Rose	xique-xique das pedras	76
60	109	<i>Quiabentia zehntneri</i> (Br. & R.)Br. & Rose		<i>Pereskia z.</i> Br. & Rose	quiabêncio, quiabento	108,90,32
61	110	<i>Stephanocereus leucosteale</i> (Gürke) Berger		<i>Cephalocereus leucosteale</i> (Gür.) B&R		90

62	111	<i>Tacinga atropurpurea</i> Werdermann var. <i>atropurpurea</i>			161	
		var. <i>zehntnerioides</i> Backeberg			161	
	112	<i>Tacinga braunii</i> Esteves			161	
	113	<i>Tacinga funalis</i> Britton & Rose		quipá voador	76,280,24,90,36	
*	63	<i>Zehntnerella squamulosa</i> Britton & Rose [ <i>Facheiroa squamosa</i> (Gür.) Br. & Esteves]	<i>Cereus squamosus</i> Gürke; <i>Leocereus sq.</i> (Gür.) Werd.	facheiro-preta, facheiro	280,90,32,168,34, 173,261,71,337	
13		CAPPARIDACEAE				
64	115	<i>Capparis flexuosa</i> L. ( <i>sensu lato</i> )	[ <i>C. cynophallophora</i> L.]	feijão-bravo, feijão-de-boi	168,180,174,51, 106,337,282, h.s.	
*	116	<i>Capparis jacobinae</i> Moric. ex Eichler	<i>Colicodendron jacobinae</i> (Mor.) Hut.	icó-prêto, icó-de-cavalo	17,18,397,168,180, 200,51,36	
*	117	<i>Cápparis yco</i> Mart.	<i>Colicodendron yco</i> (Mart.) Hutchinson	icó-branco, icó	280,17,18,397,168, 200,106,36	
65	118	<i>Cratèva tapia</i> L.		trapiá	138,415,153,51	
66	119	<i>Haplocarpum bahiense</i> Ule			349	
14		CARICACEAE				
67	120	<i>Carica quercifolia</i> (St.-Hil.) Hieron.		mamaozinho	43	
68	121	<i>Jacaratia spinosa</i> (Aublet) A.D.C.	<i>J. dodecaphylla</i> A.D.C.	jacaratiá	140,43	
	122	<i>Jacaratia</i> sp.	[ <i>J. corumbensis</i> Kuntze?]	mamaozinho, mamaozinho de veado, mamão de veado	32,34,153,400,51, 106	

15		CÉLASTRACEAE						
*	69	<i>Fraunhoffera multiflora</i> Mart.				pau-branco	17,397,33,34,153, 180,51,106,36	
*	70	<i>Maytenus rigida</i> Mart.				bon-nome, bonomeiro, casca-grossa, pau-de-colher	17,18,32,168,170, 174,51,173,337,36	
16		CHRYSOBALANACEAE						
	71	<i>Couepia uiti</i> (Mart. & Zucc.) Benth.				assicí	280,368,397,208	
*	72	<i>Licania rigida</i> Bentham			[ <i>L.sclerophylla</i> (Mart. ex Hook.f) Fritsch]	oiticica	12,22,415,368,168, 34,51,337,36	
17		COCHLOSPERMACEAE						
	73	<i>Cochlospermum vitifolium</i> (Willd.) Spreng.			[ <i>C.regium</i> (Schr.)Pilg.; <i>C.insigne</i> St.-Hil.]	algodão bravo, a.do mato, a.-de-veado, pacoté, maria-mole(?)	138,280,32,364, 153,51,173	
18		COMBRETACEAE						
	74	<i>Combretum fruticosum</i> (Loefl.) Stuntz					163	
		<i>Combretum lanceolatum</i> Pohl ex Eichl.					280,163	
		<i>Combretum laxum</i> Jacq.			<i>C.obtusifolium</i> Rich.		280,163	
*		<i>Combretum leprosum</i> Martius				mofumbo,vaqueta, vaquetinha	280,22,31,168,170, 153,174,173, 337,36	
		<i>Combretum mellifluum</i> Eichler					280,163	
		<i>Combretum monetaria</i> Martius				cipaúba	163,397	
		<i>Combretum pisonioides</i> Taub.					163	
		<i>Combretum rupicola</i> Ridl.					163	

	75	136	<i>Terminalia fagifolia</i> Mart. & Zucc.		catanga-de-porco	280,397,208,51
	76	137	<i>Thiloa glaucocarpa</i> (Mart.) Eichl.		sipaúba, vaqueiro	138,12,51,106,173
19			CONVOLVULACEAE			
	77	138	<i>Ipomoea asarifolia</i> (Desr.)R.& Schult.		salsa, rama-de-peba	208,106
		139	<i>Ipomoea carnea</i> Jacq. <b>subsp. fistulosa</b> (Mart. ex Choisy) D. Austin	<i>I. fistulosa</i> Mart. ex Choisy	matacabra	17,18,415, h.s.
20			ERYTHROXYLACEAE			
	78	140	<i>Erythroxylum betulaceum</i> Mart.	<i>E.rosuliferum</i> Schulz ?	rompe-gibão grande	280,418,106,360
		141	<i>Erythroxylum bezerrae</i> Plowman			360,359
		142	<i>Erythroxylum caatingae</i> Plowman		imbuzeiro bravo	360
		143	<i>Erythroxylum campestre</i> St.-Hil.			280,418
		144	<i>Erythroxylum flaccidum</i> Salzman			280,418
		145	<i>Erythroxylum macrochaetum</i> Miq.			280,418,360
		146	<i>Erythroxylum maracasense</i> Plowman			360
		147	<i>Erythroxylum nummularia</i> Peyritsch		rompe-gibão pequeno	280,418,400,180, 106
		148	<i>Erythroxylum oxypetalum</i> O.E. Schulz			208,360
		149	<i>Erythroxylum pelleterianum</i> St.-Hil.			280,418,360
		150	<i>Erythroxylum petrae-caballi</i> Plowman			360
		151	<i>Erythroxylum polygonoides</i> Mart.			418,360
		152	<i>Erythroxylum pungens</i> O.E. Schulz		rompe-gibão	280,418,397,360, 337

	153	<i>Erythroxylum revolutum</i> Mart.			rompe-gibão	280,418,435
	154	<i>Erythroxylum subrotundum</i> St.-Hil.				418,400,360
21		EUPHORBIACEAE				
	79	<i>Alchornea castaneaefolia</i> (Willd.) Juss.			pau-mole	280,17
	80	<i>Cnidocolus bahianus</i> (Ule) Pax & Hoff.			favela-de-gallina, orelha-de-onça	346,180,106,36
*		<i>Cnidocolus phyllacanthus</i> (Müll.Arg.) Pax & Hoffm.			favela, faveleira, favela de cachorro	280,17,18,168,34, 153,51,106,173,337
	158	<i>Cnidocolus vitifolius</i> Mill. ex Pohl var. <i>obtusifolia</i> Müll.Arg.			favela brava, cansanção, cansanção-de-vaqueiro	280,346,153,400, 200
*	81	<i>Croton argyrophyllodes</i> Müll.Arg.			marmealeiro da serra, m.branco, vassourinha, sacatinga, velame	280,208,153,180, 174,61,106,337,36
	160	<i>Croton campestris</i> St.-Hil.em.Müll.Ar.			marmealeiro, velame	168,153,36
	161	<i>Croton hemiargyreus</i> Müll.Arg.			marmealeiro	397,61
	162	<i>Croton jacobinensis</i> Baill.			marmealeiro branco	288,81,61,173
	163	<i>Croton micans</i> Sw. emend. Müll.Arg.				208
*	164	<i>Croton sincorensis</i> Mart.			marmealeiro, marmealeiro branco	17,168,61
*	165	<i>Croton sonderianus</i> Müll.Arg.			marmealeiro, marmealeiro preto	170,153,180,174,61 106,173,337, 212,36
	166	<i>Croton tricolor</i> Müll.Arg.				208
	167	<i>Croton zehntneri</i> Pax & Hoffm.			quebra-faca, canelinha	280,174,337
	82	<i>Ditaxis desertorium</i> (Müll.Arg.) Pax & Hoffm.			<i>Argythamnia desertorium</i> Müll.Arg.	347

	169	<i>Ditaxis malpighiacea</i> (Ule) Pax & Hoff.	<i>Argythamnia mal.</i> Ule	pau-de-mocó	347,208,400,106
*	83	<i>Euphorbia phosphorea</i> Mart.		pau-de-leite, barbasco, cumanan, pau-de-camaná	280,17,32,168,34, 173,36
	84	<i>Jatropha mutabilis</i> (Pohl) Baill.		pinhão, pinhão miúdo	346,208,173,36
*	172	<i>Jatropha pohliana</i> Müll.Arg.		pinhão bravo	280,18,397,168,34, 170,153,180,200, 106,173,212,36
	173	<i>Jatropha ribifolia</i> (Pohl) Baill.		pinhão, pinhão pequeno	280,346,208,106,36
*	174	<i>Jatropha urens</i> L.	<i>Chidoscolus u.</i> (L.)Art.	cansação, urtiga branca	17,32,168,208,153
	85	<i>Manihot brachyandra</i> Pax & Hoffm.			280,402
	176	<i>Manihot cærulescens</i> Pohl emend. Rogers & Appan subsp. <i>cærulescens</i>	<i>M. piauhyensis</i> Ule	manicoba brava, manicoba-de- veado	28,402
	177	<i>Manihot catingae</i> Ule		manicoba brava	280,402
	178	<i>Manihot dichotoma</i> Ule			280,402
	179	<i>Manihot epruinosa</i> Pax & Hoffm.			280,402
*	180	<i>Manihot glaziovii</i> Müll.Arg.		manicoba , manicobeira, caucho	138,402,168,173,36
	181	<i>Manihot heptaphylla</i> Ule			280,402
	182	<i>Manihot maracasensis</i> Ule		manicoba	280,402
	183	<i>Manihot pseudoglaziovii</i> Pax & Hoffm.		manicoba brava	280,402,106
	86	<i>Maprounea brasiliensis</i> St.-Hil.			348
	185	<i>Maprounea guyanensis</i> Aubl.		pau de leite	348,180,106,337
	87	<i>Sapium argutum</i> (Müll.Arg.)Huber			348,233

	187	<i>Sapium cicatricosum</i> Pax & Hoffm.				348,233
	188	<i>Sapium montevidense</i> Klotzch ex Baill.			burra leiteira	348,208,170?, 106?
	189	<i>Sapium obovatum</i> Klotzch ex Müll.Arg.				348,208
	190	<i>Sapium sceleratum</i> Ridley				348,233
88	191	<i>Sebastiania catinae</i> Ule				348
22		FABACEAE				
		CAESALPINIOIDEAE				
89	192	<i>Bauhinia acuruana</i> Moric.			miroró	262
	193	<i>Bauhinia cacovia</i> Wund. subsp. <i>blanchetiana</i> Wund. ined.				262
	194	<i>Bauhinia catinae</i> Harms				262
*	195	<i>Bauhinia cheilantha</i> (Bong.) Steud.		<i>Pauletia cheilantha</i> Bong.	mororó, mororó preto, miroró	397,34,170,153,180 106,173,262, 337,36
	196	<i>Bauhinia dumosa</i> Benth.				262
	197	<i>Bauhinia estivana</i> Wund. ined.				262
	198	<i>Bauhinia flexuosa</i> Moric.		<i>Schnella fl.</i> (M.) Walp.	guela-de-velho, cipó-de-mixla	262, h.s.
	199	<i>Bauhinia forficata</i> Link		<i>B. candicans</i> Benth.	mão (unha)-de-vaca, miroró	262
	200	<i>Bauhinia microstachya</i> (Raddi) Macbr.		<i>B. bahiensis</i> Bong.; <i>B. langsdorffiana</i> Bong.		262
*	201	<i>Bauhinia pentandra</i> (Bong.) Vog. ex Steud.		<i>B. heterandra</i> Benth.; <i>Pauletia pent.</i> Bong.	mororó, unha-de-vaca, capa bode	17,18,28,51,262



*	90	202	<i>Caesalpinia bracteosa</i> Tul.		catingueira, pau-de-rato, pau-santo	33,34,153,174,51, 262,337,36
		203	<i>Caesalpinia calycina</i> Benth.			262
*		204	<i>Caesalpinia ferrea</i> Mart. ex Tul. <b>var. ferrea</b> Huber	<i>C.f. var. cearensis</i>	pau ferro	262
			<b>var. glabrescens</b> Benth.			262
			<b>var. parvifolia</b> Benth.	[ <i>C. leiostachya</i> (Benth.) Ducke]	pau ferro, jucá	280,17,283,28,397, 170,153,180,51,106 173,262,337, 36,282
		205	<i>Caesalpinia gardneriana</i> Benth.			262
		206	<i>Caesalpinia laxiflora</i> Tul.			397,262
*		207	<i>Caesalpinia microphylla</i> Mart. ex Tul.		catingueira rastreira, c.de porco, arranca-estribo, catinga de porco	280,17,18,397,168, 153,200,106,262, 36
*		208	<i>Caesalpinia pyramidalis</i> Tul.		catingueira, catinga de porco, pau-de-rato, mussitáiba	280,17,18,22,397, 168,170,180,51,106 173,262,212, 36,282
*	91	209	<i>Cenostigma gardnerianum</i> Tul.	<i>C.angustifolium</i> Tul.	caneleiro, canela de velho	33,153,51,262
		210	<i>Cenostigma macrophyllum</i> Tul.			262
	92	211	<i>Chamaecrista acosmifolia</i> (Benth.) Irwin & Barneby <b>var. acosmifolia</b>	<i>Cassia acosmifolia</i> Benth.		262
		212	<i>Chamaecrista amiciella</i> (I&B)Ir.& Bar.	<i>Cassia amic.</i> Ir.&Bar.		262

	213	<i>Chamaecrista barbata</i> (Nees & Mart.) Irwin & Barneby	<i>Cassia barbata</i> Nees & Mart.		262
	214	<i>Chamaecrista belemii</i> (I.& B.)Ir.& Bar.	<i>Cassia belemii</i> I.& Bar.	flor-de-São João	262
	215	<i>Chamaecrista carobinha</i> (I&B)Ir.&Bar.	<i>Cassia carob.</i> Ir.&Br.		262
	216	<i>Chamaecrista desvauxii</i> (Coll.) Killip <b>var. latifolia</b> (Benth.) Irwin & Barneby	<i>Cassia uniflora</i> Mill. <b>var. latif.</b> Bth.; <i>Cassia</i> <i>piauhiensis</i> Irwin		262
	217	<i>Chamaecrista pascuorum</i> (Bth.) I.& B.	<i>Cassia pascuor.</i> Benth.		262
	218	<i>Chamaecrista rotundifolia</i> (Pers.) Greene <b>var. rotundifolia</b>	<i>Cassia rotundifolia</i> Persoon	pasto-rasteiro	280,262
	219	<i>Chamaecrista supplex</i> (Benth.) Br.& R.	<i>Cassia supplex</i> Benth.	cabeleira	174,262
	220	<i>Chamaecrista zygophylloides</i> (Taub.) Irwin & Barneby	<i>Cassia zygophylloides</i> Taub.		280,262
93	221	<i>Copaifera coriacea</i> Mart.	<i>C.cordifolia</i> Hayne	copaiv(b)a branca, pau d'óleo	144,51,262
	222	<i>Copaifera langsdorffii</i> Desf.	<i>C.grandiflora</i> (Benth.) Malme; <i>C.nitida</i> Hayne	pau d'óleo do sertão, copaiba vermelha	280,144,180,154, 51,262
	223	<i>Copaifera luetzelburgii</i> Harms			144
	224	<i>Copaifera martii</i> Hayne	<i>C. rigida</i> Benth.	pau d'óleo, jatobá	144,262
94	225	<i>Diptychandra aurantiaca</i> Tul. <b>subsp.</b> <i>epunctata</i> (Tul.) Lima, Carv. & Costa	<i>D. epunctata</i> Tul.	birro branco, biró	397,153,51,262
	95	226	<i>Goniorrhachis marginata</i> Taub.	itapicurú, itapicurú preto	397,32,35,51,262
	96	227	<i>Hymenaea courbaril</i> L. <b>var. courbaril</b>	jatobá	18,51

			<i>var. stilbocarpa</i> (Hayne) Lee & Lang.	<i>H. stilbocarpa</i> Hayne	jatobá de caatinga, jatobá-sertão	262
	228		<i>Hymenaea eriogyne</i> Benth.		jatobá	255,51,262
	229		<i>Hymenaea martiana</i> Hayne	<i>H. sellowiana</i> Hayne	jatobá	280,255,200,262
	230		<i>Hymenaea velutina</i> Ducke		jatobá de caatinga, jatobázinho	255,262
97	231		<i>Martiodendron mediterraneum</i> (Mart. ex Benth.) Koeppen	<i>Martia parvifolia</i> (Bth.) Benth.; <i>Martiusia parvifolia</i> Benth.		244,262
*	98		<i>Parkinsonia aculeata</i> L.		turco, sensitivo	280,17,18,29,33,51,262,36
	99		<i>Peltogyne pauciflora</i> Benth.	<i>P. glaziovii</i> (Taub.) Dwy. <i>Cynometra glaz.</i> Taub.	buranhe, imburanhe, jitaí	397,400,200,51,262
	100		<i>Peltophorum dubium</i> (Spreng.) Taub.	<i>Caesalpinia dubia</i> Spr. <i>P. vogelianum</i> Benth.	imbira-puitá, farinha seca, canafistula	17,32,262, h.s.
*	101		<i>Poeppegia procera</i> Presl. <i>var. conferta</i> Benth.		muquém, sabonete, lava-cabelo, pau-branco, caracu	280,17,18,397,153,51,262
*	102		<i>Pterogyne nitens</i> Tul.		madeira nova, amendoim bravo, vilão, sucupira, vassourinha	31,62,34,174,51,262,36
*	103		<i>Senna acuruensis</i> (Benth.) Ir. & Barn. <i>var. acuruensis</i>	<i>Cassia acuruensis</i> Benth.	São João, monzê-branco, pau-de-besouro	34,200,262
			<i>var. catingae</i> (Harms) Ir. & Barn.	<i>Cassia catingae</i> Harms		262
			<i>var. interjecta</i> Irwin & Barneby			262
	238		<i>Senna aversiflora</i> (Herbert) Ir. & Barn.	<i>Cassia aversiflora</i> Her.		262

	239	<i>Senna gardneri</i> (Benth.) Ir. & Barneby	<i>Cassia gardneri</i> Benth.		280,262
	240	<i>Senna harleyi</i> Irwin & Barneby			262
	241	<i>Senna macranthera</i> (Coll.) Ir. & Barn. <i>var. pudibunda</i> (Benth.) Ir. & Barneby	<i>Cassia macr.</i> DCexCol. <i>C. pudibunda</i> Bth	velame, canafistula da serra	174,262,337
	242	<i>Senna martiana</i> (Benth.) Ir. & Barneby	<i>Cassia martiana</i> Bth.	mata-pasto, besouro, canafistula	280,397,114,262, 36
	243	<i>Senna rizzinii</i> Irwin & Barneby	<i>Cassia granulata</i> Rizz.	São João	106,262
*	244	<i>Senna spectabilis</i> (DC.) Ir. & Barneby <i>var. excelsa</i> (Schrader) Ir. & Barn.	<i>Cassia spectabilis</i> DC.; <i>C. excelsa</i> Schr.; <i>C. carnaval</i> Spegazzini	canafistula, c.-de-besouro, São João, pau-de-besouro	280,17,18,28,33, 153,180,51,106, 262,337,36,282
	245	<i>Senna splendida</i> (Vog.) Ir. & Barneby <i>var. gloriosa</i> Irwin & Barneby	<i>Cassia splendida</i> Vog.		280,262
	246	<i>Senna uniflora</i> (P.Mill.) Ir. & Barneby	<i>Cassia uniflora</i> P.Mill.	mata-pasto	168,174,262
		MIMOSOIDEAE			
*	104	<i>Acacia bahiensis</i> Benth.	<i>A. tavaresorum</i> Rizzini	jurema branca, espinheiro, pau-de-fuso, unha de gato, coração de mulato	28,208,34,51,262, 36
	248	<i>Acacia farnesiana</i> (L.) Willd.		arapiraca, vinhático-de-espinho	280,394,170,153, 262
	249	<i>Acacia glomerosa</i> Benth.		braúna-mongo, maracaípe, etc.	280,394,262,337
	250	<i>Acacia langsdorffii</i> Benth.		jurema-unha-de-gato	208,153,262
	251	<i>Acacia martii</i> Benth.		espinheiro branco	280,262
	252	<i>Acacia monacantha</i> Willd.	<i>A. velutina</i> Benth.		117,262

*		253	<i>Acacia piauhiensis</i> Benth.		jurema branca, espinheiro, rama-de-boi	280,397,174,106,262
		254	<i>Acacia polyphylla</i> DC.		espinheiro	262
		255	<i>Acacia riparia</i> Kunth		unha-de-gato	394,262
	105	256	<i>Albizia blanchetii</i> (Benth.) Lewis	<i>Pithecellobium blanchetii</i> (Bth.) Benth.	canzil, canela-de-burro, saia-de-comadre	51,262
*		257	<i>Albizia polyantha</i> (Spreng.f.) Lewis	<i>Cathormion polyanthum</i> (Spr.)Bk.; <i>Pithecellobium multiflorum</i> (Kth)Benth	canafistula, muquêm, munzê, canafistula-de-boi	280,17,18,31,397,34,51,262,36
		258	<i>Albizia polycephala</i> (Benth.) Killip	<i>Pithecellobium polycephalum</i> Benth.	monzê, camunzê, camondongo, candieiro	17,51,262
*	106	259	<i>Anadenanthera colubrina</i> (Vell.) Bren. <b>var. cebil</b> (Griseb.) Altschul	<i>Piptadenia macrocarpa</i> Benth.; <i>P.m. var. cebil</i> (Gris.)Ch.&Hassl.; <i>A. macrocarpa</i> (Bent.)Br.	angico, angico-preto, angico-jacaré, angico-vermelho, angico-de-casca, angico-manso, angico-de-umbigo	17,18,11,31,32,168,34,170,153,180,200,51,106,173,262,337,36
*	107	260	<i>Calliandra depauperata</i> Benth.		carqueja, carqueijo, alecrim, umari-bravo	18,34,153,174,106,173,262,337,36
		261	<i>Calliandra leptopoda</i> Benth.			280,262,36
		262	<i>Calliandra macrocalyx</i> Harms	<i>C. villosiflora</i> Harms		397,262
		263	<i>Calliandra squarrosa</i> Benth.	<i>C. catingae</i> Harms		262

108	264	<i>Chloroleucon dumosum</i> (Benth.) Lewis	<i>Pithecollobium dumosum</i> Benth.	arapiraca, pau-rósea, mulequeduro criadinho, coronha (?)	280,153,200,51,262
*	265	<i>Chloroleucon foliolosum</i> (Benth.) Lewis	<i>Pithecollobium foliolosum</i> Benth.; <i>Calliandra aristulata</i> Rizzini	arapiraca, jurema branca	397,170,180,174,51,173,262,337,212
	266	<i>Chloroleucon mangense</i> (Jacq.) Britton & Rose	<i>Pithecollobium mangense</i> (J.) Mebr.; <i>P. parvifolium</i> (S.) Benth.; <i>P. oliganthum</i> Rizz.	arapiraca	29,180,51,106,262
109	267	<i>Desmanthus virgatus</i> Willd.	<i>Mimosa virgata</i> L.	jureminha, pena-de-saracura	170,153,262
*	110	<i>Enterolobium contortisiliquum</i> (Vell.) Morong	<i>E. timbouva</i> Mart.; <i>Mimosa cont.</i> Vellozo	timbauva, orelha de macaco, tamboril do campo, tamboril	12,17,283,31,180,51,262
111	269	<i>Mimosa acutistipula</i> Benth.		jurema preta, jureminha	397,174,262
	270	<i>Mimosa adenophylla</i> Harms <i>var. armandiana</i> (Rizzini) Barneby			49,262
		<i>var. mitis</i> Barneby			49,262
*	271	<i>Mimosa arenosa</i> (Willd.) Poir.	<i>M. malacocentra</i> (Mart.) Benth.	calumbí, jurema, jurema vermelha, avoador	280,34,174,106,173,262,337,36
	272	<i>Mimosa campicola</i> Harms <i>var. planipes</i> Barneby			49,262
*	273	<i>Mimosa caesalpiniiifolia</i> Benth.		sabiá	280,22,33,168,174,51,173,337,36

	274	<i>Mimosa coruscocæsia</i> Barneby				49,262
	275	<i>Mimosa exalbescens</i> Barneby				49,262
	276	<i>Mimosa gemmulata</i> Barn. var. <i>gemmulata</i>				49,262
	277	<i>Mimosa glaucula</i> Barneby				49,262
	278	<i>Mimosa hexandra</i> Micheli	<i>M. fascifolia</i> Rizz.; <i>M. acanthophora</i> Harms	carquejo		397,262
	279	<i>Mimosa invisã</i> Mart. ex Colla	<i>M. rhodostachya</i> Benth.	calumbí-miúdo		114,262
	280	<i>Mimosa irrigua</i> Barneby				49,262
	281	<i>Mimosa misera</i> Benth.	<i>M. franciscana</i> Benth.; <i>M. remansoana</i> Harms			280,262
	282	<i>Mimosa modesta</i> Mart.	<i>M. ursinoides</i> Harms	malícia		280,262
	283	<i>Mimosa morroënsis</i> Barneby				49,262
	284	<i>Mimosa nothopteris</i> Barneby				49,262
*	285	<i>Mimosa ophthalmocentra</i> Mart. ex Bth.				280,51,262
	286	<i>Mimosa paludosa</i> Benth.		calumbí-vermelho		280,262
	287	<i>Mimosa pigra</i> L.		calumbí, jiquiri-grande		17,262
	288	<i>Mimosa pseudosepiaria</i> Harms		espinheiro bravo		280,262
*	289	<i>Mimosa tenuiflora</i> (Willd.) Poir.	<i>M. hostilis</i> Benth.; <i>M. limana</i> Rizzini	calumbí, jurema preta, espinheiro		280,17,18,28,397, 168,170,180,51,106 173,337,212,36
	290	<i>Mimosa ulbrichiana</i> Harms				280,262

	291	<i>Mimosa ursina</i> Mart.				262	
*	292	<i>Mimosa verrucosa</i> Benth.			jurema, jurema rosada	280,397,34,262,36	
	293	<i>Mimosa xiquexiquensis</i> Barneby sp. nov. ined.				262	
	112	<i>Parapiptadenia blanchetii</i> (Benth.) Vaz & M.P. Lima	<i>Piptadenia blanchetii</i> Benth.		angico, guanambira	274,51,262	
*	295	<i>Parapiptadenia zehntneri</i> (Harms) M.P. Lima & Lima	<i>Piptadenia zehntneri</i> Harms		angico, angico monjolo, faveira, guanabira, inhambira, fava	280,34,170,274,180 174,51,106,262,337	
*	113	<i>Piptadenia moniliformis</i> Benth.			rama/angico-de-bezerro	280,17,397,262	
*	297	<i>Piptadenia obliqua</i> (Pers.) Macbr.			quipembe, quipé, catanduva, angico de bezerro, carrasco	18,34,174,200,51, 106,173,337,36	
	298	<i>Piptadenia stipulacea</i> (Benth.) Ducke	<i>Pityrocarpa stipulacea</i> (Benth.) Brenan		jurema branca, jurema-de-besta	153,174,262,337, 36	
*	299	<i>Piptadenia viridiflora</i> (Kunth) Benth.	<i>P. biuncifera</i> Benth.; <i>Pityrocarpa v.</i> (Kth) Br.		jiquiri,jacurutú,jacarutú,soroca, surucucú, espinheiro (M.Gerais)	280,17,140,22,31, 62,32,153,51,262	
*	114	<i>Pithecellobium diversifolium</i> Benth.			carcarazeiro, espinheiro, brinco de saguim, orelha-de-macaco	280,17,18,153,51, 173,262,36	
	115	<i>Stryphnodendron coriaceum</i> Benth.				293	
	302	<i>Stryphnodendron piptadenioides</i> Marts.			angico-bravo	397,293	
		PAPILIONOIDEAE					



116	303	<i>Acosmium dasycarpum</i> (Vog.) Yakovl. <b>subsp. glabratum</b> (Benth.) Yakovl.	<i>Sweetia elegans</i> (Vog.) Benth; <i>S. dasycarpa</i> (Vog.) Benth.		51?,262
	304	<i>Acosmium fallax</i> (Taub.) Yakovl.	<i>Sweetia fallax</i> Taub.	lombo preto	262
117	305	<i>Aeschynomene filosa</i> Mart. ex Benth.			17,262
	306	<i>Aeschynomene martii</i> Benth.	<i>A. arbuscula</i> Rizz.; A. <i>rizzinii</i> Schoen.&Ferr.	pau-de-fuso	397,262
*	118	<i>Amburana cearensis</i> (Fr. All.) A.Ç.Smith	<i>Torresea cearensis</i> Fr. Allem.	imburana de cheiro, cumarí, c. de cheiro, c.-da-caatinga, amburana, umburana, u. macho	280,17,18,22,33, 168,170,153,180, 106,173,262,337,36
*	119	<i>Bocoa mollis</i> (Benth.) Cowan	<i>Swartzia mollis</i> Benth. <i>S. cearensis</i> Ducke	brinquinho, chocalhinho	17,18,200,262
120	309	<i>Calopogonium velutinum</i> (Benth.) Amsh.	<i>Stenolobium velutinum</i> Benth.	caatinga-de-macaco, cipó-de- macaco	107,337?
121	310	<i>Canavalia brasiliensis</i> Mart. ex Benth.			262
	311	<i>Canavalia dictyota</i> Piper	<i>C. amazonica</i> Piper		262
122	312	<i>Coursetia rostrata</i> Benth.		cavany, caoang	262,253
	313	<i>Coursetia vicoides</i> (Nees&Mart.) Benth.			262,253
*	123	<i>Cratylia mollis</i> Mart. ex Benth.		camaratuba, camaratu	280,17,18,153,262
	315	<i>Cratylia nuda</i> Tul.			262
124	316	<i>Dalbergia cattingicola</i> Harms		jacarandá, coração-de-negro	51,262,105

*	317	<i>Dalbergia cearensis</i> Ducke			violeta, pau violeta, jacarandá	17,18,397,51,106,
	318	<i>Dalbergia decipularis</i> Rizz. & Matt.			violeta j.-cega-machado, violete	36,105
	319	<i>Dalbergia frutescens</i> (Vell.) Britt. var. <i>frutescens</i>	<i>D. variabilis</i> Vog.;		sebastião-de-arruda	262,105
	320	<i>Dalbergia glaucescens</i> (Mart.ex Benth.) Benth.	<i>Pterocarpus frut.</i> Vell. <i>Miscolobium glauc.</i> Mart. ex Benth.		mata-pulga	397,337,105
	321	<i>Dalbergia miscolobium</i> Benth.	<i>D. violacea</i> (Vog.) Malm.		canela-de-burro	262,105
125	322	<i>Dioclea glabra</i> Mart. ex Benth.	<i>D. leiophylla</i> Ducke			262
	323	<i>Dioclea grandiflora</i> Mart. ex Benth.			mucunã, mucunã de caroço	17,153,180,106, 262,337,36
	324	<i>Dioclea guianensis</i> Benth. var. <i>lasiophylla</i> (Benth.) Maxwell	<i>D. lasiophylla</i> Mart. ex Benth.			262
126	325	<i>Discolobium hirtum</i> Benth.				174,262
*	127	<i>Erythrina velutina</i> Willd.	<i>E. aurantiaca</i> Ridley		mulungú, bico-de-papagaio	280,17,18,283,248, 153,51,106,173,262
*	128	<i>Geoffroea striata</i> (Willd.) Morong	<i>G. superba</i> Kunth; <i>G.</i> <i>spinosa</i> Jacq.?		marizeiro, umari, mari, "árvore que chora" (Paraíba)	280,17,18,31,62, 34,51,262,36
*	129	<i>Lonchocarpus araripensis</i> Benth.	<i>Derris araripensis</i> ?		angelim	18,28,262
	329	<i>Lonchocarpus campestris</i> Benth.			ingá-de-porco	51,262,282
*	330	<i>Lonchocarpus sericeus</i> (Poir.) Kunth	<i>Derris sericea</i> (Kunth) Ducke ?		ingá, cabelouro da caatinga, ingazeira, angelim	17,415,28,208,51, 106,262,337



		347	<i>Pterocarpus villosus</i> (Mart. ex Benth.) Benth.	<i>Amphymenium villosum</i> Mart. ex Benth.		262
		348	<i>Pterocarpus violaceus</i> Vog. var. <i>angustifolia</i> Benth.		pau-sangue	51,262
		349	<i>Pterocarpus zehntneri</i> Harms		pau-sangue	262
137		350	<i>Riedeliella graciliflora</i> Harms	<i>R. hassleri</i> (Chod.) Harms; <i>Sweetiopsis hassleri</i> Chodat	cipó?	32,262
		351	<i>Riedeliella magalhaesii</i> (Rizz.) L. & Vaz	<i>Itaobimia mag.</i> Rizz.	levanta-foice	273
138		352	<i>Sesbania exasperata</i> Kunth		canafistula-de-lagoa, manjerioba	17,174,262
139		353	<i>Swartzia apetala</i> Raddi var. <i>apetala</i>	<i>Toumatea apetala</i> (Rad.) Taub.	coração-de-negro, fruto de urubú	127
*	140	354	<i>Zollernia ilicifolia</i> (Brongn.) Vog.	<i>Z. securidacifolia</i> Benth.	pau-santo, mocutaíba, pau-ferro, laranjeira brava, corazeiro	18,51,262
23			FLACOURTIACEAE			
	141	355	<i>Prockia crucis</i> P. Browne ex L. s. lato	<i>P. bahiensis</i> Turcz.		427,208
24			KRAMERIACEAE			
	142	356	<i>Krameria tomentosa</i> St.-Hil.			208,200,425
25			MALPIGHIACEAE			
	143	357	<i>Dicella bracteosa</i> (Adr. Juss.) Griseb.			329,208
	144	358	<i>Galphimia brasiliensis</i> (L.) Adr. Juss.			280,329,208
	145	359	<i>Heteropterys syringifolia</i> Griseb.			329,208

	360	<i>Heteropterys trichanthera</i> Adr.Juss.				329,208
	146	<i>Ptilochaeta bahiensis</i> Turcz.			estralador	329,397
	147	<i>Stigma phyllon auriculatum</i> (Cav.) A.Juss.				329,208,170
26		MALVACEAE				
	148	<i>Gaya aurea</i> St.-Hil.			malva	34,36
*	364	<i>Gaya gaudichaudiana</i> St.-Hil.				208,34
	149	<i>Herissantia crispa</i> (L.) Briz.			malva branca, m.-de-lavar-prato	34,400,106
*	366	<i>Herissantia tiubae</i> (K.Schum.) Briz.	<i>Bogenhardia tiubae</i> (Sch.) H. Mont.		mela-bode, melosa, malva- visguenta	332,168,208,34,153 106,337?,36,282
	150	<i>Pavonia andrade-lima</i> H.Mont.			tampa-cabaça	400,200
	368	<i>Pavonia humifussa</i> Juss.				200
	369	<i>Pavonia martii</i> Mart. ex Colla				208,282
*	151	<i>Sida cordifolia</i> L.			malva de veludo, malva-benta, malva-babenta, malva branca	17,34,153,106, 337,36
	371	<i>Sida galheirensis</i> Ulbr.			malva alta, malva-folha-miúda, malva grossa, malva branca	208,34,153,400, 174,106,212
	372	<i>Sida micrantha</i> St.-Hil.			malva alta, malva-capaga- garote	208,153,106
	152	<i>Wissadula contracta</i> (Link) R.E. Fries				208
	374	<i>Wissadula patens</i> (St.-Hil.) Gürke				208
27		MELIACEAE				
	153	<i>Trichilia hirta</i> L.			cedro-canjerana, jitó or gitó (?)	208,350,153?,51

28		MORACEAE					
154	376	<i>Brosimum gaudichaudii</i> Tréc.				inharé, embaré, minaré	397,153,51,337?
155	377	<i>Maclura tinctoria</i> (L.) Don ex Steudel		<i>Chlorophora t.</i> (L.) Bth.		amora, amoreira	397,51
29		MYRTACEAE					
156	378	<i>Campomanesia eugenioides</i> (Cam.) Leg. var. <i>desertorum</i> (DC.) Landrum		<i>C. dardanolimai</i> Matt. & Legr.; <i>Psidium d.</i> DC.			252
30		NYCTAGINACEAE					
157	379	<i>Bougainvillea glabra</i> Choisy					280,29?,208
158	380	<i>Pisonia tomentosa</i> Casaretto				joão-mole, pau-piranha, maria- mole	22,153?,51,106,173
31		OLACACEAE					
159	381	<i>Schoepfia brasiliensis</i> DC.		<i>S. obliquifolia</i> Turcz.; <i>S. elliptica</i> All. ex Glaz.			208,428
*	160	<i>Ximения americana</i> L.		<i>X. inermis</i> L.; <i>Amyris arborescens</i> P. Browne		ameixa	140,22,428,51,173, 337
32	383	<i>Ximения coriacea</i> Engler					208,428
		PHYTOLACCACEAE					
161	384	<i>Gallsia integrifolia</i> (Spreng.) Harms		<i>G. gorazema</i> (Vell.) Moq.		pau d'alho, muirarema	403,51,360
162	385	<i>Petiveria alliacea</i> L.				tipi	478,153
163	386	<i>Phytolacca dioica</i> L.					35,51, h.s.

164	387	<i>Seguiera aculeata</i> Jacq.	<i>S. parvifolia</i> Benth.;		403
33		POLYGONACEAE	<i>S. guaranitica</i> Speg.		
165	388	<i>Ruprechtia laxiflora</i> Meissn.	<i>R. polystachya</i> Gris.; <i>R. glauca</i> Meissn.	caixão	120,62,208,36, h.s.
*	389	<i>Triplaris gardneriana</i> Wedd.	<i>T. pachau</i> Mart.	pajeú, pajauí	17,140,18,415,31, 32,153,51
34		RHAMNACEAE			
167	390	<i>Alvimiantha trimerata</i> Grey-Wilson			208
168	391	<i>Ziziphus cotinifolia</i> Reiss.			208,51, h.s.
*	392	<i>Ziziphus joazeiro</i> Mart.		juazeiro, juá, joa, joá-babão	280,17,18,168,34, 170,153,180,51,106 173,337,36,282
35		RUBIACEAE			
169	393	<i>Alseis floribunda</i> Schott		goiabeira brava	208,435,51, h.s.
	394	<i>Alseis involuta</i> Schum.			h. s.
170	395	<i>Coccocypselum dichroolasion</i> Mart.			208
171	396	<i>Coutarea hexandra</i> (Jacq.) K. Schum.		quina-quina	208,153,435,51
172	397	<i>Guettarda angelica</i> Mart. ex Müll.Arg.		açoita cavalo, angelica	397,32,208
173	398	<i>Machaonia spinosa</i> Cham. & Schlecht.			280,51
174	399	<i>Randia armata</i> (Sw.) DC.	<i>R. spinosa</i> (J.) Karst.; <i>Bas anacantha</i> s. (J.) Sch.	quatro-espinhos, limão-bravo	280,439,208,153?, 435

175	400	<i>Simira</i> sp. Aublet		<i>Sickingia</i> sp. Willd.	pereiro-vermelho, pereiro da tinta, candeia-braba	439,32,153,435, 180,51,106, h.s.
36		RUTACEAE				
176	401	<i>Balfourodendron riedelianum</i> (Engler) Engler			mucambo, pau-chumbo	208,400,51
37		SAPINDACEAE				
177	402	<i>Sapindus saponaria</i> L.			sabão-de-soldado, sabonete	138,397,180,51
178	403	<i>Serjania comata</i> Radlk.			ariú, saia-de-ariú	36,282
	404	<i>Serjania glabrata</i> Kunth			saia-de-cunhá	375,208
38		SAPOTACEAE				
179	405	<i>Micropholis gnaphaloclados</i> (Mart.) Pierre		<i>Lucuma gnaphaloclados</i> Mart.		351
180	406	<i>Pouteria gardneriana</i> (DC.) Radlk.		<i>Lucuma gard.</i> DC.		153,351
*	181	<i>Sideroxylon obtusifolium</i> (Roem. & Schult.) Pennington subsp. <i>obtusifolium</i>		<i>Bumelia obtusifolia</i> Roem. &Schul.; <i>B. sartorum</i> Mart.; <i>B. fragrans</i> Ridley	quixabeira, quixabá preta, rompe-gibão	17,22,168,170,435, 51,106,173,36, 351
39		SOLANACEAE				
182	408	<i>Brunfelsia clandestina</i> Plowman				358
	409	<i>Brunfelsia uniflora</i> (Pohl) D. Don		<i>Franciscea unifl.</i> Pohl	manacá	140,357,208, h.s.
183	410	<i>Solanum chaetacanthum</i> Dunal			budim	208,106



	411	<i>Solanum granuloso-leprosum</i> Dunal	<i>S. riparium</i> Pers.; <i>S. verbascifolium</i> L.		208, h.s.
40		STERCULIACEAE			
184	412	<i>Ayenia blanchetiana</i> K.Schum.			128
	413	<i>Ayenia erecta</i> Mart. ex Schum.		cabacinha	128,106,409
	414	<i>Ayenia hirta</i> St.-Hil. & Naud.			128
	415	<i>Ayenia tomentosa</i> L.			128,208
185	416	<i>Byttneria scabra</i> L.	<i>B. salicifolia</i> Humb. & Bonpl. ex Schultes		280,208
186	417	<i>Helicteres eichleri</i> K.Schum.		saca-rolha	280,400,106
	418	<i>Helicteres mollis</i> K.Schum.		saca-rolha, guaxumba, cachimbeira	138,400,200?
	419	<i>Helicteres veluina</i> K.Schum.			208,400
187	420	<i>Melochia betonicifolia</i> St.-Hil.	<i>M. cordiformis</i> St.-Hil.; <i>M. nepetooides</i> St.-Hil.		196
	421	<i>Melochia tomentosa</i> L. var. <i>tomentosa</i>			196,208,34,153,200
188	422	<i>Sterculia striata</i> St.-Hil. & Naud.		chichá, xixá, castanheta	138,12,31,32,444
*	423	<i>Waltheria ferruginea</i> St.-Hil.			34,153,200
41		TILIACEAE			
190	424	<i>Luehea candicans</i> Mart. & Zucc. var. <i>candicans</i>	<i>L. villosa</i> Mart. & Zucc.; <i>L. uniflora</i> St.-Hil.; <i>L. microphylla</i> Pohl	açoita-cavalo, malvão-bravo	397,208,130,51

42		ULMACEAE			
	191	425	<i>Celtis pubescens</i> (Kunth) Sprengel	<i>C. boliviensis</i> Pl.ex DC; <i>C. brasiliensis</i> Gard. ex Planchon	44, h.s.
	192	426	<i>Phyllostylon brasiliensis</i> Capanema		carne-d'anta, pau-branco, vareteiro 103,35,400,51
43		VELLOZIACEAE			
	193	427	<i>Xerophyta cinerascens</i> Roem. & Schult.	<i>Vellozia ciner.</i> Mart.	canela-de-ema, perna-d'ema 207,153,36
		428	<i>Xerophyta plicata</i> (Mart.) Spreng.	<i>Vellozia plicata</i> Mart.	canela-de-ema 280,32,36(p.12)
44		VERBENACEAE			
	194	429	<i>Amasonia campestris</i> (Aubl.) Mold.		208,153?
	195	430	<i>Lantana caatingensis</i> Moldenke		208
		431	<i>Lantana camara</i> L.		cambará, camara 280,32,153,400, 106,173,337,282
	196	432	<i>Lippia bahiensis</i> Moldenke		208
		433	<i>Lippia gracilis</i> Schauer		280,208,400
	197	434	<i>Stachytarpheta sanguinea</i> Mart.ex Sch.		280,208
*	198	435	<i>Vitex gardneriana</i> Schauer		salgueiro, jaramataia, jeremataia 138,17,18,415, 397,51,337,36
45		VITACEAE			
	199	436	<i>Cissus coccinea</i> Mart. ex Planch.		cipó-gordo, cipó-de-cobra 32,106,36
		437	<i>Cissus simsiana</i> Roem. & Schult.		cipó-de-vaqueiro, parreira 32,208,106

#### 4.3- Woody and succulent species of the Subandean Piedmont Forests:

In the floristic list of the woody and succulent species of the Subandean Piedmont Forests, those indicated with an asterisk (\*) correspond to taxa known to occur only in the Bolivian sector of this vegetation unit, and whose presence in the southern Argentine sector is yet to be proved. The taxa indicated with a capital letter (C) are regarded as Chaco intruders into the Subandean Piedmont Forests, generally coming from the adjoining Sierra Chaco. In the 'Main Synonym' column the names between brackets ([...]) are common identification mistakes or binomials wrongly applied to the entities shown in the 'Species Name' column, not to be treated as taxonomic synonyms. In the 'References' column, h.s. stands for 'herbarium specimens' in those cases in which exsiccata have been taken by the present author as evidence of the alleged presence of the species in the area.

Fly N°	Gen N°	Sp N°	SPECIES NAME	MAIN SYNONYM	VERNACULAR NAME	REFERENCES
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1			ACHATOCARPACEAE			
	1	1	<i>Achatocarpus praecox</i> Gris.	<i>A. nigricans</i> Triana	palo de tinta, palo mataco, ruma caspi, tala negro	9,77
2			AMARANTHACEAE			
	2	2	<i>Chamissoa altissima</i> (Jacq.) Kunth			97
3			ANACARDIACEAE			
	3	3	<i>Astronium urundeuva</i> (Fr.All.) Engler		urundel, cuchi	48,97
	4	4	<i>Loxopterigium grisebachii</i> Hieron. & Lorentz ex Griseb.		urundel amarillo	46,379

*	5	<i>Schinopsis brasiliensis</i> Engler var. <i>brasiliensis</i>		quebracho, cuchi, soto	217,304
*		var. <i>glabra</i> Engler	<i>S. glabra</i> (En.)B.&Mey.		217,304
C	6	<i>Schinopsis haenkeana</i> Engler	<i>S. marginata</i> Engler; <i>S. lorentzii</i> var. <i>marginata</i> (Eng.)Cabr.	horco quebracho, q. colorado del cerro, q. serrano	136,379
	6	<i>Schinus gracilipes</i> Johnston var. <i>gracilipes</i>		molle de la quebrada, molle del cerro, horco-molle	134,45
		var. <i>pilosus</i> Barkley			45
	8	<i>Schinus piliferus</i> I.M.Johnston var. <i>piliferus</i>		molle, m.blanco, m. de Tucumán	45
		var. <i>cabreræ</i> (Barkl.)Barkley		molle, m.blanco, m.colorado	45
	9	<i>Schinus venturii</i> Barkley			45
4		ANNONACEAE			
	7	<i>Rollinia occidentalis</i> R.E. Fries		chirimoya, chirimoya del monte	256
5		APOCYNACEAE			
*	8	<i>Aspidosperma parvifolium</i> A.DC.		palo amarillo	286
	9	<i>Rawolfia schuelii</i> Speg.		lecherón negro, leche-leche	256
6		ARALIACEAE			
	10	<i>Pentapanax angelicifolius</i> Griseb.		sacha-paraiso, pino, albiche	134,302,136,77
7		ARECACEAE			
	11	<i>Acrocomia chunta</i> Covas & Ragonese		chonto, chunta	302,97,355

C	12	<i>Copernicia alba</i> Morong	<i>C. australis</i> Becc.	carandá, caranday	183,132
	13	<i>Trithrinax schizophylla</i> Drude		palma, saro, saho	379,354
8		ASCLEPIADACEAE			
	14	<i>Marsdenia altissima</i> (Jacq.) Dugand	<i>M. mollissima</i> Fourn.		302,317
	15	<i>Schubertia schreiteri</i> Desc. & Meyer			134,302,97
9		ASTERACEAE			
	16	<i>Barnadesia odorata</i> Griseb.		trampa de gato, clavel	134
	17	<i>Chaenocephalus heterophyllus</i> Griseb.			210,134
	18	<i>Cnicothamnus lorentzii</i> Griseb.	= <i>C. azafra</i> n ? [379]	azafrán, cejranilla, dominguillo	134,136,97
	19	<i>Dasyphyllum brasiliense</i> (Spreng.) Cabrera	<i>Flotovia brasiliensis</i> (Sp.)Cabr.; <i>Chuquiraga glabra</i> (Spr.)Baker; <i>Ch. brasiliensis</i> (Spr.)OK.		93,94
	20	<i>Eupatorium lasiophthalmum</i> Griseb.	<i>E. hiemale</i> Lillo	malvón	134,256
	24	<i>Eupatorium saltense</i> Hieron.			256
	21	<i>Lagascea mollis</i> Cav.			440
	22	<i>Pseudogynoxys benthamii</i> (Gris.) Cabr.			97
	23	<i>Senecio deferrens</i> Griseb.			210
	28	<i>Senecio peregrinus</i> Griseb.			303
	24	<i>Tessaria integrifolia</i> Ruiz & Pavón		palo bobo, aliso, a.del río, bobo,etc	9,256
	25	<i>Vernonia cincta</i> Griseb.			183
	31	<i>Vernonia fulva</i> Griseb.	= <i>V. squamulosa</i> ?	Santa Rosa	303,379?,97

10	BIGNONIACEAE				
26	<i>Amphilophium sandwithii</i> Fabris				164
33	<i>Amphilophium vauthieri</i> DC.		<i>A.paraguariense</i> Hassl. ex Schulz		164
27	<i>Arrabidea corallina</i> (Jacq.) Sandwith		<i>Bignonia</i> cor. Jacq.; <i>A. rhodantha</i> Bur. & Sch.		164
35	<i>Arrabidea selloi</i> (Spreng.) Sandwith		<i>Bignonia selloi</i> Spreng.		164
28	<i>Clytostoma callistegioides</i> (Cham.) Bur. ex Griseb.		<i>Bignonia</i> call. Cham.; <i>B. speciosa</i> Tw. ex Hook.	alegría de la mañana, dama del monte	164, 191
29	<i>Jacaranda cuspidifolia</i> Mart. ex DC.		<i>J. chelonias</i> Gris. [Symb]		164, 306
38	<i>Jacaranda mimosifolia</i> D. Don		<i>J. chelonias</i> Gris. [P.L.]; <i>J. ovalifolia</i> R.Br.	jacarandá, tarco	303, 164, 136, 306
30	<i>Macfadyena unguis-cati</i> (L.) Gentry		<i>Doxantha</i> uc. (L.) Miers		164, 97
31	<i>Melloa populifolia</i> (DC.) Britton		<i>Bignonia populifolia</i> DC		164
32	<i>Paradolichandra chodatii</i> Hassler				164
* 33	<i>Tabebuia aurea</i> (Manso) ? [Gentry, in litt.]		<i>T. caraiba</i> (Mart.) Bur.	paratodo	h. s.
43	<i>Tabebuia impetiginosa</i> (Mart. ex DC.) Standley		<i>T. avellaneda</i> Lorentz ex Griseb.; <i>T. ipe</i> (Mart. ex Schum.) Standley	lapacho, lapacho rosado	303, 164, 97

	44	<i>Tabebuia ochracea</i> Cham. subsp. <i>heteropoda</i> (DC.) A. Gentry <sup>1</sup>	<i>T. lapacho</i> (Schum.) Sandw.	lapacho amarillo, lapacho amarillo salteño	164,256,190, h.s.
34	45	<i>Tecoma garrocha</i> Hieron.		guaranguay colorado, guarán colorado, nosto, garrocha	134,164,379
	46	<i>Tecoma stans</i> (L.) Juss. ex Kunth		guaranguay amarillo, guarán amarillo	134,303,164,136, 379
	47	<i>Tecoma tenuiflora</i> (DC.) Fabris BOMBACACEAE	<i>Bignonia tenuiflora</i> DC	guaranguay del cerro	164
11	48	<i>Ceiba chodatii</i> (Hassler) Gibbs & Semir comb. ined.	<i>Chorisia insignis</i> Kunth	palo borracho, yuchán, painero, algodonero, etc.	303,136,9,97, 77, Gibbs (p. comm.)
	36	<i>Eriotheca roseorum</i> (Cuatrecasas) A. Robyns	<i>Bombax roseorum</i> <i>Cuat. Tartagalía rubra</i> <i>Capurro; T. roseorum</i> (Cuatr.) Meyer		102,399
	37	<i>Pseudobombax argentinum</i> (Fries) Robyns	<i>Bombax argentinum</i> Fries; <i>B. marginatum</i> (St.-Hil., Juss. & Camb.) K. Schum.	soroche	134,399,97,256
12		BORAGINACEAE			
	38	<i>Cordia alliodora</i> (Ruiz & Pavon) Oken			210,193

<sup>1</sup> Specimens of *T. lapacho* at K have been identified by Gentry as *T. ochracea* subsp. *heteropoda*, whereas in Gentry (1982) he states they are subsp. *ochracea*.

	52	<i>Cordia trichotoma</i> (Vell.) Arrab. ex Steud.	[complex with <i>C. alliodora</i> (R.&P.) Oken]	afata, afata blanca, afata grande	9,97,256,193
39	53	<i>Patagonula americana</i> L.		guayaibí, g.blanco, sauquillo, guayabil	134,97,256
	40	<i>Saccolium lanceolatum</i> Humb.& Bonpl.		guayabil, g.negro, guayibil	134,302,256
	41	<i>Tournefortia lilloi</i> Johnst.			134
		56 <i>Tournefortia rubicunda</i> Salzm. ex DC.			134
13		BROMELIACEAE			
	42	57 <i>Aechmea distichantha</i> Lemaire		caraguatá	379,432
C	43	58 <i>Bromelia serra</i> Grisebach		chaguar, cardo gancho	9
C	44	59 <i>Dyckia ferox</i> Mez		chaguar	432
C		60 <i>Dyckia floribunda</i> Grisebach	<i>D. chaguar</i> Castell.	chaguar	432
		61 <i>Dyckia velascana</i> Mez			432
14		BUDDLEJACEAE			
	45	62 <i>Buddleja albotomentosa</i> R.E. Fries			97
15		CACTACEAE			
	46	63 <i>Brasiliopuntia brasiliensis</i> (Willd.) Berger	<i>Opuntia argentina</i> Gr.; <i>O.hieronimi</i> Gris.		76,112,90
C	47	64 <i>Cereus validus</i> Haworth	<i>C.forbesii</i> Otto	ucle	9
C	48	65 <i>Cleistocactus smaragdiflorus</i> (Web.)Br.& Rose	<i>Cereus smaragdiflorus</i> Weber	uvillinche, cogote de suri	240



* 49	66	<i>Espositoa guentheri</i> (Kupp.) Buxbaum	<i>Vatricania guentheri</i> (Kupp.) Backeberg		89,90,42
C 50	67	<i>Opuntia discolor</i> Britton & Rose			76,9
C	68	<i>Opuntia kiskaloro</i> Spegazzini		quiscaloro	9
51	69	<i>Pereskia sacharosa</i> Grisebach	<i>P. moorei</i> Br. & Rose	sacha-rosa, cuguchi, guyapa	90,9,260
52	70	<i>Quiabentia pflanzii</i> (Vaupel) Berger	<i>Q. chacoensis</i> Back.; <i>Pereskia pflanzii</i> Vaup	sacha-rosa, amendacaru, achuma, tunilla	108
*	71	<i>Quiabentia verticillata</i> (Vaupel) Berger		amendacaru-rai, achuma, oreja de perro	108
*	72	<i>Quiabentia zehntneri</i> (Br. & R.) Br. & Rose	<i>Pereskia</i> z. Br. & Rose		108
53	73	<i>Trichocereus terscheckii</i> (Parm.) Br. & R.	<i>Cereus terscheckii</i> Pm.	cardón grande	239
	74	<i>Trichocereus thelegonoides</i> (Speg.) Britton & Rose	<i>Cereus thelegonoides</i> Speg.		239
	75	<i>Trichocereus thelegonus</i> (Web.) Br. & R. CAPPARIDACEAE	<i>Cereus thelegonus</i> Web	cola de león	239
C 54	76	<i>Capparis retusa</i> Grisebach var. <i>retusa</i>	<i>C. cynophallophora</i> L. var. <i>retusa</i> (Gris.) OK	sacha-poroto	9
	77	<i>Capparis tweediana</i> Eichler		sacha membrillo, s.coca, yerba de la comadreja, cayampa	302
17		CARICACEAE			
55	78	<i>Carica glandulosa</i> Pavón ex A.D.C.	<i>C. gossypiifolia</i> Gris.	higuera/mamón del monte	134,43

	79	<i>Carica quercifolia</i> (St.-Hil.) Hieron.	<i>C.l. anceolata</i> (A.DC.) Hier.; <i>Vasconcellea quercifolia</i> St.-Hil.	sacha-higuera, higuera/mamón del monte, higerón, papaya silvestre	134,303,379,43, h.s.
18	56	<i>Jacaratia corumbensis</i> Kuntze	<i>J. hassleriana</i> Chod.	yacón, Akol-yacón, cipoy	302,43
		CELASTRACEAE			
	57	<i>Maytenus cuezzoi</i> Legneme			256
C	82	<i>Maytenus viscifolia</i> Grisebach		tapia, palta, asperillo, chasqui yuyo, mucamo	136
	58	<i>Plenckia integerrima</i> Lundell	<i>Viposia integerrima</i> (Lundell) Lundell	palo blanco	134,136,379
19		COCHLOSPERMACEAE			
	59	<i>Cochlospermum tetraporum</i> Hallier	<i>C.zahlbruckneri</i> Ost.; <i>C.argentinensis</i> (Speg.) Haum.	queñoa, palo papel, árbol de papel	134,379,9,364, 256
*	85	<i>Cochlospermum vitifolium</i> (Willd.) Spreng.	[ <i>C.regium</i> (Schr.) Pilg.; <i>C.insigne</i> St.-Hil.]		364
20		COMBRETACEAE			
*	60	<i>Combretum guanaiense</i> Rusby			163
*	87	<i>Combretum leprosum</i> Martius		mapaiso	163
	61	<i>Terminalia triflora</i> (Griseb.) Lillo	<i>T.balanseae</i> (OK.) K.Sch. <i>T.hassleriana</i> Chod.	lanza amarilla, lanza, amarillo de río	162,134,303,136, 410,97
21		CONVOLVULACEAE			

62	89	<i>Ipomoea carnea</i> Jacq. <b>subsp. fistulosa</b> (Mart. ex Choisy) D. Austin	<i>I. fistulosa</i> Mart. ex Choisy	floripón	333
	90	<i>Ipomoea crinicalyx</i> Moore			333
C	91	<i>Ipomoea hieronymi</i> (OK.) O'Donnell			333
22		ELAEOCARPACEAE			
63	92	<i>Muntingia calabura</i> L.		sacha guinda	134,97,256
23		ERYTHROXYLACEAE			
64	93	<i>Erythroxylum argentinum</i> O.E. Schulz		ajicillo, sacha ají, coca del monte	418,136
	94	<i>Erythroxylum cuneifolium</i> (Mar.)Schulz		coca del monte	418,256
24		EUPHORBIACEAE			
65	95	<i>Cnidocolus vitifolius</i> Mill. ex Pohl var. <i>cnidodendron</i> (Griseb.) Pax	<i>C. cnidodendron</i> Griseb.	ortiguilla, ortiga, cerraña árbol, piñón de ortiga	134,9,256
66	96	<i>Croton beetlei</i> Croiz.			256
	97	<i>Croton densiflorus</i> Pax & Hoffmann		sacha-chirimoya, sangre de drago	134,256
67	98	<i>Ditaxis breviramea</i> (Müll. Arg.) Pax & Hoffm.	<i>Argythamnia</i> <i>breviramea</i> Müll.Arg.		335
68	99	<i>Euphorbia oranensis</i> (Croizat) Subils			142
C	100	<i>Jatropha hieronymi</i> O.Ktze		piñón, sacha higuera	134,346,256
70	101	<i>Manihot anomala</i> Pohl emend. Rogers & Appan <b>subsp. pavoniana</b> (Müll.Arg.) Rogers & Appan	<i>M. heterophylla</i> Pohl; <i>M. pavoniana</i> Müll.Arg.		402
	102	<i>Manihot grahami</i> Hooker	<i>M. tweediana</i> M.Arg.	mandioca brava	402

		103	<i>Manihot guaranitica</i> Chodat & Hassler <b>subsp. guaranitica</b>	<i>M. fiebrigii</i> Pax & Hoffm.; <i>M. recognita</i> Pax		402
71		104	<i>Parodiendron marginivillosum</i> (Speg.) A.T. Hunziker	<i>Phyllanthus marginivillosa</i> Spegaz.	lenteja	256
72		105	<i>Phyllanthus acuminatus</i> Vahl		chirrincha	256
73		106	<i>Sapium saltense</i> (O'Don.&Lour.) Jablonski	<i>S. haematospermum</i> M. Arg. var. <i>saltensis</i> O&L.	lecherón, curupí	302,136,233
74		107	<i>Sebastiania brasiliensis</i> Spreng.		leche-leche, palo de leche	136,379
		108	<i>Sebastiania klotzschiana</i> (M.A.) M. Arg.		blanquillo, amarillo	134,379
25			FABACEAE			
			CAESALPINIOIDEAE			
75		109	<i>Bauhinia argentinensis</i> Burkart var. <i>megasiphon</i> (Burk.) Fortunato	<i>B. megasiphon</i> Burkart		178
		110	<i>Bauhinia forficata</i> Link <b>subsp. pruinosa</b> (Vog.) Fort. & Wund.	<i>B. candicans</i> Benth.; <i>B. pruinosa</i> Vog.	pata de vaca, pata de buey, caoba, falsa caoba	136,178
		111	<i>Bauhinia mollis</i> (Bong.) D. Dietrich var. <i>notophila</i> (Gris.) Fortunato	<i>B. notophila</i> Gris.	pata de vaca, uña de tigre	177,178
76		112	<i>Caesalpinia floribunda</i> Tul.		morochillo, momoqui	84,256
C		113	<i>Caesalpinia paraguayensis</i> (D.Parodi) Burkart	<i>C. melanocarpa</i> Gris.	guayacán, guayacán negro	302,84

77	114	<i>Chamaecrista calycioides</i> (Coll.)Greene var. <i>calycioides</i>			232	
*	78	<i>Copaifera paupera</i> (Herzog) Dwyer	<i>Copaiba paupera</i> Herz. <i>C. langsdorffii</i> Desf. var. <i>peruviana</i> Mcbr.	copaiba blanca	144	
	79	<i>Gleditsia amorphoides</i> (Gris.) Taub.	<i>Garugandra amorphoides</i> Gris.	coronillo, espina corona, caranchí, carandí	84,97,256	
*	80	<i>Peltophorum dubium</i> (Spreng.) Taub.	<i>Caesalpinia dubia</i> Spr. <i>P. vogelianum</i> Benth.		h.s.	
	81	<i>Pterogyne nitens</i> Tul.		tipa, tipa colorada, palo mortero, palo coca	302,84,9,97	
	82	<i>Seina pendula</i> (Willd.) Irwin & Barneby	<i>Cassia bicapsularis</i> L. var. <i>eriocarpa</i> Gris.	yerba de burro, sen, muveva, pitó- movéva	134,84,97,232	
	120	<i>Seina spectabilis</i> (DC.) Ir. & Barneby var. <i>spectabilis</i>	<i>Cassia spectabilis</i> DC.; <i>C. carnaval</i> Spegazzini	carnaval, palo flojo	84,9,97,256, 232	
		MIMOSOIDEAE				
	83	<i>Acacia albicorticata</i> Burkart		tusca blanca, aroma, tataré, espinillo blanco, espino blanco	84,97,256,117	
	122	<i>Acacia etilis</i> Spegazzini		garabato guiador, g.de 4 caras, g. blanco, guayacán	379,117	
	123	<i>Acacia parviceps</i> (Speg.) Burkart	<i>A. adhaerens</i> (Mart.) Bth. var. <i>parviceps</i> Sp.	garabato blanco, yapán	379,117	

	124	<i>Acacia tucumanensis</i> Grisebach	<i>A. riparia</i> auct.	garabato, g. negro, g. blanco	84,9,117
84	125	<i>Albizia polyantha</i> (Spreng.f.) Lewis	<i>Cathormion polyanthum</i> (Spr.)Bk.; <i>Pithecellobium</i> <i>multiflorum</i> (Kth)Benth	palo flojo, timbó, timbó blanco, pacará blanco, tarco, sachamonte	134,9
85	126	<i>Anadenanthera colubrina</i> (Vell.) Bren. var. <i>cebil</i> (Griseb.) Altschul	<i>Piptadenia macrocarpa</i> Benth.; <i>P.m.</i> var. <i>cebil</i> (Gris.)Ch.&Hassl.; <i>A.</i> <i>macrocarpa</i> (Bent.)Br.	cebil, cebil moro, cebil colorado	134,302,84,303, 11,9,97
86	127	<i>Calliandra formosa</i> (Kunth) Benth.			302,84
87	128	<i>Desmanthus virgatus</i> Willd.	<i>Mimosa virgata</i> L.		84
88	129	<i>Enterolobium contortisiliquum</i> (Vell.) Mprong	<i>E. timbouva</i> Mart.; <i>Mimosa cont.</i> Vellozo	pacará, timbó colorado, oreja de negro	84,303,136,97, 77
89	130	<i>Inga saltensis</i> Burkart		pacay, inga	84,256
90	131	<i>Mimosa polycarpa</i> Kunth			84
	132	<i>Mimosa sensibilis</i> Grisebach			84
	133	<i>Mimosa stenoptera</i> Benth.			84
	134	<i>Mimosa velloziana</i> Mart.			84
91	135	<i>Parapiptadenia excelsa</i> (Gris.) Burkart	<i>Piptadenia ex.</i> (Gris.) Lil.; <i>P.communis</i> Bth. var. <i>excelsa</i> Gris.	horco cebil, cebil blanco, sachamonte cebil	134,136,97,77

92	136	<i>Piptadenia viridiflora</i> (Kunth) Benth.	<i>P. biuncifera</i> Benth.;	vilcarán, tjarca, garabato, carancho, guaranchillo	84,379,256
93	137	<i>Pithecellobium chacoense</i> Burkart	<i>Pityrocarpa</i> v. (Kth) Br.	palo overo, palo barroso	84,379,220,256
	138	<i>Pithecellobium grisebachianum</i> Harms	<i>Calliandra grisebachiana</i> Speg.	palo barroso, guayacán, guayacán blanco	84,220,256
	139	<i>Pithecellobium scalare</i> Grisebach	<i>P. tortum</i> Mart. f. <i>scalare</i> (Gris.) Hassler	palo cascarudo, espinillo, tatané	84,97,220
C	140	<i>Prosopis nigra</i> (Grisebach) Hieronymus var. <i>nigra</i>	<i>P. dulcis</i> Kunth var. <i>australis</i> Bentham	algarrobo negro, árbol negro	9
		PAPILIONOIDEAE			
95	141	<i>Aeschynomene rudis</i> Benth.			84
96	142	<i>Amburana cearensis</i> (Fr. All.) A.C. Smith	<i>Torreseia cearensis</i> Fr. Allem.	roble del país, roble, cedro salteño, palo trébol, roble salteño	303,84,9,97
97	143	<i>Canavalia brasiliensis</i> Mart. ex Benth.	<i>C. gladiata</i> Lor. & Gris.		84
98	144	<i>Cascaronia astragalina</i> Grisebach		cascarón, tipa amarilla	84,136,256
99	145	<i>Coursetia brachyrhachis</i> Harms	<i>Tephrosia craccoides</i> Lillo		84,253
	146	<i>Coursetia hassleri</i> Chodat 2	<i>C. guaranitica</i> Chod.; <i>Cracca corumbae</i> Hoeh		84,9,253, Lavin, in litt.
	147	<i>Coursetia hypoleuca</i> (Spegazzini) Lavin	<i>Poissonia</i> <i>hy.</i> (Sp.) Lill.; <i>Chioendaea</i> <i>hy.</i> Speg.		84,253

2 See footnote 4 in Section 4.1.

100	148	<i>Erythrina dominguezii</i> Hassler	<i>E. chacoensis</i> Speg.	ceiba, ceibo, c.rosado, seibo chaqueño, seibo rosado	134,84,248,256
	149	<i>Erythrina falcata</i> Benth.	<i>E.crista-galli</i> L. var. <i>inermis</i> Speg.& Girola	ceiba, ceibo, seiba, seibo, s. de la selva,s.rosado,s.salteño, s.jujeño	134,84,136,379,248
101	150	<i>Geoffroea decoricans</i> (H.& Arn.) Burk. var. <i>subtropicalis</i> (Lillo) Burk.	<i>Gourleia dec.</i> Gill. var. <i>subtropicalis</i> Lillo	chañar, chañar arbóreo	83,84
*	151	<i>Geoffroea striata</i> (Willd.) Morong	<i>G.superba</i> Kunth; <i>G.</i> <i>spinosa</i> Jacq.?	almendrón (Peru)	83,84, h.s.
102	152	<i>Lonchocarpus lilloi</i> (Hassler) Burkart	<i>L.nitidus</i> (Vog.)Benth. var. <i>lilloi</i> Hassler	sacha quina, quina blanca	84,97,256
*	103	<i>Machaerium acutifolium</i> Vog.			84, h.s.
104	154	<i>Myroxylon balsamum</i> (L.) Harms	<i>M.peruiferum</i> L.f. [Sturton ( <i>in sched.</i> .)]	quina, kina, quina-quina, kina- kina, kina morada	134,84,9,97,256,77
*	105	<i>Platypodium elegans</i> Vog.			h. s.
106	156	<i>Psoralea higuera</i> Gill.	<i>P.higuera</i> Gris.	higuera	84
107	157	<i>Sesbania exasperata</i> Kunth			84
*	108	<i>Swarzizia jorori</i> Harms		jorori	127
109	159	<i>Tipuana tipu</i> (Benth.) O.Kuntze	<i>Machaerium tipu</i> Benth.	tipa, tipa blanca, tipú, palo mortero	84,303,136,97,77
26		FLACOURTIACEAE			
110	160	<i>Casearia silvestris</i> Sw.		palo rajador, rajador, yerba de lagarto, quillero	256
111	161	<i>Prockia crucis</i> P.Browne ex L. s. lato	<i>P.bahiensis</i> Turcz.		136,97



27		Lauraceae				
112	162	<i>Ocotea puberula</i> (Nees. & Mart.) Nees	<i>O. suaveolens</i> (Meissn.) Hassler ?	laurel, laurel del río, l. blanco, l. amarillo, l. mestizo, guaica	183,134	
113	163	<i>Phoebe porphyria</i> (Griseb.) Mez	<i>Nectandra</i> por. Gris.	laurel, l. de la falda, l. del cerro, l. tucumano, l. del monte	303,136	
28		MALPIGHIACEAE				
*	114 164	<i>Galphimia brasiliensis</i> (L.) Adr.Juss.			329	
	115 165	<i>Heteropterys syl vatica</i> Adr.Juss.			336	
*	166	<i>Heteropterys syringifolia</i> Griseb.			329	
	167	<i>Heteropterys umbellata</i> Adr.Juss.			336	
	116 168	<i>Ptilochaeta nudipes</i> Grisebach		amarillo	336,329,256	
*	117 169	<i>Stigma phyllon coloratum</i> Rusby			329	
29		MALVACEAE				
	118 170	<i>Abutilon molle</i> ?			97	
	119 171	<i>Pavonia eurychlamys</i> Ulbrich			247	
	172	<i>Pavonia hirta</i> Sprengel	<i>P. glechomoides</i> St.-Hil.		247	
	173	<i>Pavonia malvacea</i> (Vell.) Krap. & Crist.	<i>P. sepium</i> St.-Hil.		247	
	120 174	<i>Sida cordifolia</i> L.			401	
30		MELIACEAE				
	121 175	<i>Cedrela fissilis</i> Vellozo	<i>C. balansae</i> C.DC.; <i>C. macrocarpa</i> Ducke		430,350	

			176	<i>Cedrela lilloi</i> C.DC.	<i>C. boliviiana</i> Rusby; <i>C. steinbachii</i> Harms	cedro	183,430,136,350
			177	<i>Cedrela odorata</i> L.	<i>C. paraguariensis</i> Mart [ <i>C. angustifolia</i> Sessé & Mociño ex C.DC.]	cedro, cedro salteño, cedro paraíso	97,256,350
		122	178	<i>Trichilia claussoni</i> C.DC.	<i>T. hieronymi</i> Gris.; <i>T. tartagalensis</i> C.DC.	dominguillo, mayan jitara, catiguá blanco, catiguá moroti	210,134,97,256,350
31				MORACEAE			
		123	179	<i>Ficus maroma</i> Castellanos		maroma, gomero, aguaray	302,468,256,469
		124	180	<i>Maclura tinctoria</i> (L.) Don ex Steudel subsp. <i>mora</i> (Griseb.) Vázquez Ávila	<i>Chlorophora tinct.</i> (L.) Gaud. subsp. <i>mora</i> (Gr.) Hassl.; <i>M. mora</i> Gris.	mora, mora colorada, mora amarilla, mora de la pampa	302,97,256,469
32				MYRSINACEAE			
		125	181	<i>Rapanea laetevirens</i> Mez		canelón, San Antonio	426,303,136
33				MYRTACEAE			
		126	182	<i>Eugenia uniflora</i> L.	<i>Stenocalyx micheli</i> (Lam.) Berg	arrayán	257,303,136,379
		127	183	<i>Myrcianthes cisplatensis</i> (Camb.) Berg	<i>Eugenia cisplatensis</i> Camb.	vil-vil, güili, sachá mato, arrayán, lapachillo, palo pelao	136,406
			184	<i>Myrcianthes mato</i> (Gris.) Mc Vaugh	<i>Acreugenia mato</i> (Gr.) Kaus.; <i>Eugenia m.</i> Gr.	mato, horco-mato, alpa-mato, sachá-mato	257,303,136,406,77

	185	<i>Myrcianthes pungens</i> (Berg) Legrand	<i>Acreugenia p.</i> (Berg) Kaus.; <i>Eugenia p.</i> Berg	mato, guabiyú, arrayán negro, arrayán	257,134,9,406, 77
	128	<i>Siphoneugena occidentalis</i> Legrand		frutilla	256,371
34		NYCTAGINACEAE			
C	129	<i>Bougainvillea stipitata</i> Grisebach		alfiler, alfilerillo, tala falso, guáncar blanco, coronillo blanco	134,136
	130	<i>Pisonia zapallo</i> Grisebach	<i>P. ambigua</i> Heimerl	zapallo-caspi, mata pájaro, caspi zapallo	303,9,452,97, 256
	131	<i>Pisoniella arborescens</i> (Lag. & Rodr.) Standley var. <i>glabrata</i> Heimerl	<i>Pisonia hirtella</i> Kunth		210,134,452
35		OLACACEAE			
*	132	<i>Schoepfia tetramera</i> Herzog	<i>S. obliquifolia</i> Rusby		428
C	133	<i>Ximения americana</i> L. var. <i>argentinensis</i> De Filippis	<i>X. americana</i> L. var. <i>oblonga</i> Gris.	pata, albaricoque, pata del monte	256,428
36		OPILIACEAE			
	134	<i>Agonandra excelsa</i> Grisebach		sacha pera, pata, meloncillo, sacha naranjo, caona	134,256
37		PHYTOLACCACEAE			
	135	<i>Hillieria latifolia</i> (Lam.) H.Walt.	<i>Mohlana latifolia</i> Moq.		302,9
	136	<i>Petiveria alliacea</i> L.		pipí	302,478,9,453
	137	<i>Phytolacca bogotensis</i> Kunth			303

	138		<i>Seguiera aculeata</i> Jacq.		<i>S. parvifolia</i> Benth.;	verdenaza, espina del infierno	134,302,403
*	197		<i>Seguiera paraguayensis</i> Morong		<i>S. guaranítica</i> Speg.		
38			PIPERACEAE		<i>S. inernis</i> Walter		134,403
	139		<i>Piper aduncum</i> L.		<i>P. angustifolium</i> R. & P.		134,302,256
			<i>var. cordulatum</i> (C.DC.) Yunquer		<i>var. cordulatum</i> C.DC.		
	199		<i>Piper medium</i> Jacq.				134,302
	200		<i>Piper tucumanum</i> C.DC.			no duro, lata de pobre, matico	134,136
39			POLYGONACEAE				
	140	201	<i>Coccoloba cordata</i> Chamisso			morilla, duraznillo morado, yana poco, mandor	134,302,136
		202	<i>Coccoloba tiliacea</i> Lindau			sacha pera, sacha mora	134,302,256,77
C	141	203	<i>Ruprechtia apetala</i> Weddell		<i>R. corylifolia</i> Gris.; <i>R. mollis</i> Wedd.; <i>R. boliviensis</i> Herzog	manzano del campo, duraznillo, d. colorado, sacha manzana, manzanillo	119,9,77
		204	<i>Ruprechtia laxiflora</i> Meissn.		<i>R. polystachya</i> Gris.; <i>R. glauca</i> Meissn.	virarú, viraró, virarú blanco	119,136,97
40			RHAMNACEAE				
	142	205	<i>Scutia buxifolia</i> Reissek		<i>Adolia bux.</i> (Reiss.)OK.	coronillo, coronillo colorado	155,234,97
C	143	206	<i>Ziziphus mistol</i> Grisebach			mistol, sacha mistol	9
		207	<i>Ziziphus oblongifolius</i> S. Moore				155
		208	<i>Ziziphus piurensis</i> Pilger				155

41		RUBIACEAE				
144	209	<i>Calycophyllum multiflorum</i> Grisebach			palo blanco	210,183,302,93, 9,97,256
145	210	<i>Coutarea hexandra</i> (Jacq.) K. Schum.			quina, cascarilla, dominguillo	134,302,256
146	211	<i>Hoffmannia australis</i> Lillo				210,134,303
147	212	<i>Manettia cordifolia</i> Martius				302
148	213	<i>Pegonopus tubulosus</i> (DC.) K.Schum.			sacha-quina, virreina, flor del diablo, cascarilla, quina-quina	97,256
149	214	<i>Randia armata</i> (Swartz) DC.			sacha limón, sacha lima	303,136,64
42		RUTACEAE				
C	150	<i>Fagara coco</i> (Gill.) Engler			coco, cocucho, sauco hediondo, cochucho	156,303,136,379, 97
	216	<i>Fagara naranjillo</i> (Griseb.) Engler			sacha limón, naranjillo, sacha-naranja	156,136,9
	217	<i>Fagara nigrescens</i> Fries			sauquillo, sauco hediondo, naranjillo negro	156,256
	218	<i>Fagara pterota</i> L.			uña de tigre, uña de gato, teatín	156,256
	219	<i>Fagara rhoifolia</i> (Lam.) Engler				156,136,9

43		SANTALACEAE					
C	151	220	<i>Acanthosyris falcata</i> (Mart. & Eichl.) Grisebach			sacha pera, saucillo, sombra de toro hembra	136,9,150
44			SAPINDACEAE				
	152	221	<i>Allophyllus edulis</i> (St.-Hil.) Radlkofer		<i>Schmidelia edulis</i> St.-Hil.	chalchal, comida de paloma	136,9,97
	153	222	<i>Athyana weinmannifolia</i> (Gris.) Radlk.		<i>Thouinia wein.</i> Gris.	quebrachillo, q.colorado, tarco	134,302,9,256
	154	223	<i>Cupania vernalis</i> Cambessedes			ramo, ramo colorado, guayabo colorado	134,77
	155	224	<i>Diatenopteryx sorbifolia</i> Radlkofer		<i>Thouinia ornifolia</i> Gris	quebrachillo, saucillo	256
*	156	225	<i>Diplokeleba herzogi</i> Radlkofer				374
	157	226	<i>Sapindus saponaria</i> L.			quillai, palo jabón, jaboncito, saponaria, casita	256
	158	227	<i>Serjania glabrata</i> Kunth				375
45			SAPOTACEAE				
	159	228	<i>Chrysophyllum gonocarpum</i> (Mart. & Eichler) Engler		<i>Sapota g.</i> Mart. & Eich.; <i>C. lucumifolium</i> Gris.	aguay	302,256,351
		229	<i>Chrysophyllum marginatum</i> (Hook. & Arn.) Radlk. <b>subsp. marginatum</b>		<i>C. maytenoides</i> Mart.; <i>C. grisebachii</i> (Hier.) Mez	lanza blanca, carapún, blanquillo colorado	303,136,351
*	160	230	<i>Pouteria gardneriana</i> (DC.) Radlk.		<i>Lucuma gard.</i> DC.		352

161	231	<i>Sideroxylon obtusifolium</i> (Roem. & Schult.) Pennington subsp. <i>obtusifolium</i>	<i>Bumelia obtusifolia</i> Roem. &Schul.; <i>B. sartorum</i> Mart.	molle blanco, m. del monte, m.crespo, m.negro, horco-molle, chiri-molle, lanza colorada	93,136,351
46		SCROPHULARIACEAE			
* 162	232	<i>Basistemon silvaticus</i> (Herzog) Baehni & Macbr.	<i>Saccanthus silvaticus</i> Herzog		50
	233	<i>Basistemon spinosus</i> (Chodat) Moldenke	<i>Hassleropsis spinosus</i> Chod.; <i>Saccanthus violaceus</i> Herzog		50
47		SIMARUBACEAE			
163	234	<i>Alvarodoa puberulenta</i> (Monachino) Sleumer	<i>A.amorphoides</i> Liebm. var. <i>puberulenta</i> Mon.	pichi blanco, tipilla	134,136,410
48		SOLANACEAE			
* 164	235	<i>Brunfelsia boliviana</i> Plowman		bella unión	358
	236	<i>Brunfelsia uniflora</i> (Pohl) D.Don	<i>Francisea unifl.</i> Pohl	bella unión	357, h.s.
165	237	<i>Cestrum lorentzianum</i> Grisebach	<i>C.calycinum</i> Willd.? <i>C. viridiflorum</i> Hook.?	hediondilla	210?,134?,303,97
C 166	238	<i>Lycium cestroides</i> Schlechtendal	<i>Acnistus cestroides</i> (Schlech.) Miers	comida devbora, ischivil, chile/i, tala churqui, chivil, tailla, etc.	134,256,60
167	239	<i>Solanum granuloso-leprosum</i> Dunal	<i>S. riparium</i> Pers.; <i>S. verbascifolium</i> L.	tabaquillo, lata de pobre	302,303,136,319, 64,77

168	240	<i>Vassobia breviflora</i> (Sendtner) Hunziker	<i>Acnistus brev.</i> Sendt.; <i>A. parviflorus</i> Gris.; <i>Dunalia b.</i> (Sen.) Sleum.	candelilla, chalchal de gallina, yuá, ischivil, palo negro, sachá perilla, pucancho, etc.	134,303,256,229, 77
49		STERCULIACEAE			
169	241	<i>Ayenia subtilis</i> Cristóbal			128
*	242	<i>Ayenia tomentosa</i> L.			128
170	243	<i>Byttneria oranensis</i> Cristóbal			129
*	244	<i>Byttneria scabra</i> L.	<i>B. salicifolia</i> Humb. & Bonpl. ex Schultes		129
	245	<i>Byttneria tucumanensis</i> Cristóbal			129
171	246	<i>Melochia argentina</i> R.E. Fries	<i>M. argentina</i> Hassler		196
*	247	<i>Sterculia striata</i> St.-Hil. & Naud.			h.s.
50		TILIACEAE			
173	248	<i>Heliocarpus popayanensis</i> Kunth		afata blanca	303,136
174	249	<i>Luehea grandiflora</i> Mart. & Zucc.	[ <i>L. speciosa</i> Willd.]	tabaquillo	256,130
51		ULMACEAE			
175	250	<i>Celtis chichape</i> (Wedd.) Miquel	<i>C. tala</i> Gill. var. <i>ch.</i> Pl.; <i>C. pubescens</i> (Kth) Spr. var. <i>ch.</i> (Wedd.) Baehni		405
	251	<i>Celtis pubescens</i> (Kunth) Sprengel	<i>C. boliviensis</i> Pl. ex DC; <i>C. brasiliensis</i> Gard. ex Planchon	tala gateador, tala trepadora, tala de la selva	134,303,9,97, 405



	252	<i>Celtis spinosa</i> Sprengel	<i>C.tala</i> Gill. γ <i>gaudichaudiana</i> Plan.		405
176	253	<i>Phyllostylon rhamnoides</i> (Poisson) Taubert	<i>Samaroceltis</i> <i>rhamnoides</i> Poisson	palo amarillo, palo de lanza, palo lanza, palo blanco	302,136,9,97
177	254	<i>Trema micrantha</i> (L.) Blume		palo pólvora, afata colorada	303,136
52		URTICACEAE			
178	255	<i>Urera baccifera</i> (L.) Gaud.		ortiga brava, ortiga colorada	136,97,256
	256	<i>Urera caracasana</i> (Jacq.)Gaud.ex Gris.		ortiga blanca, ortiga de monte	302,136
53		VERBENACEAE			
179	257	<i>Aloysia triphylla</i> (L'Her.) Britton	<i>Lippia citriodora</i> (Ortega) Kunth	cedrón, yerba Luisa, yerba de la princesa	134,68
	258	<i>Aloysia virgata</i> (Ruiz & Pavón) Juss.	<i>A.uriticoides</i> Cham.	niño-rupá	68
180	259	<i>Lantana fiebrigii</i> Hayek			458
	260	<i>Lantana trifolia</i> L.			458
181	261	<i>Lippia grisebachiana</i> Moldenke			458
	262	<i>Lippia suffruticosa</i> (Gris.) Ktze			458
54		ZYGOPHYLLACEAE			
C	263	<i>Porhiera microphylla</i> (Baill.) Desc., O'Don. & Lourt.		cucharero, palo cuchara, chucupí, guayacán, chucupí	9, 97,256

## 5. PATTERNS OF DISTRIBUTION OF CHACO AND CAATINGAS SPECIES IN THE NEOTROPICS

### 5.1- Chaco endemics and other characteristic species of the Chaco:

In the previous chapter the woody and succulent species of the Chaco have been listed; 136 genera and 297 species occur in what is here understood as Chaco *sensu stricto*. Only eight genera are strictly endemic to the phytogeographical province, all of them monotypic: *Stetsonia*, *Setiechinopsis*, and *Castellanosia* in the Cactaceae, *Lophocarpinia*, *Mimozyanthus* and *Stenodrepanum* in the Leguminosae, and *Amhipetalum* and *Grahamia* in the Portulacaceae. Table 5.1 lists 92 species here regarded as exclusive to the Chaco, which represent ca. 31% of the total number of woody and succulent Chaco species. Distribution maps are given for 12 of these species: *Aspidosperma triternatum*, *Lophocarpinia aculeatifolia*, *Maytenus spinosa*, *M. vitis-idaea*, *Prosopis fiebrigii*, *P. kuntzei*, *P. ruscifolia*, *P. vinalillo*, *Schinopsis cornuta*, *S. quebracho-colorado*, *Tabebuia nodosa* and *Ziziphus mistol* (Figs. 5.1 to 5.12, respectively).

Some of the remaining species are virtually endemic to the Chaco since they extend only marginally into neighbouring provinces, such as *Aspidosperma quebracho-blanco* and *Schinopsis balansae* (Figs. 5.13 & 5.14), which are two of the most characteristic trees of the Chaco, but they extend to transitional communities in Mato Grosso do Sul (Prado et al., in press, b). Similarly, although *Prosopis affinis* is a typical chaquenian species, it extends as far east as to Rio Grande do Sul in Brazil or W Uruguay (Fig. 5.15). However, the Chaco shares the highest number of species with the Monte province of the arid west of Argentina (Sarmiento, 1972 & 1975; Solbrig, 1976). Some of these are of mainly chaquenian distribution but can also be important members of the Monte province (*sensu* Morello, 1958), such as *Geoffroea decorticans* (Fig. 5.16), which also extends to the Chilean Espinal and dry inter-andean valleys in Bolivia and Peru. *Prosopis alba* does not cross the Andes, but it extends to the Monte and dry valleys of Bolivia and Peru (Fig. 5.17), whereas *P. nigra* and *P. sericantha* only extend from typical Chaco into neighbouring Monte (Figs. 5.18 & 5.19). The low shrub *P. reptans* shows a more marked disjunction: whilst *P. reptans* var. *reptans* is largely restricted to the Chaco and it is absent from any

TABLE 5.1**GENERA ENDEMIC TO CHACO S.S.**

	Nº of spp
<b>CACTACEAE</b>	
<i>Castellanosia</i>	1
<i>Setiechinopsis</i>	1
<i>Stetsonia</i>	1
<b>FABACEAE</b>	
<i>Lophocarpinia</i>	1
<i>Mimozyganthus</i>	1
<i>Stenodrepanum</i>	1
<b>PORTULACACEAE</b>	
<i>Amhipetalum</i>	1
<i>Grahamia</i>	1

## SPECIES ENDEMIC TO CHACO

## ANACARDIACEAE

- 1-*Schinopsis cornuta* Loes.  
 2-*Schinopsis heterophylla* Rag.& Cast.  
 3-*Schinopsis quebracho-colorado* (Schlecht.) Barkley & Meyer

## APOCYNACEAE

- 4-*Aspidosperma triternatum* Rojas Acosta  
 ? 5-*Vallesia glabra* (Cav.)Link.

## ARECACEAE

- 6-*Trithrinax biflabellata* Barb. Rodr.

## ASCLEPIADACEAE

- 7-*Marsdenia castillonii* Lillo ex Meyer

## ASTERACEAE

- 8-*Flourensia campestris* Gris.  
 9-*Flourensia oolepis* Baker  
 10-*Heterothalamus alienus* OK.

## BIGNONIACEAE

- 11-*Tabebuia nodosa* (Grisebach) Grisebach

## BROMELIACEAE

- ? 12-*Bromelia hieronymi* Mez  
 ? 13-*Bromelia urbaniana* (Mez) L.B.Smith  
 14-*Dyckia ragonesei* Castellanos  
 15-*Dyckia tweediei* Mez

## CACTACEAE

- 16-*Castellanosia caineana* Cárd.  
 ? 17-*Cereus comarapanus* Cárd.  
 ? 18-*Echinopsis chacoana* Schütz  
 ? 19-*Echinopsis minuana* Spegazzini  
 ? 20-*Echinopsis schaferi* Br. & Rose  
 ? 21-*Eriocereus guelichii* (Speg.)Berg  
 ? 22-*Eriocereus martinii* (Lab.)Ricc.  
 ? 23-*Eriocereus pomanesis* (Web.) ?  
 ? 24-*Gymnocalycium capillensis* Hosseus  
 ? 25-*Gymnocalycium ragonesei* Castellanos  
 26-*Monvillea cavendishii* (Monv.)Br.& Rose  
 27-*Monvillea spegazzinii* (Weber)Br.& Rose  
 ? 28-*Opuntia brunnescens* Br. & Rose

- 29-*Opuntia quimilo* Schumann  
 ? 30-*Opuntia retrorsa* Spegazzini  
 ? 31-*Opuntia salagria* Castellanos  
 32-*Setiechinopsis mirabilis* (Speg.) Backg. ex de Haas  
 33-*Stetsonia coryne* (Salm-Dyck) Br. & Rose  
 34-*Trichocereus andalgalensis* (Web.) Hos.  
 35-*Trichocereus lamprochlorus* (Lem.) Br. & Rose  
 36-*Trichocereus spachianus* (Lem.) Ricc.

## CAPPARIDACEAE

- ? 37-*Capparis retusa* Grisebach  
 38-*Capparis salicifolia* Grisebach  
 39-*Capparis speciosa* Grisebach  
 ? 40-*Capparis tweediana* Eichler

## CELASTRACEAE

- 41-*Maytenus spinosa* (Gris.) Lour. & O'Don.

## CHENOPODIACEAE

- 42-*Atriplex eximia* Soriano

## EUPHORBIACEAE

- 43-*Jatropha chacoana* Fernández Casas  
 44-*Jatropha matacensis* Castellanos

## FABACEAE

## CAESALPINIOIDEAE

- 45-*Bauhinia argentinensis* Burkart **var. argentinensis**  
 ? 46-*Caesalpinia paraguariensis* (D. Parodi) Burkart  
 ? 47-*Caesalpinia stuckertii* Hassler  
 48-*Lophocarpinia aculeatifolia* (Burk.) Burk.  
 ? 49-*Senna acanthoclada* (Gris.) Irwin & Barneby  
 50-*Senna chacöensis* (Bravo) Irwin & Barneby  
 ? 51-*Senna spiniflora* (Burkart) Irwin & Barneby  
 52-*Stenodrepanum bergii* Harms

## MIMOSOIDEAE

- 53-*Acacia curvifructa* Burkart  
 54-*Mimosa detinens* Benth.  
 55-*Mimozyanthus carinatus* (Gris.) Burkart  
 56-*Prosopis elata* (Burkart) Burkart  
 57-*Prosopis fiebrigii* Harms  
 58-*Prosopis hasslerii* Harms  
 59-*Prosopis kuntzei* Harms

60-*Prosopis pugionata* Burkart

61-*Prosopis rojasiana* Burkart

62-*Prosopis ruscifolia* Gris.

63-*Prosopis vinalillo* Stuckert

PAPILIONOIDEAE

64-*Apurimacia dolichocarpa* (Gris.) Burkart

65-*Sophora linearifolia* Gris.

MALVACEAE

66-*Wissadula densiflora* R.E.Fries

MENISPERMACEAE

67-*Odontocarya asarifolia* Barneby

NYCTAGINACEAE

68-*Bougainvillea campanulata* Heim.

69-*Bougainvillea infesta* Gris.

70-*Bougainvillea praecox* Gris.

POLYGONACEAE

71-*Ruprechtia triflora* Gris.

PORTULACACEAE

72-*Amphipetalum paraguayense* Bacigalupo

73-*Grahamia bracteata* Gill. ex Hook. & Arn.

RHAMNACEAE

74-*Condalia montana* Castellanos

75-*Ziziphus mistol* Gris.

SANTALACEAE

76-*Acanthosyris falcata* (Mart. & Eichl.) Gris.

SIMARUBACEAE

77-*Castela coccinea* Gris.

SOLANACEAE

78-*Capsicum chacöense* A.T.Hunziker

79-*Lycium athium* Bernardello

80-*Lycium morongii* Britton

81-*Lycium nodosum* Miers

82-*Solanum argentinum* Bitt. & Lillo

83-*Solanum chroniotrichum* Morton

STERCULIACEAE

? 84-*Ayenia acalyphifolia* Gris.

85-*Ayenia cordobensis* (Hieron.) Hieron.

? 86-*Ayenia eliae* Cristóbal

? 87-*Ayenia lingulata* Gris.

? 88-*Ayenia o'donellii* Cristóbal

VERBENACEAE

? 89-*Aloysia gratissima* (Gill. & Hk.) Tr. var. *chacoensis* (Mold.)

Botta

ZYGOPHYLLACEAE

90-*Bulnesia bonariensis* Gris.

91-*Bulnesia foliosa* Gris.

92-*Bulnesia sarmientoi* Lorentz ex Gris.

neighbouring phytogeographical area, Burkart (1976) cites this variety for a reduced area in Peru (Fig. 5.20); more strikingly, *P. reptans* Benth var. *cinerascens* (A.Gray) Burkart is found on saline soils in Texas and adjoining Mexico (Burkart, *op .cit .*).

On the other hand, some typical Monte species extend deep into the Chaco (e.g. *Larrea cuneifolia* and *L. divaricata* , see Morello & Adámoli, 1974), or sometimes with more peripheral intrusions, e.g. *Bulnesia retama* , and *B. schickendantzii* in the Llanos district of the Chaco in La Rioja (Ragonese & Castiglioni, 1970), or *Monttea schickendantzii* and *Ramorinoa girolae* in very reduced areas of the Sierra Chaco (Ragonese & Castiglioni, *op .cit .*; Luti et al., 1979).

Some species are restricted in the Chaco to the mountainous areas of central Argentina in the Sierra Chaco where they are not only typical but also dominant, such as *Lythraea ternifolia* and *Schinopsis haenkeana* (Figs. 5.21 & 5.22). However, neither is exclusive to the Chaco; the former is occasionally found in the Monte province (Morello, 1958; Digilio & Legname, 1966) while the latter, in much less abundant populations than in the Sierra Chaco, is a member of the so-called Transitional Forests in NW Argentina and S Bolivia (Digilio & Legname, 1966; Ragonese & Castiglioni, *op .cit .*). Fig. 5.22 shows a cluster of dots for *Schinopsis haenkeana* in central Bolivia, based on herbarium material seen by the present author. According to Herzog's travel notes (1910 & 1912), which provide virtually the only data available for the vegetation of this sector, *S. haenkeana* seems to be both a member of deciduous forests on the eastern slopes of the Altiplano (Herzog, 1910) linked to the Argentine Subandean Piedmont Forests, and also member of communities in dry inner valleys (Herzog, 1912). The geographical area and floristic list coincides fairly well with Unzueta's (1975, p.101) 'monte espinoso subtropical', but he cites *S. cornuta* instead (probably a misidentification for *S. haenkeana* ), of which there are no known collections for dry interandean valleys but only within Chaco s.s. (see Fig. 5.9, and Meyer & Barkley, 1973).

## 5.2- Caatinga endemics and other characteristic species of the Caatingas:

It has been proposed by both Rizzini (1963) and Andrade-Lima (1982) that the level of endemism in the Caatingas is "too small to suggest



that the caatinga has its own unique flora which arose in the region" (Andrade-Lima, 1982, p. 247) at the specific and particularly the generic level. Andrade-Lima (1982) cited only three genera as endemic: *Fraunhoffera*, *Auxemma* and *Apterokarpos*. The latter is a somewhat contentious generic split from *Loxopterigium* (*apud* Barkley, 1962a), which was invalidly published by Rizzini (1975) since no basionym was cited. However, the number of endemic genera is in fact much higher since, as far as this author is able to ascertain from the available literature and herbarium material, there may be 12 endemic genera (and one endemic section) out of a total of 199 for the Caatingas (see Sect. 4.2), as follows: *Auxemma* (Boraginaceae; see map of Fig. 5.23), *Haptocarpum* (Capparidaceae), *Fraunhoffera* (Celastraceae; see map of Fig. 5.24), *Neoglaziovia* (Bromeliaceae), *Neesiochloa* (Graminae), *Arrojadoa*, *Stephanocereus*, *Tacinga* and *Zehntnerella* (Cactaceae), *Blanchetia* and *Telmatophila* (Asteraceae), and the recently described *Alvimiantha* of the Rhamnaceae (Grey-Wilson, 1978).

At the specific level the degree of endemism is even more impressive, since within the Caatingas area *sensu* Andrade-Lima (1966a) there appear to be *ca.* 183 endemic and possibly endemic species (Table 5.2) out of a total of 437 species as ascertained from literature and herbarium material. This gives a level of endemism of *ca.* 42% of the Caatingas species. Some examples of this kind of distribution are: *Bauhinia catinae*, *B. estivana* and *B. flexuosa* (Fig. 5.25), *Cordia dardani* and *C. leucocephala* (Fig. 5.26), *Cratylia mollis* and *C. nuda* (Fig. 5.27), *Hymenaea eriogyne* (Fig. 5.28), which appears to overlap slightly into the neighbouring Cerrados in W Bahia, *Maytenus rigida* (Fig. 5.29), *Mimosa adenophylla*, *M. glaucula* and *M. morroënsis* (Fig. 5.30), *Patagonula bahiensis* (Fig. 5.47), *Mimosa coruscocæsia*, *M. nothopteris* and *M. xique-xiquensis* (Fig. 5.37), *Alseis involuta* and what seems to be a new species in the genus *Simira* of the Rubiaceae (Fig. 5.31), the typical 'umbuzeiro' of the Caatingas *Spondias tuberosa* (Fig. 5.32), and the two endemics of the genus *Ziziphus*, *Z. cotinifolia* and *Z. joazeiro* (Figs. 5.33 & 5.34).

There are also some peculiar kinds of distributional patterns which deserve separate comment. *Commiphora leptophloeos* (sub *Bursera leptophloeos*) was assumed until very recently to be another

TABLE 5.2**GENERA ENDEMIC TO THE CAATINGAS**

	Nº of spp
ASTERACEAE	
<i>Telmatophila</i>	1
<i>Blanchetia</i>	1
BORAGINACEAE	
<i>Auxemma</i>	2
BROMELIACEAE	
<i>Neoglaziovia</i>	1
CACTACEAE	
<i>Arrojadoa</i>	2
<i>Stephanocereus</i>	1
<i>Tacinga</i>	3
<i>Zehntnerella</i>	1
CAPPARIDACEAE	
<i>Haptoctarpum</i>	1
CELASTRACEAE	
<i>Fraunhoffera</i>	1
EUPHORBIACEAE	
<i>Manihot</i> sect. <i>Glaziovianae</i>	7
POACEAE	
<i>Neesiochloa</i>	1
RHAMNACEAE	
<i>Alvimiantha</i>	1

## SPECIES ENDEMIC TO THE CAATINGAS

## ANACARDIACEAE

1-*Loxopterigium gardneri* Engler2-*Spondias tuberosa* Arruda

## APOCYNACEAE

3-*Aspidosperma riedelii* Müll. Arg. **subsp. oliganthum**  
(Wood.) Marc.-Ferr.

## ARECACEAE

4-*Copernicia cerifera* (Arr.Cam.) Mart.5-*Syagrus coronata* (Mart.) Becc.6-*Syagrus microphylla* Burret7-*Syagrus vagans* (Bondar) Hawkes8-*Syagrus wedermannii* Burret9-*Syagrus x matafome* (Bondar) Glassm.

## ASTERACEAE

10-*Blanchetia heterotricha* DC.11-*Telmatophila scolymastrum* Mart. ex Baker

## BIGNONIACEAE

12-*Godmania dardanoi* (J.C.Gomes) Gentry13-*Jacaranda irwinii* A.H. Gentry14-*Tabebuia spongiosa* Rizzini

## BOMBACACEAE

? 15-*Eriotheca parvifolia* (Mart.& Zucc.) Robyns16-*Pseudobombax simplicifolium* Robyns

## BORAGINACEAE

17-*Auxemma glazioviana* Taub.18-*Auxemma oncocalyx* (Fr.All.) Taub.19-*Cordia dardani* Taroda20-*Cordia globosa* (Jacq.) Kunth21-*Cordia leucocephala* Moricand22-*Patagonula bahiensis* Moricand

## BROMELIACEAE

23-*Aechmea eurycorymbus* Harms24-*Bromelia laciniosa* Mart. ex Schult.25-*Cottendorfia florida* Schultes f.26-*Dyckia limae* L.B. Smith27-*Dyckia pernambucana* L.B. Smith

28-*Encholirium spectabile* Mart. ex Schult.

29-*Hohenbergia catinae* Ule

30-*Neoglaziovia variegata* Mez

#### CACTACEAE

31-*Acanthocereus? albicaulis* Br. & Rose

32-*Acanthocereus brasiliensis* Br. & Rose

33-*Arrojadoa penicillata* (Gürke) Br. & Rose

34-*Arrojadoa rhodantha* (Gürke) Br. & Rose

35-*Austrocephalocereus dybowskii* (Gosselin) Backeberg

36-*Austrocephalocereus purpureus* (Gürke) Backeberg

37-*Brasiliopuntia bahiensis* (Britt. & Rose) Berger

38-*Cereus jamacaru* P.DC. non SD. ex Pfeiffer

39-*Discocactus bahiensis* Britt. & Rose

? 40-*Discocactus placentiformis* (Leh.) Sch.

41-*Discocactus zehntneri* Britt. & Rose

42-*Eriocereus adscendens* (Gürke) Berger

43-*Espostoa ulei* (Gürke) Buxbaum

44-*Leocereus bahiensis* Britt. & Rose

? 45-*Melocactus bahiensis* Britt. & Rose

46-*Melocactus horridus* Werdermann

47-*Melocactus oreas* Miquel

? 48-*Melocactus zehntneri* (Br. & Rose) Back.

49-*Opuntia palmadora* Britt. & Rose

50-*Pereskia aureiflora* Ritter

51-*Pereskia bahiensis* Gürke

52-*Pereskia stenantha* Ritter

53-*Pilosocereus catincola* (Gür.) B. & Row.

54-*Pilosocereus chrysostele* (Vaup.) Byl. & Rowl.

55-*Pilosocereus glaucescens* (Lab.) Byl. & Rowl.

56-*Pilosocereus gounellei* (Web.) Byl. & Rowl.

57-*Pilosocereus piauhiensis* (Gürke) Byl. & Rowl.

? 58-*Pilosocereus tuberculatus* (Werd.) Byl. & Rowl.

59-*Pilosocereus zehntneri* (Br. & R.) Byl. & Rowl.

60-*Quiabentia zehntneri* (Br. & R.) Br. & Rose

61-*Stephanocereus leucostele* (Gürke) Berger

62-*Tacinga atropurpurea* Werdermann

63-*Tacinga braunii* Esteves

64-*Tacinga funalis* Britton & Rose

65-*Zehntnerella squamulosa* Britton & Rose

CAPPARIDACEAE

66-*Capparis jacobinae* Moric. ex Eichler

67-*Capparis yco* Mart.

68-*Haplocarpum bahiense* Ule

CELASTRACEAE

69-*Fraunhoffera multiflora* Mart.

70-*Maytenus rigida* Mart.

CHRYSOBALANACEAE

71-*Licania rigida* Bentham

COMBRETACEAE

72-*Combretum monetaria* Martius

? 73-*Combretum pisonioides* Taub.

74-*Combretum rupicola* Ridl.

ERYTHROXYLACEAE

75-*Erythroxylum betulaceum* Mart.

76-*Erythroxylum bezerrae* Plowman

77-*Erythroxylum caatingae* Plowman

78-*Erythroxylum maracasense* Plowman

79-*Erythroxylum macrochaetum* Miq.

80-*Erythroxylum petrae-caballi* Plowman

81-*Erythroxylum polygonoides* Mart.

82-*Erythroxylum pungens* O.E. Schulz

EUPHORBIACEAE

? 83-*Cnidoscolus bahianus* (Ule) Pax & Hoff.

84-*Croton argyrophyloides* Müll.Arg.

85-*Croton sincorensis* Mart.

86-*Croton sonderianus* Müll.Arg.

? 87-*Croton zehntneri* Pax & Hoffm.

88-*Ditaxis desertorum* (Müll.Arg.)Pax & Hoffm.

89-*Ditaxis malpighiacea* (Ule)Pax & Hoffm.

? 90-*Jatropha mutabilis* (Pohl) Baill.

91-*Manihot brachyandra* Pax & Hoffm.

92-*Manihot catingae* Ule

93-*Manihot dichotoma* Ule

94-*Manihot epruinosa* Pax & Hoffm.

95-*Manihot glaziovii* Müll.Arg.

96-*Manihot heptaphylla* Ule

97-*Manihot maracasensis* Ule

98-*Manihot pseudoglaziovii* Pax & Hoffm.

? 99-*Sapium argutum* (Müll.Arg.)Huber

? 100-*Sapium cicatricosum* Pax & Hoffm.

101-*Sapium sceleratum* Ridley

#### FABACEAE

##### CAESALPINIOIDEAE

? 102-*Bauhinia acuruana* Moric.

103-*Bauhinia catinae* Harms

? 104-*Bauhinia cheilantha* (Bong.) Steud.

105-*Bauhinia estivana* Wund. ined.

106-*Bauhinia flexuosa* Moric.

? 107-*Bauhinia pentandra* (Bong.) Vog. ex Steud.

? 108-*Caesalpinia bracteosa* Tul.

? 109-*Caesalpinia calycina* Benth.

? 110-*Caesalpinia laxiflora* Tul.

111-*Caesalpinia microphylla* Mart. ex Tul.

112-*Caesalpinia pyramidalis* Tul.

? 113-*Chamaecrista amiciella* (I&B)Ir.& Bar.

? 114-*Chamaecrista barbata* (Nees & Mart.) Irwin & Barneby

? 115-*Chamaecrista carobinha* (I&B)Ir.&Bar.

116-*Diptychandra aurantiaca* Tul. **subsp. epunctata** (Tul.)

Lima, Carv. & Costa

117-*Hymenaea eriogyne* Benth.

? 118-*Peltogyne pauciflora* Benth.

119-*Senna acuruensis* (Bth.)I&B **var. catinae** (Harms)I.&B.  
**var. interjecta** Ir. & Barn.

? 120-*Senna gardneri* (Benth.)Ir. & Barneby

? 121-*Senna martiana* (Benth.)Ir. & Barneby

? 122-*Senna rizzinii* Irwin & Barneby

##### MIMOSOIDEAE

123-*Acacia bahiensis* Benth.

? 124-*Acacia piahuiensis* Benth.

? 125-*Calliandra depauperata* Benth.

? 126-*Calliandra leptopoda* Benth.

? 127-*Calliandra squarrosa* Benth.

? 128-*Chloroleucon dumosum* (Benth.) Lewis

? 129-*Chloroleucon foliolosum* (Benth.) Lewis

- 130-*Mimosa adenophylla* Harms  
 131-*Mimosa coruscaesia* Barneby  
 132-*Mimosa glaucula* Barneby  
 ? 133-*Mimosa misera* Benth.  
 134-*Mimosa morroënsis* Barneby  
 135-*Mimosa nothopteris* Barneby  
 ? 136-*Mimosa pseudosepiaria* Harms  
 137-*Mimosa xiquexiquensis* Barneby sp. nov. ined.  
 138-*Parapiptadenia blanchetii* (Benth.) Vaz & M.P. Lima  
 139-*Parapiptadenia zehntneri* (Harms) M.P. Lima & Lima  
 ? 140-*Piptadenia obliqua* (Pers.) Macbr.  
 ? 141-*Piptadenia stipulacea* (Benth.) Ducke  
 ? 142-*Pithecellobium diversifolium* Benth.  
 ? 143-*Stryphnodendron piptadenioides* Marts.

## PAPILIONOIDEAE

- ? 144-*Acosmium fallax* (Taub.) Yakovl.  
 145-*Coursetia rostrata* Benth.  
 146-*Coursetia vicioides* (Nees&Mart.) Benth.  
 147-*Cratylia mollis* Mart. ex Benth.  
 148-*Cratylia nuda* Tul.  
 149-*Dalbergia catiingicola* Harms  
 150-*Dalbergia cearensis* Ducke  
 151-*Dalbergia decipularis* Rizz. & Matt.  
 ? 152-*Discolobium hirtum* Benth.  
 ? 153-*Lonchocarpus araripensis* Benth.  
 154-*Luetzelburgia andrade-limae* Lima  
 ? 155-*Luetzelburgia bahiensis* Yakovl.  
 ? 156-*Poecilanthe ulei* (Harms) Arr. & Rudd  
 157-*Pterocarpus ternatus* Rizzini  
 ? 158-*Pterocarpus villosus* (Mart. ex Benth.) Benth.  
 ? 159-*Pterocarpus zehntneri* Harms  
 160-*Riedeliella magalhaesii* (Rizz.) L. & Vaz

## MALVACEAE

- ? 161-*Gaya aurea* St.-Hil.  
 ? 162-*Herissantia crispa* (L.) Briz.  
 ? 163-*Herissantia tiubae* (K.Schum.) Briz.  
 164-*Pavonia andrade-limae* H.Mont.  
 ? 165-*Sida galheirensis* Ulbr.

? 166-*Wissadula contracta* (Link) R.E. Fries

? 167-*Wissadula patens* (St.-Hil.) Gürke

#### MYRTACEAE

168-*Campomanesia eugenioides* (Cam.) Leg. **var.**  
*desertorum* (DC.) Landrum

#### NYCTAGINACEAE

? 169-*Bougainvillea glabra* Choisy

#### OLACACEAE

170-*Ximenia coriacea* Engler

#### RHAMNACEAE

171-*Alvimiantha tricamerata* Grey-Wilson

172-*Ziziphus cotinifolia* Reiss.

173-*Ziziphus joazeiro* Mart.

#### RUBIACEAE

174-*Alseis involuta* Schum.

? 175-*Guettarda angelica* Mart. ex Müll. Arg.

176-*Simira* sp. Aublet

#### STERCULIACEAE

177-*Melochia betonicifolia* St.-Hil.

? 178-*Waltheria ferruginea* St.-Hil.

#### VELLOZIACEAE

179-*Xerophyta cinerascens* Roem. & Schult.

180-*Xerophyta plicata* (Mart.) Spreng.

#### VERBENACEAE

181-*Lantana caatingensis* Moldenke

? 182-*Lippia gracilis* Schauer

? 183-*Vitex gardneriana* Schauer



exclusive species of the Caatingas, where it is a frequent and typical contorted tree. However, Ratter (1987), Ratter et al. (1988b), and above all the taxonomic treatment of this species by Gillet (1979) have shown that there are isolated disjunctions away from the main center in the Caatingas. On calcareous ground in Corumbá (Mato Grosso do Sul) and in the Ilha do Bananal (Goiás) this tree is found in deciduous forests which have a floristic composition strongly related to that of the Caatingas in NE Brazil. Moreover, Ule collected this species in hills in Roraima state (Fig. 5.35). A different case is posed by *Hymenaea velutina* (Fig. 5.36), which whilst certainly a caatinga species (Lee & Langenheim, 1975) can also be found in cerrado in N Piauí and neighbouring Maranhão. This pattern seems to be followed by some other typical caatinga species which when extending into Piauí mix with cerrado elements in the 'carrasco' vegetation (see Sect. 3.4). Such is the case of *Piptadenia obliqua* (the 'catanduva' tree), *Cenostigma gardnerianum*, both characteristic species of the carrasco (Andrade-Lima, 1978; Emperaire, 1983), and sometimes *Luetzelburgia auriculata* (Lima, 1982). The famous and useful 'sabiá' of the sertão in Ceará is not an endemic either of that state nor even to the Caatingas as a whole (Fig. 5.37), contrary to Fernandes (1989); *Mimosa caesalpiniiifolia* has also been collected in Maranhão state, in the Amazon close to Manaus, and in the Atlantic Forest in Bahia (Lewis, 1987), although its occurrence in such areas is rather occasional and never as massive as in Ceará. Another similar case is *Mimosa exalbescens* (Fig. 5.30), which is not only a caatinga species but can also appear in secondary vegetation in Maranhão (Barneby, 1985).

### 5.3- Neotropical seasonal forests pattern:

In the Neotropics, from Mexico to Argentina, there is a discontinuous extension of deciduous and semideciduous forests which occur at low to mid-altitude and usually on mineral-rich soils, under a more or less strongly seasonal climate with a well-defined dry season of variable length. The similarity between the different fragments of this formation is not only physiognomical but also floristic. Thus, there are a number of woody species (which includes the most important Caatinga elements) whose pattern of distribution in the Neotropics closely follows the geographical dispersion of these seasonal forests, and many of them are exclusive to this formation.

### 5.3.1- Residual Pleistocenic Seasonal Formations Arc (Pleistocenic Arc):

A number of taxa seem to be restricted to a peculiar pattern of distribution in central South America which must have originated in the wet-dry climatic oscillations in the late Pleistocene. During the last dry period in South America, equivalent to the northern hemisphere Würm-Wisconsin glaciation, about 18,000 to 12,000 years ago, there appears to have been an expansion of semiarid vegetation in the continent (Damuth & Fairbridge, 1970; Ab' Sáber, 1977b; Brown & Ab' Sáber, 1979; Ab' Sáber, 1982). Ab' Sáber (1977b) postulates that during this period caatinga-like vegetation, which has an adaptive link to mineral-rich soils, may well have surrounded a central core area of cerrado vegetation in central Brazil, which in turn very probably extended into the Amazon region, whereas tropical rain-forests contracted everywhere into relatively small pockets in climatically more privileged areas. After the climax of the dry period there was a slow and gradual return to present-day wetter conditions during the last 12,000 years. The return of the more humid climate would be accompanied by leaching and acidification of soils, therefore fragmenting the originally much more widespread semi-arid vegetation.

Some isolated areas with caatinga-related vegetation can be found nowadays elsewhere in Brazil, in localities where rainfall is well above the 1,000 mm threshold (shown to represent one of the main limitant factors for the existence of this kind of vegetation, see Sect. 3.2), such as deciduous forests on calcareous outcrops (Ratter et al., 1978; Ratter, 1987; Ratter et al., 1988b; Prado et al., in press b), but in these cases it is the geopedological substratum that is determining their presence. They are on much more fertile ground than that surrounding the limestone outcroppings (e.g. mineral-poor cerrado soils, with toxic levels of aluminium), since the calcareous rock is permanently replenishing their shallow soil with essential elements. Thus, isolated refugia of the semiarid types of formations, left behind by the Pleistocenic corridors of caatinga-like vegetation (see discussion in Sect. 8.3), remain wherever suitable environmental conditions occur, i.e. on base-rich soils such as calcareous outcrops within the Cerrados, or in the Pantanal region.

A number of the woody species which are likely to have been involved in such expansion-retreat movements of the Pleistocene are today relevant members of the tropical and subtropical deciduous forest communities south of the Equator in South America, such as the Caatingas of NE Brazil, some semideciduous Planalto forests in São Paulo and Paraná states, the forests in the upper Uruguay river valley, most of the surrounding of the Paraguay-Paraná rivers system, the Serranías of Santiago and Chiquitos in SE Bolivia, the piedmont forests in the so-called Transitional areas in NW Argentina and SW Bolivia (running parallel to the Subandean mountains from Tucumán in Argentina to Santa Cruz de la Sierra in Bolivia), and more scattered outposts in semi-dry and dry Andean valleys in N Bolivia, throughout Peru and sometimes even reaching SW Ecuador. Some of these species are not only important members of these communities but also dominant in several cases.

One such case, and here taken as paradigm, is that of the Mimosoideae *Anadenanthera colubrina* var. *cebil* ('angico', 'cebil') (Fig. 5.38). There are three continuous distribution nuclei of this taxon in the Neotropics, from which discontinuous extensions radiate. The first and major nucleus consists of the Caatingas of NE Brazil, where the 'angico' is a very important and frequent tree. It is present in most of Andrade-Lima's vegetation units (see Sect. 3.4). Outwith the Caatingas, it has been reported in the 'brejos' from Pernambuco (Andrade-Lima, 1964b), particularly in the dry forests of the slopes of the 'serras', and in the so-called 'caatingas' in Maranhão state (Galvão, 1955). Eiten (1965, 1972) has repeatedly denied any link of this latter kind of vegetation to the true Caatingas province further east, although several of the vernacular plant names he mentioned are certainly employed for caatinga species ('angico', 'aroeira', 'pau d'arco', 'jóá', 'mandacarú'). Bigarella et al. (1975) claim that disjunctions of Caatingas occur on the road Coroatá-Vargem Grande (Maranhão), while the exsiccatum marked on this map corresponds to Presidente Dutra, which is not too far south of these localities, and where caatinga-like vegetation can be assumed to exist. This NE Brazil nucleus for the 'angico' type of distribution is intermittently linked to the second nucleus, which occurs along the Paraguay-Paraná rivers system, by way of mesotrophic cerrado

woodlands in Goiás and Mato Grosso (Ratter et al., 1978), and in Mato Grosso do Sul (Ratter et al., 1988b; Prado et al., in press, b).

The second nucleus has a somewhat triangular shape with its northernmost apex on the axis Puerto Suárez-Corumbá (Bolivian-Brazilian border), a straight meridian side reaching south on the axis Resistencia-Corrientes in Argentina and thus paralleling the Paraguay river up to its confluence with the Paraná river, a latitudinal side eastwards from that confluence to the upper Uruguay river valley in Misiones (Argentina) and Santa Catarina (Brazil) and from here a diagonal side returning in NW direction to Pto Suárez-Corumbá. Thus, this nucleus includes nearly all of E Paraguay and a good deal of the western bank of the river Paraguay, that is a north-south strip parallel to the river and several kilometers inland in the geographical Gran Chaco region. Within this triangle *Anadenanthera colubrina* var. *cebil* is common but rarely dominant. It has been reported by Fiebrig (1933) along the western bank of the river Paraguay, by Tortorelli (1967) and Esser (1982) for several areas of E Paraguay, by Morello & Adámoli (1967) for eastern Formosa, and by Eskuche (1986) for NE Argentina in the Paranense phytogeographical province (Cabrera & Willink, 1980).

This second nucleus connects with the third one, located in SW Bolivia and NW Argentina, via the Santiago and Chiquitos hill ranges, forming a curved line uniting Corumbá to Santa Cruz de la Sierra. The flora of this region has scarcely been studied and even less collected, but Herzog (1910 & 1912) gives a fairly accurate impression of what the vegetation is like in the area. In the sector enclosed by this previous line and hills, by the western limit of the second nucleus, and by the north-south narrow strip of the third nucleus the true Chaco vegetation is encased. There are very few outposts of *Anadenanthera colubrina* var. *cebil* within the Chaco area (as is the case with most of the species with this pattern of distribution). The Cerro León records of this tree are not an exception to its absence from the plains of the Chaco s.s. , because the vegetation on the slopes of this tectonic horst (which comprises Silurian and Devonian rocks, as opposed to the æolian sediments surrounding the hill) shows strong links with the Subandean Piedmont Forests in NW Argentina (Ramella & Spichiger, 1989, *sub* Transitional Forests).

The third nucleus extends from Santa Cruz de la Sierra south to Tucumán and the sierras of E Catamarca in Argentina. This follows the piedmont area of the Subandean Mountains, which is the area of the so-called Transitional Forests, so-named because their floristic composition has been considered to be intermediate between that of the Chaco thorn forests and the upland subtropical rainforests (the 'Yungas' s.s.). *Anadenanthera colubrina* var. *cebil* was so important in the southern half of this nucleus in Argentina that Lillo (1919, as cited in Hauman, 1931, and Digilio & Legname, 1966) called it 'zona del cebil', but today there is little left of the original vegetation in this area. The northern remainder of the nucleus where the 'angico' occurs comprises the 'Palo blanco' forest, dominated by *Calycophyllum multiflorum* and *Phyllostylon rhamnoides*, and which extends from mid-eastern Jujuy in Argentina to, presumably, Santa Cruz de la Sierra. *Anadenanthera colubrina* var. *cebil* is one of the five commonest members of both these forests (Cabrera, 1976, p. 7).

From this third nucleus this species, and the pattern of distribution dealt with here, becomes scattered along the NE-facing slope of the Andes in Bolivia and S Peru, i.e. from Santa Cruz to Cuzco, to even more scattered localities in dry interandean valleys such as those of the Apurímac, Huállaga and Marañón rivers (Weberbauer, 1936), finally reaching southern Ecuador in what corresponds to the 'Savannah and Dry Scrub vegetational types' (see map in Harling, 1979). The distribution of the typical variety, *Anadenanthera colubrina* var. *colubrina*, further extends the range of the species (Fig. 5.39) since although it occurs sympatrically with var. *cebil* in the southern area of the Caatingas in Bahia, and also in Misiones in Argentina, it is distributed allopatrically in Rio de Janeiro state and the Planalto forests of São Paulo and Paraná states. Altschul (1964) has argued cogently that the typical variety evolved from var. *cebil*, in which case var. *colubrina* has developed in wetter areas than those of its parental stock.

An important number of woody Caatingas species have a similar, sometimes virtually identical, distribution pattern to that of *Anadenanthera colubrina* var. *cebil*. For example, *Amburana cearensis* (Fig. 5.40) is a frequent, albeit not abundant, characteristic tree of the Caatingas even in the more shrubby types of communities, and it

occupies a similar niche in the 'Palo blanco' forest (3<sup>rd</sup> nucleus), whilst it is rather rare in the 2<sup>nd</sup> nucleus except for some dense populations on calcareous substrate on the Apa river region in Paraguay (Fiebrig, 1933; Tortorelli, 1967). It has also been reported for the Cerro León (Ramella & Spichiger, 1989), and it appears very occasionally in the Andean sector of this pattern of distribution; a collection from Acre state in Brazil should be noted. The tree *Astronium urundeuva* (Fig. 5.41) is usually an important member of whichever the community it occurs in: this is certainly the case for the arboreal caatinga, in which it is characteristic and dominant (Andrade-Lima, 1981), but it also extends into the shrubby caatinga as an isolated low tree (as does *Amburana cearensis* according to Egler, 1951). *Astronium urundeuva* is considered an indicator species of mesotrophic facies cerradão (Ratter et al., 1978) within the Cerrados area in central Brazil. It has been collected in the Cerro León, and it is very frequent in the Subandean Piedmont Forests of Argentina and Bolivia, but there are no records from the Andean dry valleys.

The beautiful tree *Enterolobium contortisiliquum* is usually conspicuous not for its frequency but rather for its size. Somewhat scarce in the Caatingas (Fig. 5.42), it has been reported for the agreste (Andrade-Lima, 1954) and arboreal caatinga (Andrade-Lima, 1975). In the Planalto forests its presence is recorded by collections and phytosociological works (Martins, 1979), and it is an important component of the vegetation on the banks of the Paraguay-Paraná system (Reboratti & Neiff, 1986; Prado et al., in press, a), and also of the Subandean Piedmont Forests (particularly in the 'Tipa-pacará' variant, see Sect. 2.3.8), but again is absent from the Andean area. *E. contortisiliquum* has also been collected in gallery forest within the Chaco (see map 5.42 and Morello & Adámoli, 1974), where it occurs with other non-chaquenian subtropical species, on the alluvial levees bordering the main rivers (Adámoli et al., 1972). *Pterogyne nitens* has a very similar distribution (Fig. 5.43) and is also reported for gallery forest and humidity dependant communities within the Chaco (Morello, 1967; Morello & Adámoli, 1974), but as a rather rare element of the latter. The species *Ruprechtia laxiflora* (Fig. 5.44) was originally described by Meisner (*in* Martius, 1855) from *Blanchet exsiccata* collected in the Caatingas (Cocucci, 1961), but it was not recorded subsequently in this area until recent collections by Harley et al. from around Camaleão in

Bahia. It was, however, abundantly collected in Paraguay and Argentina in both the 2<sup>nd</sup> and 3<sup>rd</sup> nuclei (Paraguay-Paraná system and Subandean Piedmont), where it is a very important element. The scandent shrub or treelet *Celtis pubescens* follows much more closely the *Anadenanthera colubrina* var. *cebil* pattern (although it is far less frequent in the Caatingas) and it reaches central Ecuador (Fig. 5.45) and is also recorded from Acre state in Brazil.

One of the most important and characteristic trees in the Caatingas is *Schinopsis brasiliensis* (Anacardiaceae). Engler (*in* Martius, 1876) recognized two varieties, var. *glabra* and the typical variety of this species. Meyer & Barkley (1973) subsequently considered the former variety to merit specific status, based on its lack of indumentum and larger leaflets when compared to var. *brasiliensis*. However, from numerous exsiccata this author has examined it would seem that although presence-absence of indumentum is a fairly consistent character, leaflet size is unreliable. A traditional view has been taken of *S. brasiliensis*, therefore, to include the two sympatric varieties, *brasiliensis* and *glabra*, and they have been mapped together (Fig. 5.46). This tree is not only present and abundant in the Caatingas, from where it extends into isolated localities in the Federal District of Brazil and in Minas Gerais (where it has been reported to form a dense community in a flood-prone area by Pinto, 1985), but also it is the dominant species in forests in Mato Grosso do Sul (Prado et al., in press, b). *Schinopsis brasiliensis* extends also from Corumbá to the west along the Santiago and Chiquitos ranges (Herzog, 1910), and there are abundant exsiccata from the humid slopes of the Andes in NW Bolivia, but it has not been recorded for Peru, where, however, it seems to be replaced by a similar and little known species, *S. peruviana*, which has been collected only twice (Fig. 5.46).

The genus *Patagonula* L. (Boraginaceae) seems to be endemic to the Pleistocenic Arc (Fig. 5.47). This genus comprises only two species: *P. bahiensis* is endemic to the Caatingas, whereas the type species *P. americana* has been collected or reported for the Planalto Forests in Paraná state in Brazil, the upper Uruguay river basin (Klein, 1972), E Paraguay, NE Argentina in subtropical forests from Misiones to the Eastern Chaco district (Cabrera, 1976; Lewis & Pire, 1981). It is also

the third most important species in the Subandean Piedmont Forests of NW Argentina and S Bolivia (Cabrera, 1976). Although *Patagonula* has not been reported from other areas of the Pleistocenic Arc, it would not be surprising for it to be encountered in the future in the rather poorly studied areas of Cerro León, the Santiago and Chiquitos ranges or south of Santa Cruz de la Sierra.

The species *Piptadenia viridiflora* poses a very interesting case since it is an important element of the Caatingas frequently reported in the literature (Fig. 5.48), while it is a relatively rare species in NW Argentina in the piedmont deciduous forests. Burkart (1952) cited this tree for Colombia and Venezuela (presumably for the dry Caribbean area), but no exsiccata or reference have been encountered to confirm this assertion. Both the species and the genus seem to be missing from the 2<sup>nd</sup> nucleus of this pattern of distribution, that is the Paraguay-Paraná system, but this may simply be due to a problem of taxonomic interpretation, since all previously considered *Piptadenia* species for this area have been transferred to other genera (*Anadenanthera*, *Goldmania*, *Parapiptadenia*). It is noteworthy that the species *Goldmania paraguensis*, endemic to this sector, is very close to section *Pityrocarpa*, to which Burkart (1952) referred *Piptadenia paraguensis* (Benth.) Lindm. (= *Goldmania paraguensis*), while Brennan (1955) transferred *Piptadenia viridiflora* to his genus *Pityrocarpa*.

There is only one collection of *Carica quercifolia* known from the Caatingas, from Irecê in Bahia (Badillo, 1971), and this would represent a very wide disjunct occurrence from the main, 'amphi-Chaco', area of distribution of this species (Fig. 5.49) if it was not for three additional isolated collections in Goiás, Minas Gerais and São Paulo states, which tenuously link the Bahian record to the 2<sup>nd</sup> nucleus of the Pleistocenic Arc. The rest of the distribution is divided into two more or less continuous zones separated by the Chaco plains. One corresponds to the Paraguay-Paraná system, extending eastwards along the upper Uruguay basin to include the Planalto forests, but also with an extension westwards into the Eastern Chaco. The second corresponds to the piedmont deciduous forests on the Subandean slopes. *Carica quercifolia* is also common in dry valleys between Andean ranges in NW Bolivia and S Peru.



The shrub *Combretum leprosum* is another typical caatinga species which follows relatively well the Pleistocenic Arc (Fig. 5.50). It is also common in Maranhão state in those areas suspected of having links with the Caatingas, and it has been collected in the river Paraguay valley and in Santa Cruz de la Sierra area, but seems to be missing from there to the south and north-west. The pattern followed by *Pouteria gardneriana* (Fig. 5.51) is somewhat more uncertain since although it is well recorded in the Caatingas and in the Paraguay-Paraná system, it is unclear whether it spreads into the Subandean Piedmont Forests apart from one collection in Santa Cruz in Bolivia.

The small tree *Tabebuia caraiba*, typically a cerrado species (Fig. 5.52), is also relatively common in the Caatingas of Pernambuco (Andrade-Lima, 1954 & 1960) and Bahia, and it can be found in the Amazon valley around Santarem. It has been frequently collected in the Paraguay river valley sector from Brazil to Argentina, while Ramella & Spichiger (1989) report it for cerrado-like communities on top of the plateau in Cerro León. This species also appears occasionally in central Bolivia, including a specimen collected near Santa Cruz de la Sierra, thus conforming somewhat to the Pleistocenic Arc here described, although the main core of *T. caraiba* distribution is the central Brazilian Cerrados area.

A rather different case is that of *Sterculia striata* (Fig. 5.53), which only marginally appears in tall, arboreal caatinga (Andrade-Lima, 1975; Ratter et al., 1978). It is much commoner in mesophilous forests within the Cerrados expanse or in mesotrophic cerradão (Ratter et al., 1978 & 1988b), but it shuns the poor soils of the Cerrados s.s.. It extends into the Amazon valley (Taroda, 1984) as well as to the river Paraguay area particularly on calcium-rich soils (Ratter et al., 1988b; Prado et al., in press, b), and its westernmost collections come from the area of Santa Cruz, thus overlapping a good deal with the *Tabebuia caraiba* distribution, albeit in different environments.

### 5.3.2- Tropical and Subtropical Seasonal Forests in South America:

Some caatinga species are widely distributed in South America but rarely appear away from deciduous seasonal formations. Such is the

case of *Aspidosperma cuspa* (Fig. 5.54), which has been collected in dry forests of Hispaniola and Martinique and it is a frequent tree in the dry Caribbean sectors of Colombia and Venezuela, countries in which it extends to some dry, interandean valleys. It reappears in SW Ecuador (Woodson, 1951), and at nearly the same latitude but on the opposite side of the continent in Rio Grande do Norte (NE Brazil). Rather an infrequent plant in the Caatingas, it can also be found scattered in the Cerrados of central Brazil, and finally in Paraguay on the rock outcroppings of the Cordillera de Altos (Marcondes-Ferreira, 1988). The taxonomically closely related *Aspidosperma polyneuron* (Fig. 5.55) coincides in part with the pattern of *A. cuspa* : it has also been collected in the western half of the dry Caribbean sector, and also in dry interandean valleys in Colombia, but has not been recorded, so far, from the eastern zone. No collections in Ecuador are reported, but it has been collected from N Peru in an area known to share a very similar kind of vegetation with SW Ecuador (Weberbauer, 1936; Harling, 1979). This N Peruvian locality is separated by some thousand kilometers from the next easterly records in central Bahia, Brazil. Thus, in the east, *A. polyneuron* occurs in the southern caatingas of Bahia, and then in a more or less continuous NE-SW arc spreading in mesophyllous forests in Minas Gerais, Espírito Santo, Rio de Janeiro, São Paulo and Paraná, extending from there to neighbouring Paraguay and a very reduced area in N Misiones (Argentina).

Another very interesting case is posed by the genus *Brunfelsia* (Solanaceae). Recently Plowman (1979) drew attention to the fact that *B. uniflora* forms a link between the older Andean species and the eastern Brazilian ones within section *Franciscea* (Fig. 5.56). It has been collected in N Venezuela, in Roraima (Brazil) and neighbouring Guyana (cf. *Commiphora leptophloeos* , Fig. 5.35), in the Yungas area of the eastern-facing slopes of the Andes in SW Bolivia and NW Argentina, to then reappear sporadically in the Caatingas and more abundantly in the Atlantic forests and Planalto forests in E Brazil. Two additional species are apparently derived from *B. uniflora* : *B. pilosa* and *B. australis* . The latter taxon, previously treated as a subspecies of *B. uniflora* , fills in the southernmost gap corresponding to the 2<sup>nd</sup> nucleus in the distribution of its mother species in Paraguay and NE Argentina (Fig. 5.57).

The unresolved taxonomic problem of the *Geoffroea striata* / *G. spinosa* complex (see comments in Burkart, 1949, and Lewis, 1987) provides another example of the Seasonal Forests Arc (Fig. 5.58), since in our experience the diagnostic characters provided by Burkart (1949) fail to clearly separate these alleged species. This complex is treated here as one polymorphic unit which, however, segregates very well from the other species of the genus, the typically but not exclusively chaquenian *G. decorticans* (cf. Fig. 5.16). The *G. striata* / *spinosa* complex appears in N Venezuela, E Ecuador and adjoining Peru, and in central Bolivia in the Yungas-like area of the Río Grande or Piraí, for the Andean related part, whereas in the lowlands there are essentially two nuclei: the Caatingas and the Paraguay-Paraná system. A very similar pattern is followed by the attractive *Ipomoea carnea* ssp. *fistulosa* (Fig. 5.59), including some Caribbean islands, N Colombia and Venezuela, the same sectors of Ecuador and Peru previously mentioned, and in riverine environments linked to the Subandean Piedmont Forests in NW Argentina but where the exsiccata might have escaped from cultivation (O'Donnell, 1959b). In the east of the continent it occurs in the Caatingas and the Paraguay-Paraná system, and some odd appearances in the Amazon river valley area (around Santarem and Belém) have to be taken into account. This pattern is also followed in part by *Peltophorum dubium* (Fig. 5.60), which has been recorded for seasonal forests in Venezuela, but is more frequent in the SE of the continent, namely in the Caatingas, in mesophyllous forests in Minas Gerais, São Paulo and Paraná, in the upper Uruguay river valley in Santa Catarina, and it was frequently collected in E Paraguay. Once again this species is entirely absent from the Chaco, only to reappear in Yungas-like areas close to Santa Cruz de la Sierra in Bolivia.

The genus *Loxopterigium* in the Anacardiaceae presents five disjunct species in South America (Fig. 5.61). The scarcely known *L. gutierrezii* was collected only once in the Caribbean sector of Colombia, while *L. sagotii* is better known from the Guianas. The tree *L. huasango* appears only in seasonal semiarid to arid formations in coastal SW Ecuador and neighbouring Peru, whilst the caatinga woodlands of a small area of Piauí and Bahia contain the few recorded populations of *L. gardneri* (= *Apterokarpos gardneri*). Finally, *L.*

*grisebachii* is an important member of the Subandean Piedmont Forests in NW Argentina and S Bolivia, which separates Chaco vegetation from the rain and cloud forests of the Yungas. In this case, therefore, the allopatric species within a small genus together comprise the familiar distribution pattern of this Seasonal Forests Arc in South America.

A similar situation, but in this case with the component elements segregated as varietal taxa, occurs in *Senna spectabilis* (Irwin & Barneby, 1982). The var. *spectabilis* extends from coastal Venezuela to Andean valleys in the Mérida area of the same country and the Magdalena and Cauca river valleys in Colombia, to then reappear in seasonal formations in Ecuador and further south in dry valleys in the Peruvian Andes (Fig. 5.62). This variety is also a conspicuous member of the Yungas forests in Bolivia, and very particularly of the deciduous Piedmont forests in S Bolivia and NW Argentina where it is called 'carnaval'. As usual in this kind of distributional pattern this tree is entirely absent from the Chaco, only to reappear in E Paraguay. The other taxon, var. *excelsa*, is virtually restricted to the Caatingas in NE Brazil, where it is called 'canafistula'.

The shrub to small tree *Solanum granuloso-leprosum* also follows the tropical and subtropical seasonal forests pattern in South America (Fig. 5.63). It has been found in N Colombia and Guyana, disappearing completely from the Amazon but reappearing in the Caatingas of Bahia and Minas Gerais, continuing further south in mesophyllous forests in Rio de Janeiro, Paraná and Santa Catarina, and also extending into adjoining Paraguay - NE Argentina, particularly in the Austro-Brazilian Transitional Forest (see Sect. 2.3.3. a). As usual, it is absent from the Chaco but occurs in the eastern slopes of the Andes in NW Argentina and Bolivia.

This distributional pattern is also followed by another two-species-complex: *Cordia alliodora*/*C. trichotoma* (Fig. 5.64). Gibbs & Taroda (1983) studied this complex and concluded that both taxa should remain separate in view of the different kinds of heterostylous condition shown by plants of each species, together with differences in flower size, pollen grain size and mirmecophily. However, these taxa have had a confusing history and have been treated as conspecific by some authors,

whereas those who tried to differentiate them employed gross morphological characters (e.g. leaf indumentum) which are very variable within either species *sensu* Gibbs and Taroda (*op .cit .*). This complex seems to show a high degree of ecological plasticity, perhaps more important in *C. alliodora* , which extends from the semiarid Caribbean coast of Colombia and Venezuela, and the dry interandean valleys of these countries, but also occurs in the more humid Orinoco river valley and even in the Amazon. From western coastal Ecuador and Peru, the distribution follows the more characteristic dry valley systems to reach the Yungas area in Bolivia. The specimens collected in NW Argentina in the Subandean Piedmont Forests had been traditionally attributed to *C. trichotoma* , but from Gibbs & Taroda (*op .cit .*, Fig. 1) point of view they must be regarded as *C. alliodora* , based both on morphology and geographical range. The specimens on the eastern half of the complex distribution are nearly all considered *C. trichotoma* , which thus extends from the Caatingas, where this species can appear not only in the 'sertão' but also in the wetter hills ('brejos'), to mesophyllous forests on the Brazilian Planalto (Minas Gerais, São Paulo, Paraná and Santa Catarina), E Paraguay and NE Argentina.

Some species, such as *Platypodium elegans* (Fig. 5.65), which are more typical of the central Brazilian Cerrados vegetation, seem to shadow somewhat this distributional pattern. This species is a canopy tree in seasonal forest in Panamá (Porter, 1973), and it is also present in Venezuela, but it then disappears in the whole of north and central South America to reappear in the Caatingas, the Cerrados in Goiás, Mato Grosso, Minas Gerais and São Paulo, and further extends into E Paraguay and E Bolivia. *Astronium fraxinifolium* (fig. 5.66) is a tree found in N Colombia and Venezuela, and although it is absent from the Caatingas *s.s.* it has been recorded in semideciduous communities on higher ground within the general Caatingas area. In central Brazil, it has been considered one of the indicator species of mesotrophic cerradão by Ratter et al. (1977), a kind of deciduous forest linked to mineral-rich soils, and it extends also to E Paraguay and central Bolivia. There is a surprising collection of this species in the Cañadón Platanillos, in central Paraguayan Chaco, which must undoubtedly be linked to one of the watercourses which cross this region in a general E-W direction.

### 5.3.3- Amphitropical Seasonal Forests:

A number of species have a much more indistinct distribution pattern which can perhaps be referred to the extension of seasonal forests at both sides of the tropics. This sort of distribution is shown by a few caatinga species, although in each case they show fairly wide ecological plasticity and also occur in more humid habitats. One such is *Coutarea hexandra* (Fig. 5.67), which also occurs along the Amazon river, and also *Crateva tapia* (Fig. 5.68), which has been collected in the Amazon basin and also besides the ephemeral watercourses in the Caatingas. *Hymenaea courbaril* var. *courbaril* (Fig. 5.69), and the outstanding caatinga tree *Tabebuia impetiginosa* (Fig. 5.70) have similar distributions. Some such taxa are primarily restricted to seasonal habitats, such as *Myroxylon balsamum* (Fig. 5.71) and *Poeppigia procera* (Fig. 5.72), although these species also appear in the Amazon, or as in the case of *Phyllostylon brasiliense* in the Brazilian Atlantic rainforest (see distribution of the genus in Fig. 5.73).

The distribution of the only three woody species (*Parkinsonia aculeata*, *Sideroxylon obtusifolium* and *Ximenia americana*) which are common to the Chaco and Caatingas follow this sort of pattern. *Parkinsonia aculeata* (Fig. 5.74) is a very widespread ruderal plant whose ecological amplitude includes the Pacific coastal desert of Peru and the arid Monte province of Argentina. *Sideroxylon obtusifolium* (fig. 5.75) seems to show the highest fidelity to the seasonal formations out of the nine amphitropical species shown here. Thus, and contrary to the rest of the species of amphitropical distribution which avoid temperate areas of Latin America, these latter species are exceptional in that they spread into areas such as Chaco, Monte, or even Patagonia in the case of *Ximenia americana*.

### 5.4- Other patterns of distribution:

A consistent group of caatinga species is relatively widespread in E South America but does not show the full sequence of links with other seasonal formations as do most of the cases considered above. However, a number of these species have a distribution which can be considered as a restriction to the eastern half of the Pleistocenic Arc. One such case is *Aspidosperma pyriformis* (Fig. 5.76), which has also been collected and reported for Cerro León in Paraguay (Ramella &

Spichiger, 1989). It is a characteristic species of the Caatingas which spreads extensively into Minas Gerais, but then there is a disjunction with the populations on the river Paraguay (see map). There is also a puzzling exsiccatum from Faro (Marcondes-Ferreira, 1988), in the Pará state, a locality in a small sector of the Amazon valley where several other caatinga elements have also been collected (Andrade-Lima, 1959). The tree *Aspidosperma riedelii* has recently been treated by Marcondes-Ferreira (1988) as comprising two subspecies: ssp. *oliganthum*, a Bahian endemic, and ssp. *riedelii* with two disjunct populations in the Planalto forests of São Paulo and in central Paraguay (Fig. 5.77).

The valuable timber tree *Balfourodendron riedelianum* (Rutaceae) is a caatinga member (Fig. 5.78) extending south to the Planalto forests in São Paulo and Paraná states, along the upper Uruguay river valley, and reaching E Paraguay and NE Argentina. A similar case is that of *Hymenaea martiana* (Fig. 5.79), but it spreads from the Caatingas into the cerrado savannas in Goiás, the Federal District and Minas Gerais, as well as occurring in the forests in the Paraguayan area. *Machaerium acutifolium* is another cerrado species which occurs in the Caatingas (Fig. 5.80) and extends south into the Mata Atlântica in Rio de Janeiro, isolated 'campo' areas in Minas Gerais and São Paulo, and in forests in E Paraguay. The soft-wooded tree *Phytolacca dioica* has been relatively recently collected in the caatinga of Campo Formoso, Bahia (see specimen at K), and its presence there has been considered a proof of ancient floristic links between the Caatingas and the rest of this species distribution in South America via climatic changes (Andrade-Lima, 1982). This species is a common member of subtropical forests in the Paraguay-Paraná system (e.g. in the Austro-Brazilian Transitional forest), and extends eastwards through Planalto forests to coastal rainforests in Santa Catarina (Fig. 5.81). Some other more infrequent caatinga species extend only to the coastal rainforests of E Brazil, such as *Alseis floribunda* (Fig. 5.82) which is disjunct in coastal Rio de Janeiro, Paraná and Santa Catarina, as is *Astronium concinnum* (Fig. 5.83).

There is also a group of woody species which are entirely restricted to either the 2<sup>nd</sup> or 3<sup>rd</sup> nuclei (or both) within the Pleistocenic Arc (see sect. 5.3.1). The monotypic genus *Athyana* (Sapindaceae) is

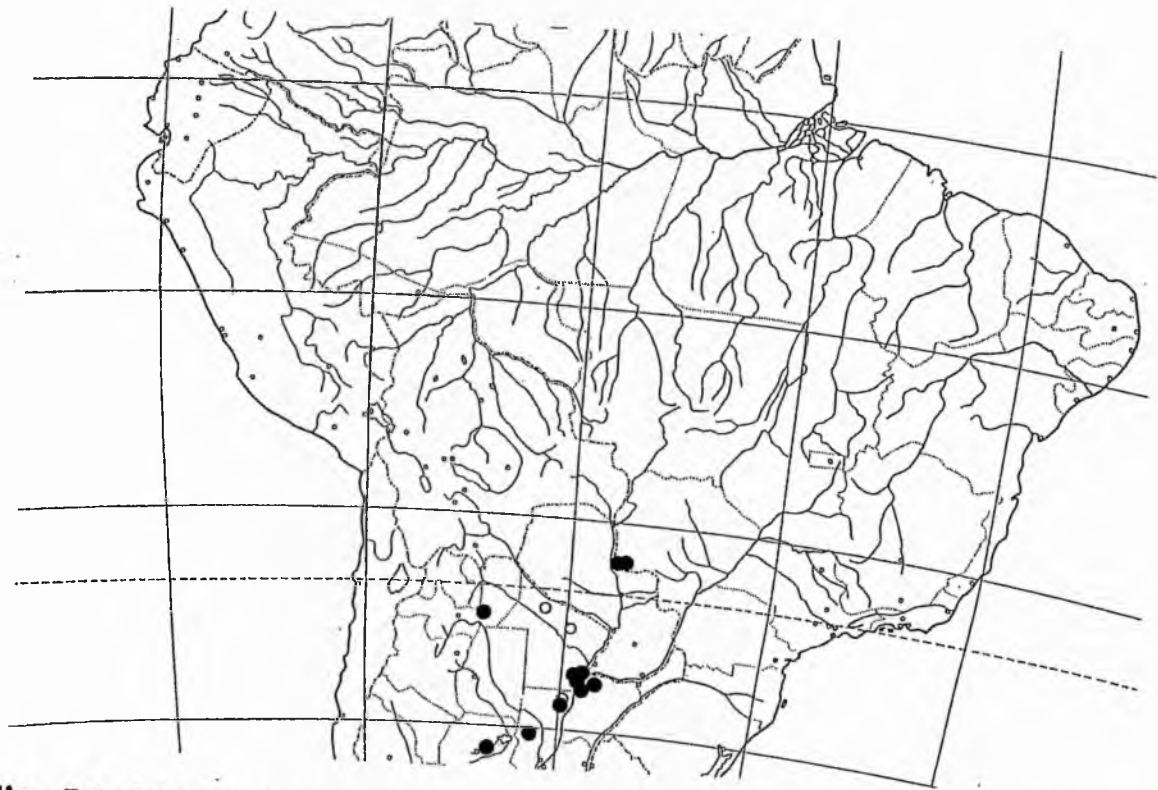
endemic to the seasonal Subandean Piedmont forests of NW Argentina and S Bolivia (Fig. 5.84). Likewise, the monotypic genus *Diatenopteryx* (also Sapindaceae) occurs in both nuclei, leaving a large blank in the middle for the Chaco, and it extends into the Planalto forests and along the upper Uruguay (Fig. 5.85). In the ditypic genus *Diplokeleba* one species, *D. floribunda*, is abundant on the Paraguay-Paraná system, while the other, *D. herzogii*, is known only from the type collection in Cabezas, Bolivia (Fig. 5.86), most likely from the deciduous forests frequent in that area (Coro, 1956). Similarly distributed is *Ziziphus oblongifolius* (Fig. 5.87), a very frequent shrub in the north of the Paraguay-Paraná system (Prado et al., in press, b), and cited by Herzog (1910) for Bolivia and Escalante (1946) for Orán in Salta (Argentina).

The elegant Rubiaceous tree *Calycophyllum multiflorum* is the dominant and characteristic species of the 'Palo blanco' forest in the Piedmont of the Subandean chains (Fig. 5.88), to which it gives its vernacular name, and it is also common in the river Paraguay area and in the Cerro León (Ramella & Spichiger, 1989). Some isolated populations of *C. multiflorum* have been occasionally found within the Chaco s.s. (Castellanos, 1958; Morello, 1967; Morello & Adámoli, 1974), where it is likely they occur in the remains of a previously more expanded seasonal forest in the Pleistocene. Three other species can be considered to be confined to the Paraguay-Paraná system: *Astronium balansae* (Fig. 5.83), *Maytenus ilicifolia* (Fig. 5.89), the latter reaching Santa Catarina to the east, and *Ziziphus guaranítica* (Fig. 5.90).

Finally, it is necessary to consider the distribution of three caatinga species which seem to link with Amazonia, or at least to wet tropical formations. One such is *Albizia polyantha* (Fig. 5.91), which extends from the Guianas and Ilha de Maracá (Lewis & Owen, 1989), to the Amazon river valley and tributaries, and to the Caatingas, the Paraguay-Paraná system and Cerro León. The distribution of this species seems to be associated with permanent watercourses except in the Caatingas. *Aspidosperma discolor* appears in the Venezuelan Guayana and the Guianas, has been profusely collected in the lower and middle Amazon river valley and in the Rondônia state, but it is also frequent in Bahian caatinga and in a central area of the Cerrados (Fig. 5.92). *Couepia uiti* (Chrysobalanceae) is essentially an Amazonian

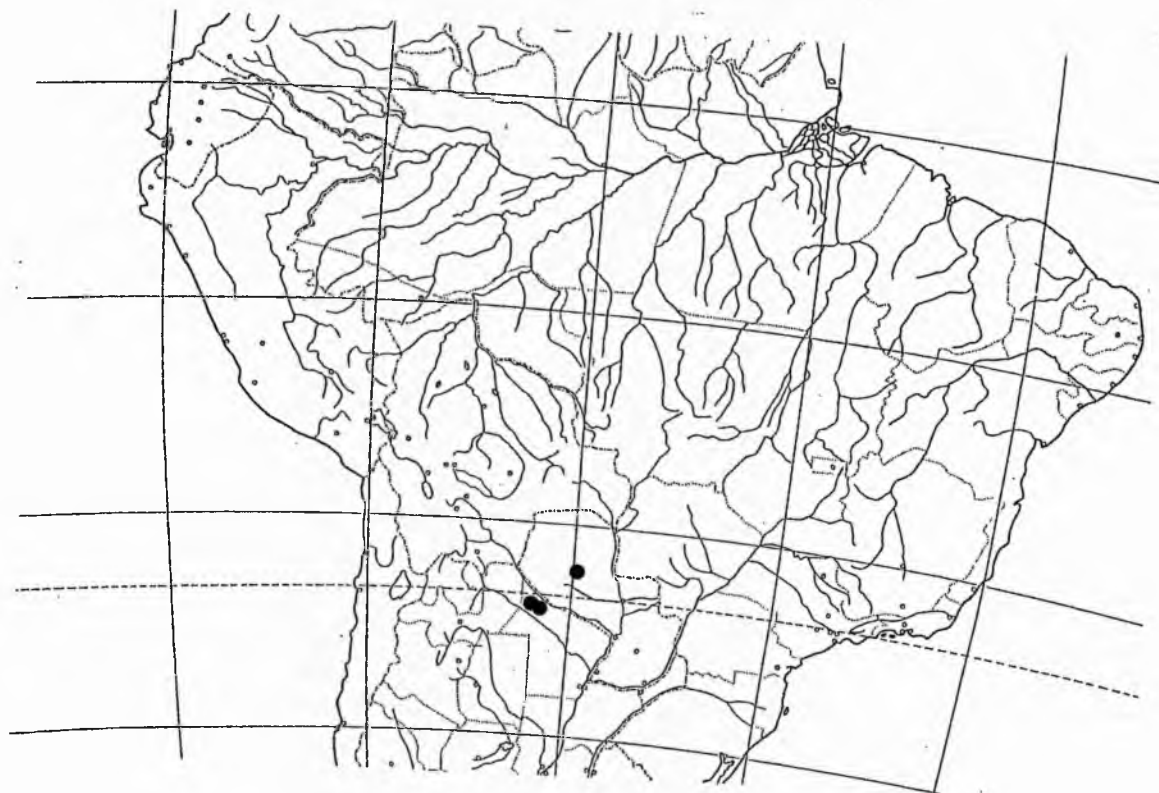


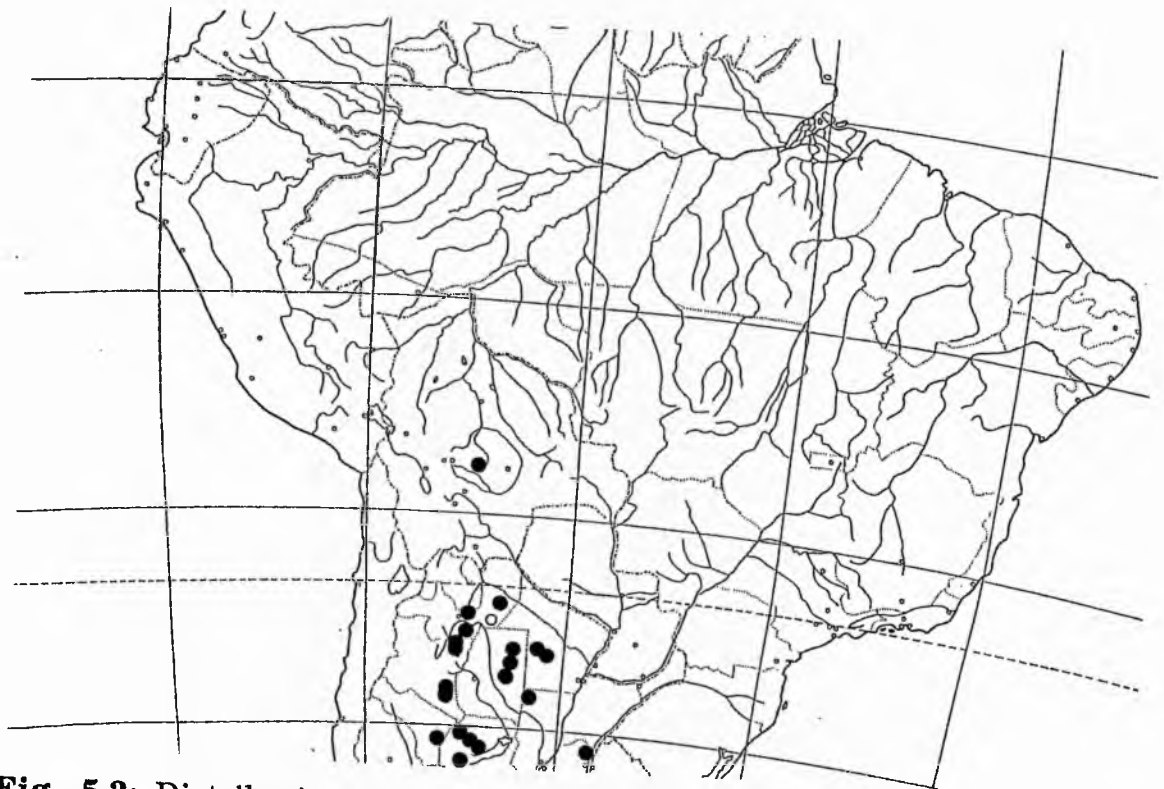
element, but via gallery forest it extends within the Cerrados and Caatingas (Fig. 5.93).



**Fig. 5.1:** Distribution map of *Aspidosperma triternatum*. Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.

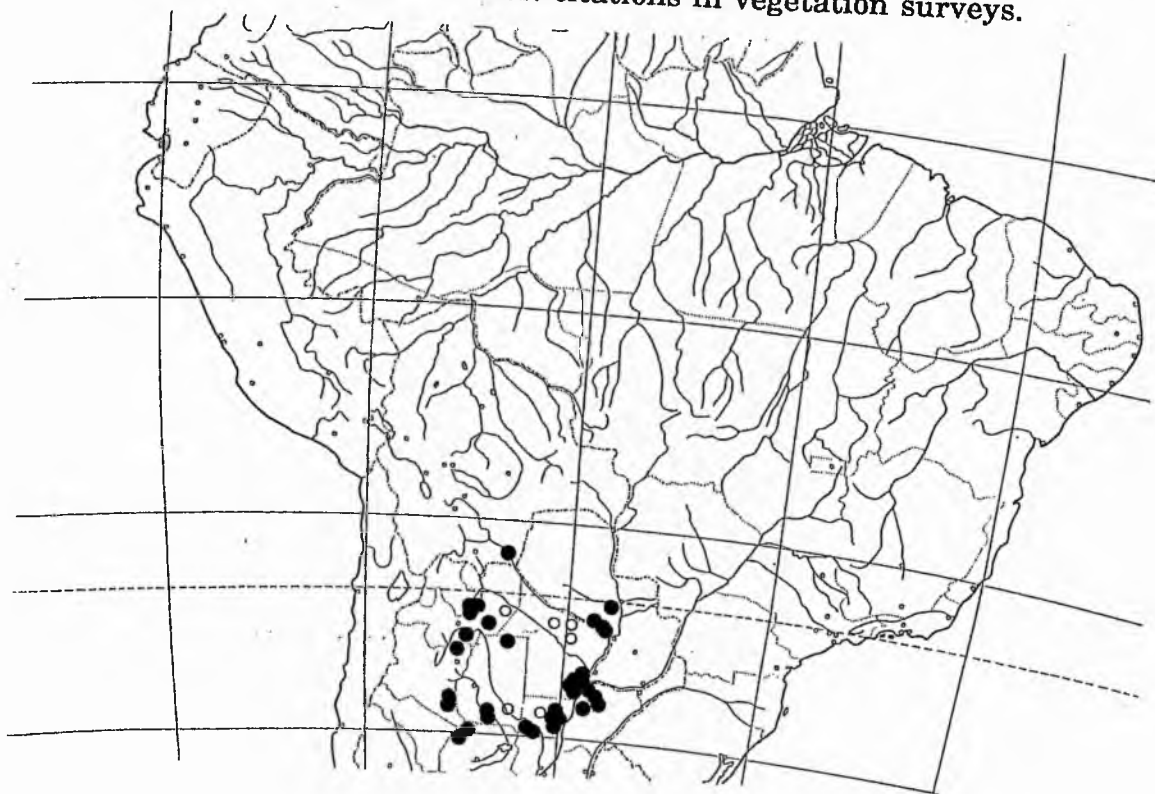
**Fig. 5.2:** Distribution map of *Lophocarpinia aculeatifolia*.

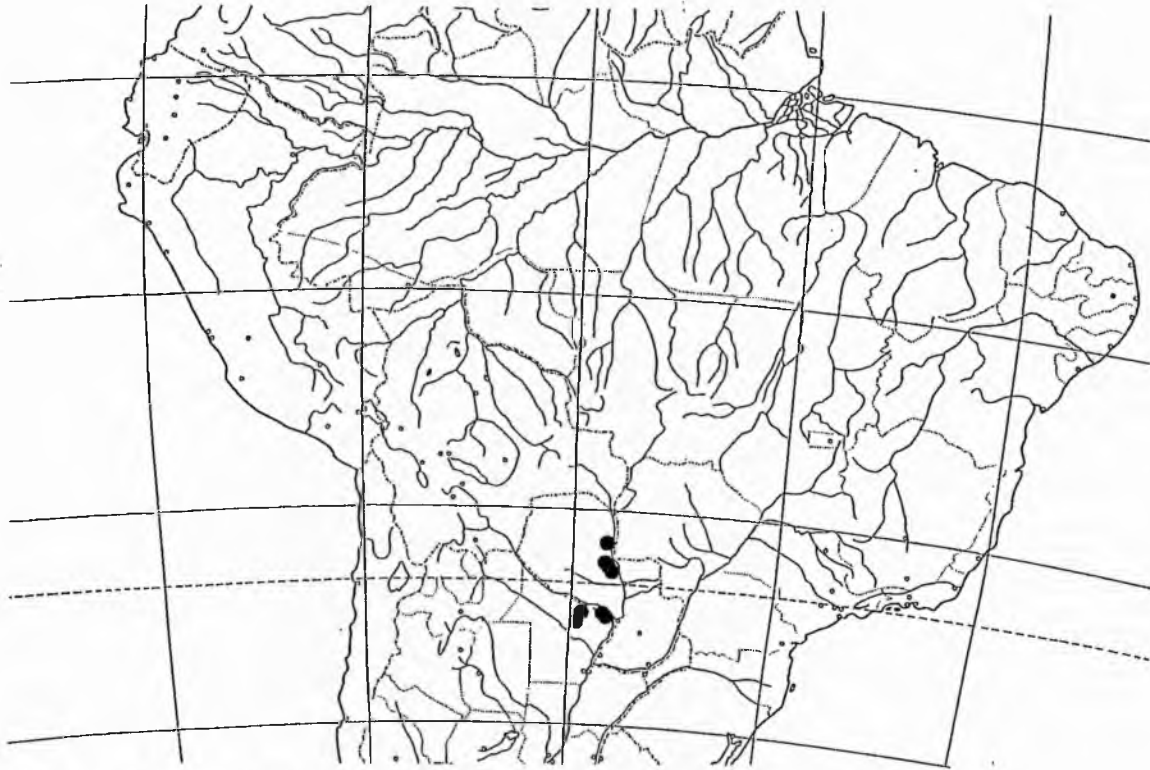




**Fig. 5.3:** Distribution map of *Maytenus spinosa*. Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.

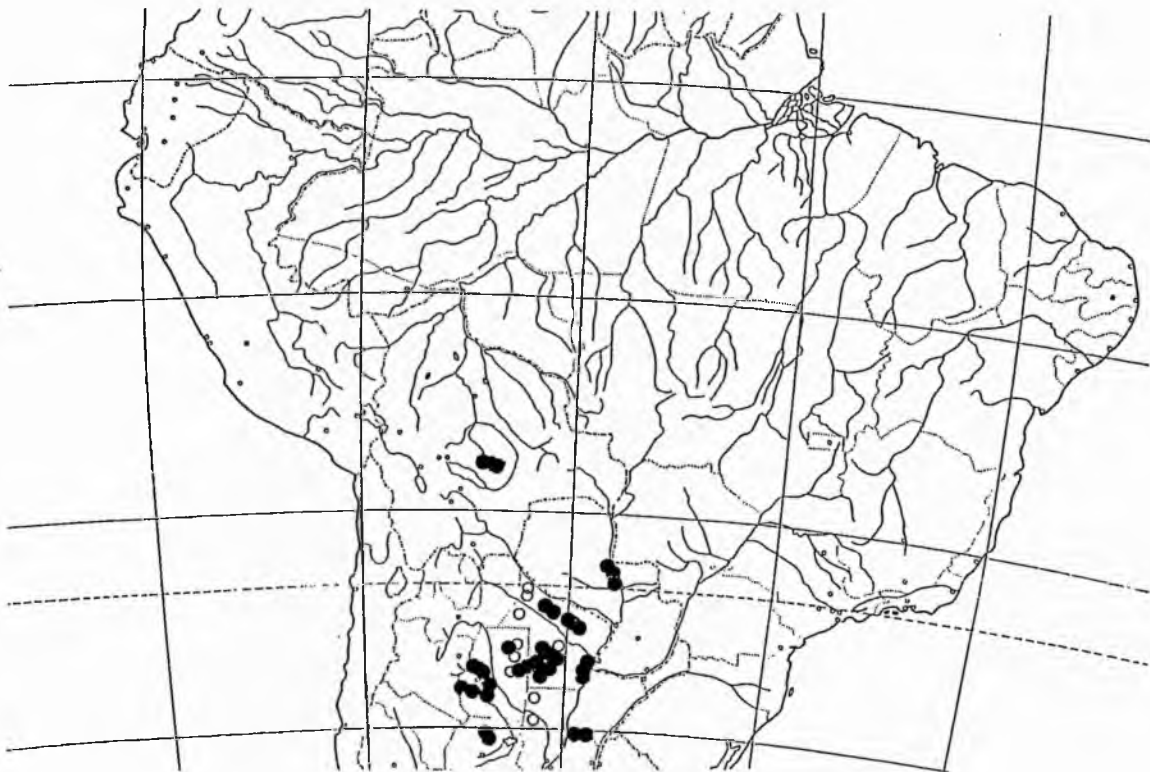
**Fig. 5.4:** Distribution map of *Maytenus vitis-idaea*. Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.

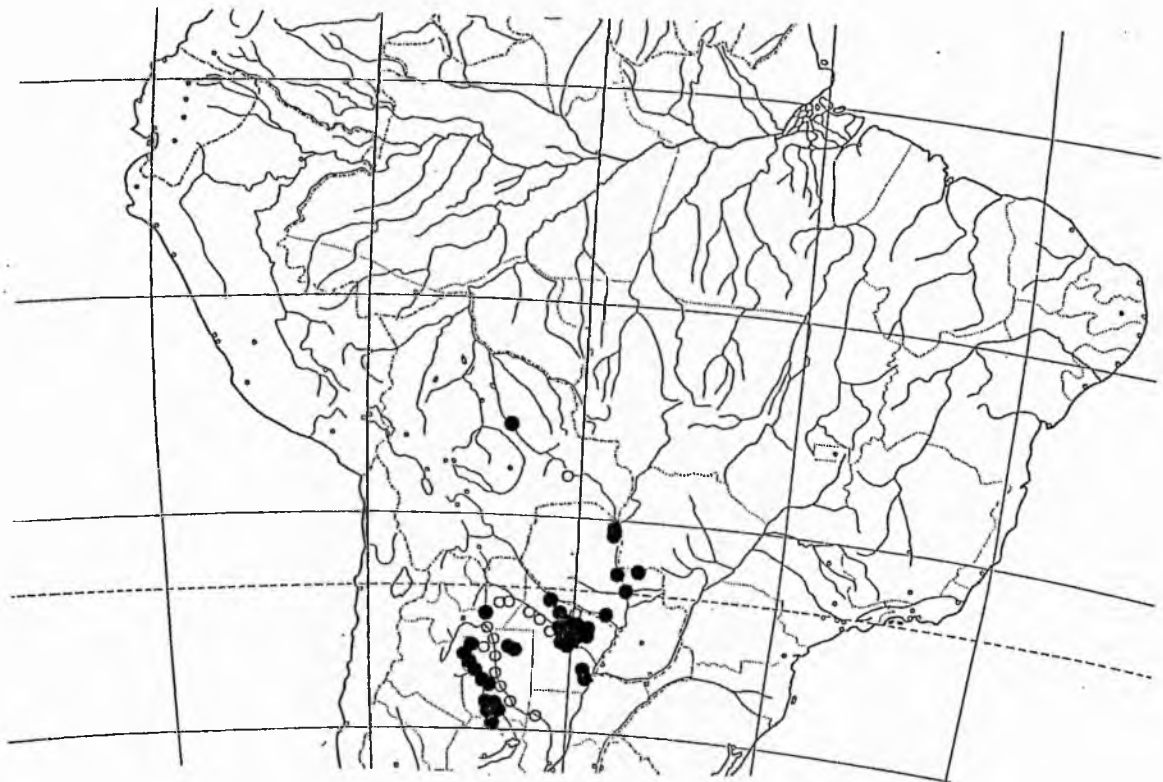




**Fig. 5.5:** Distribution map of *Prosopis fiebrigii*.

**Fig. 5.6:** Distribution map of *Prosopis kuntzei*. Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.





**Fig. 5.7:** Distribution map of *Prosopis ruscifolia*. Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.

**Fig. 5.8:** Distribution map of *Prosopis vinalillo*. Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.

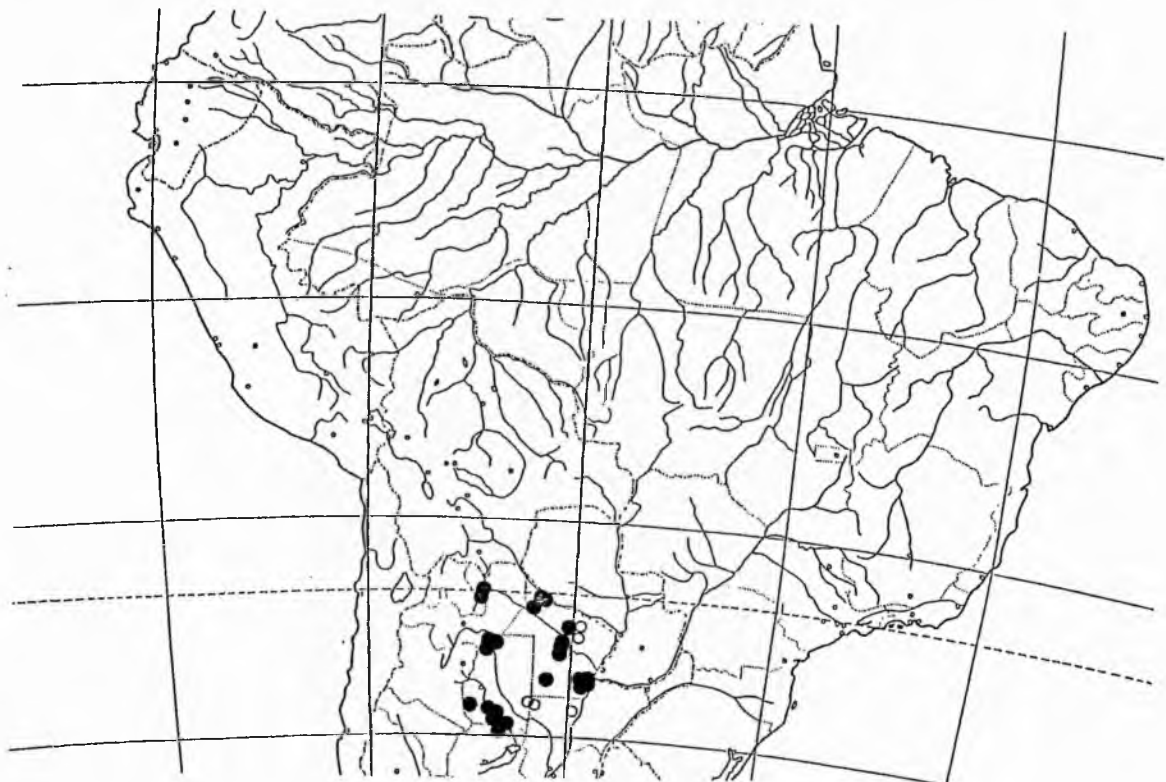




Fig. 5.9: Distribution map of *Schinopsis cornuta*.

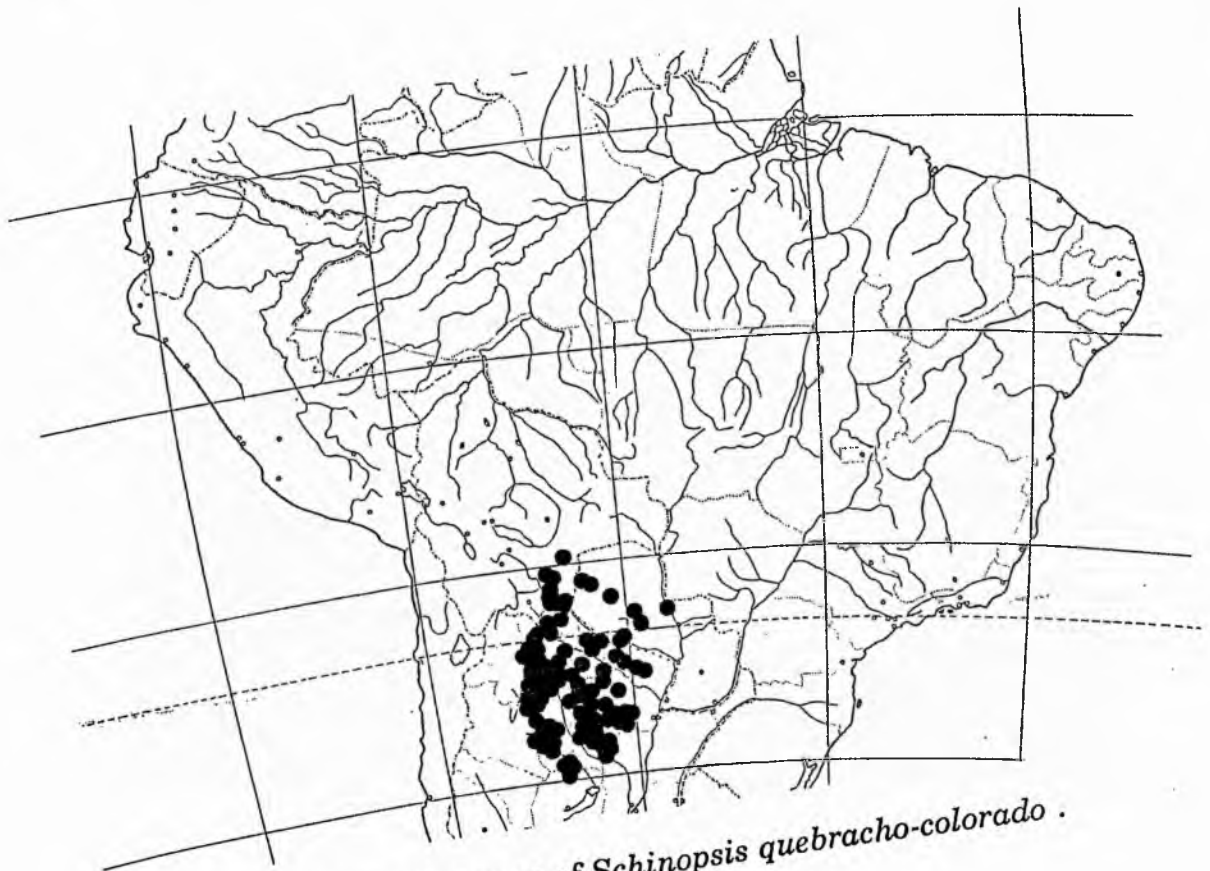


Fig. 5.10: Distribution map of *Schinopsis quebracho-colorado*.

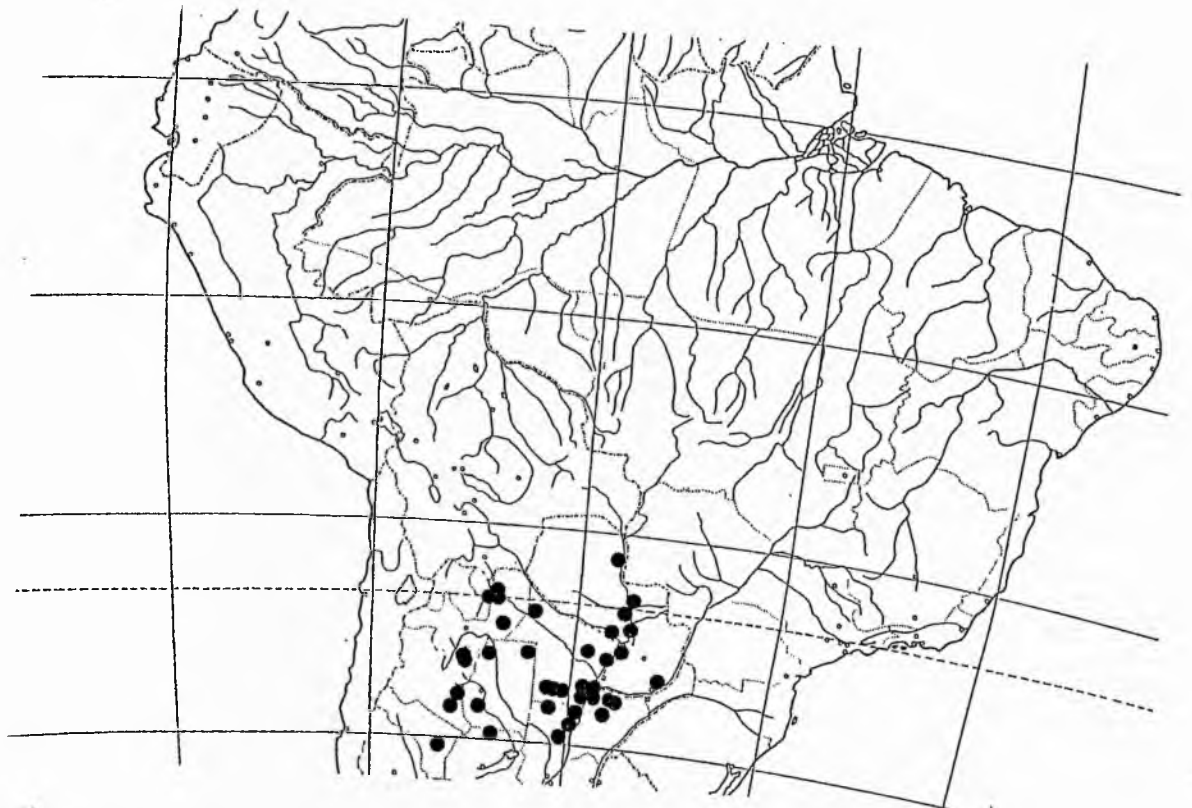
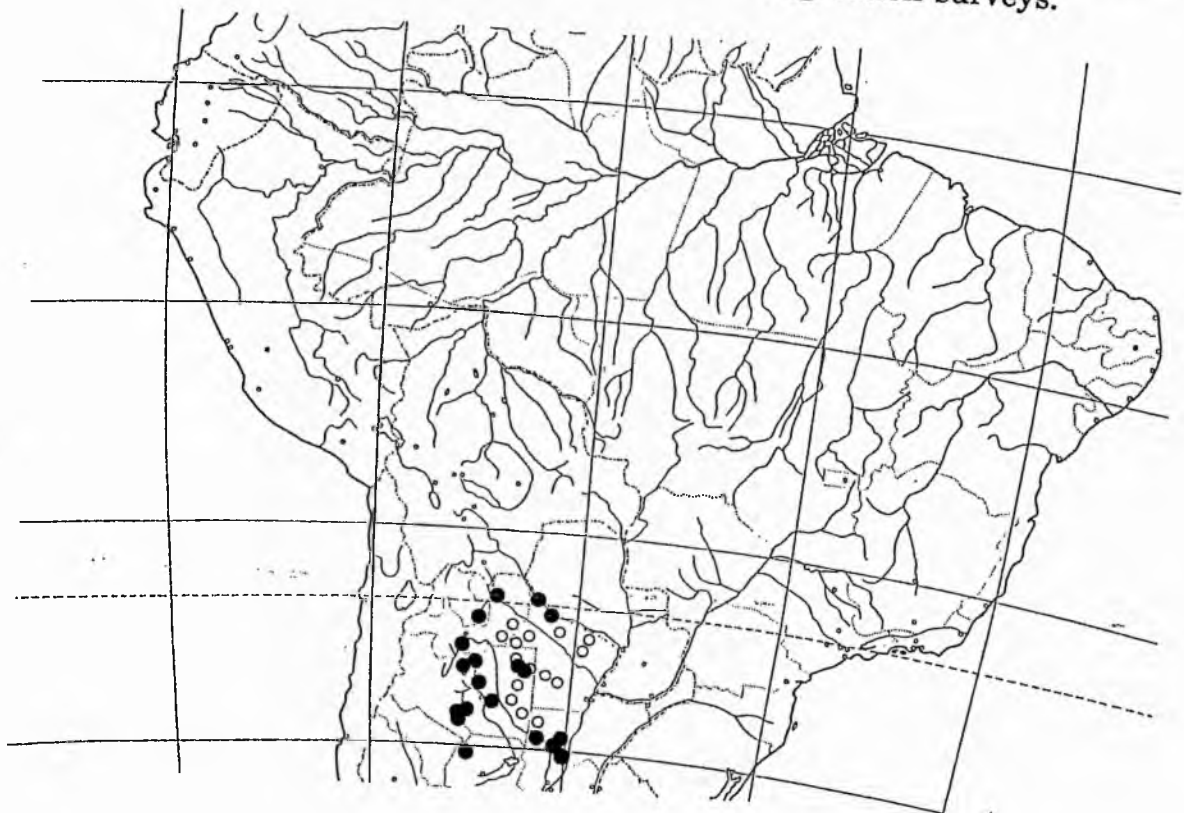
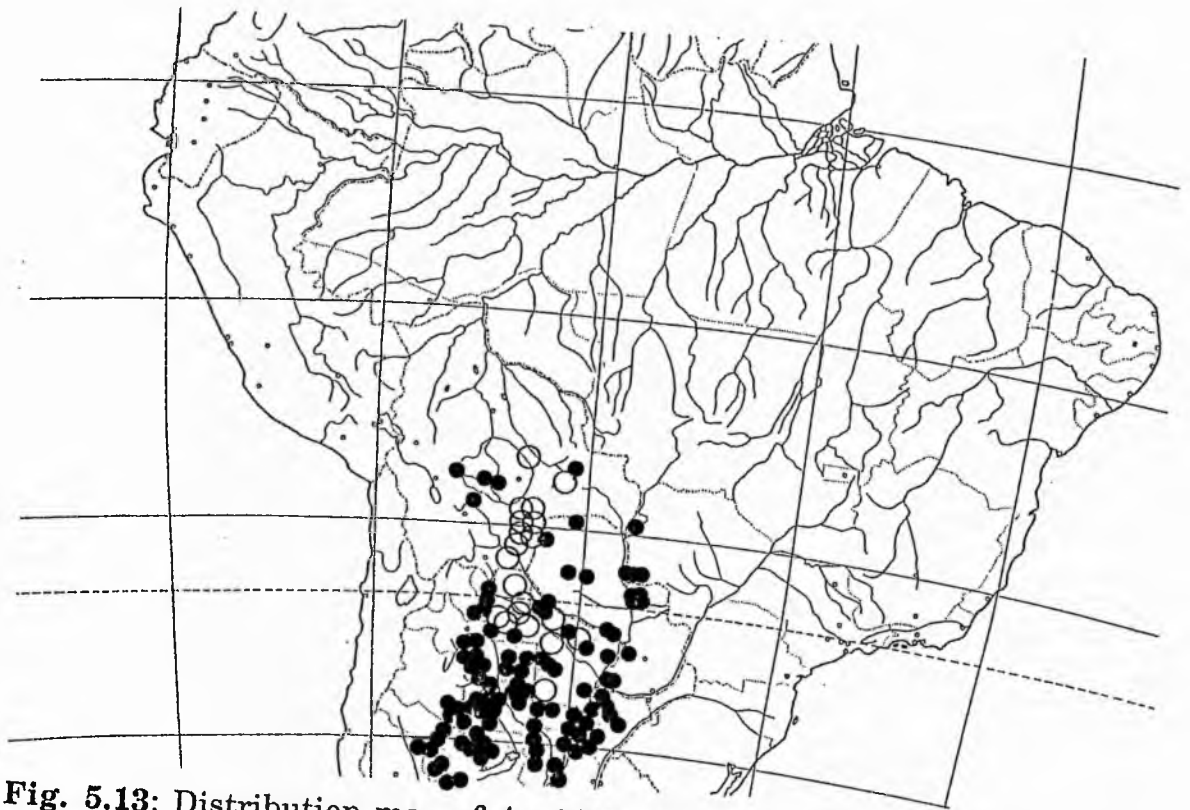


Fig. 5.11: Distribution map of *Tabebuia nodosa*.

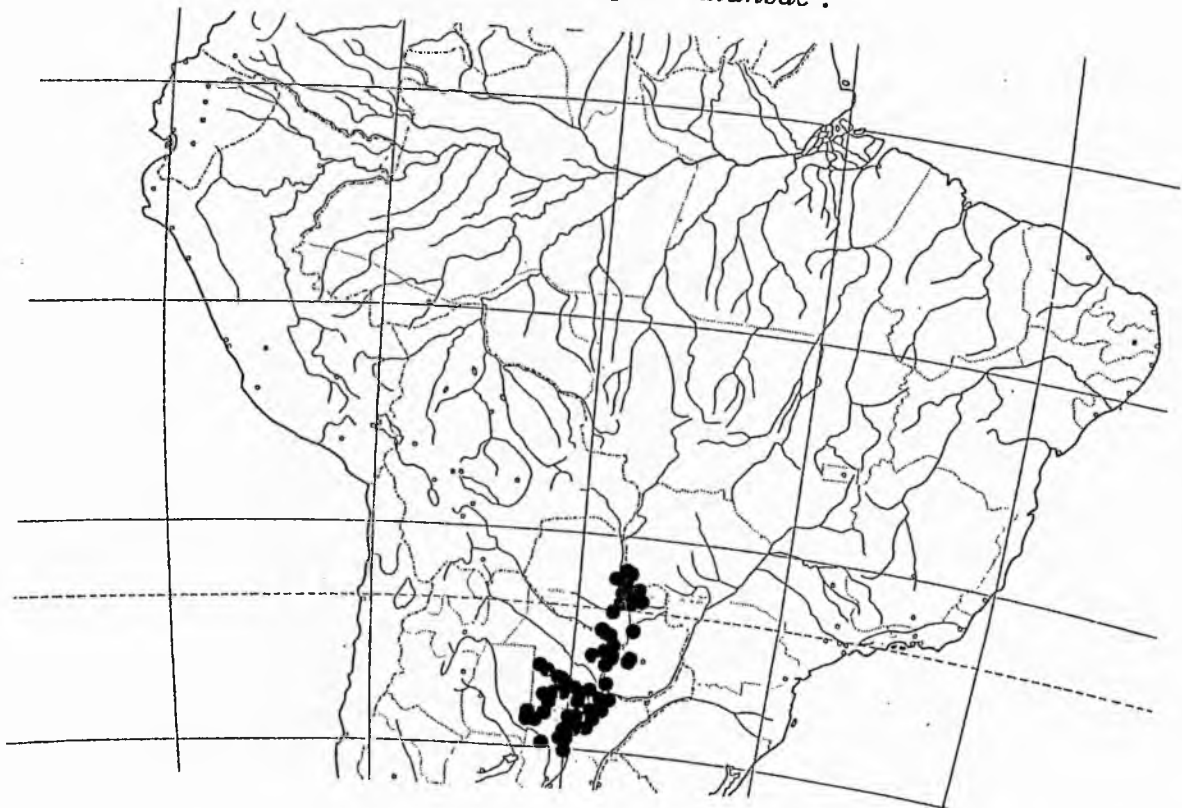
Fig. 5.12: Distribution map of *Ziziphus mistol*. Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.



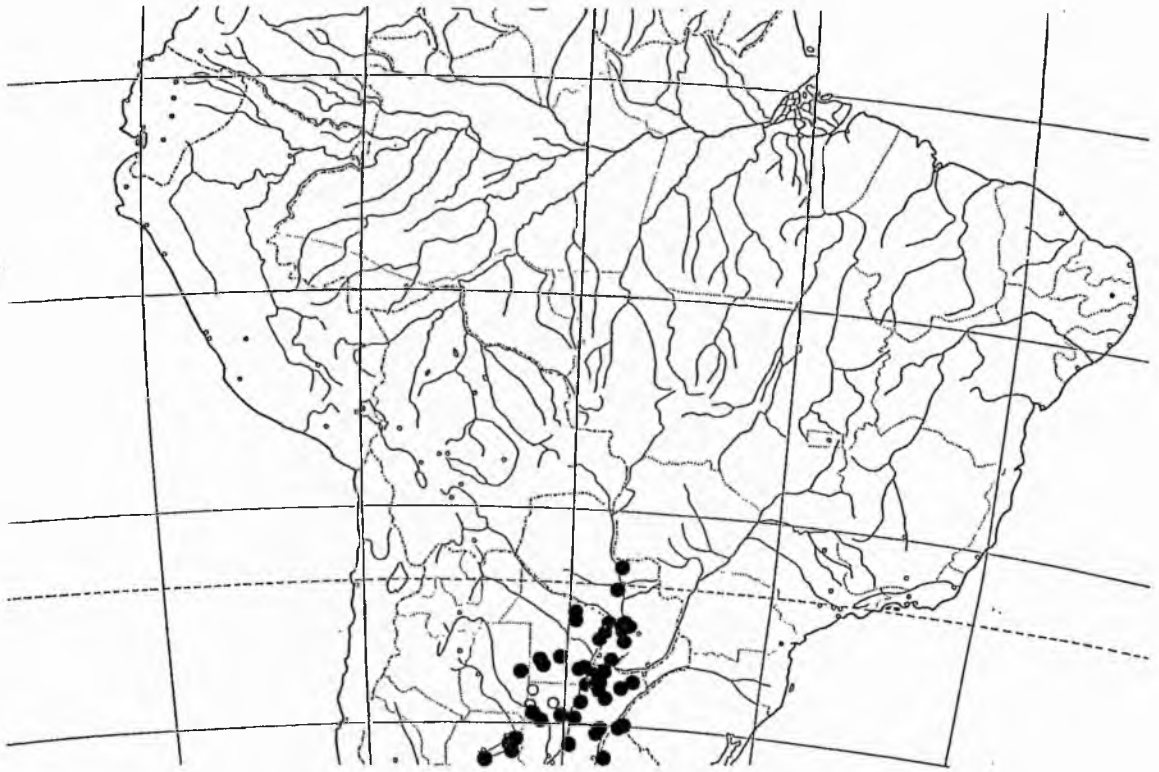


**Fig. 5.13:** Distribution map of *Aspidosperma quebracho-blanco* . Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.

**Fig. 5.14:** Distribution map of *Schinopsis balansae* .

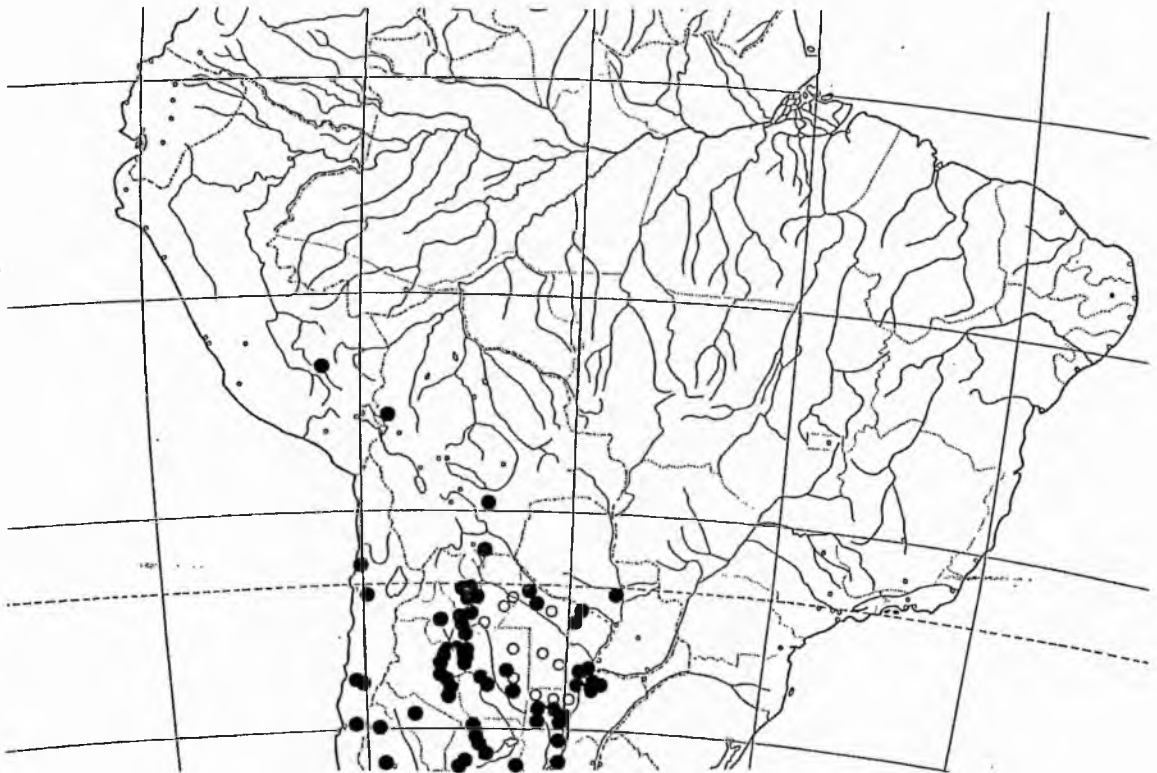


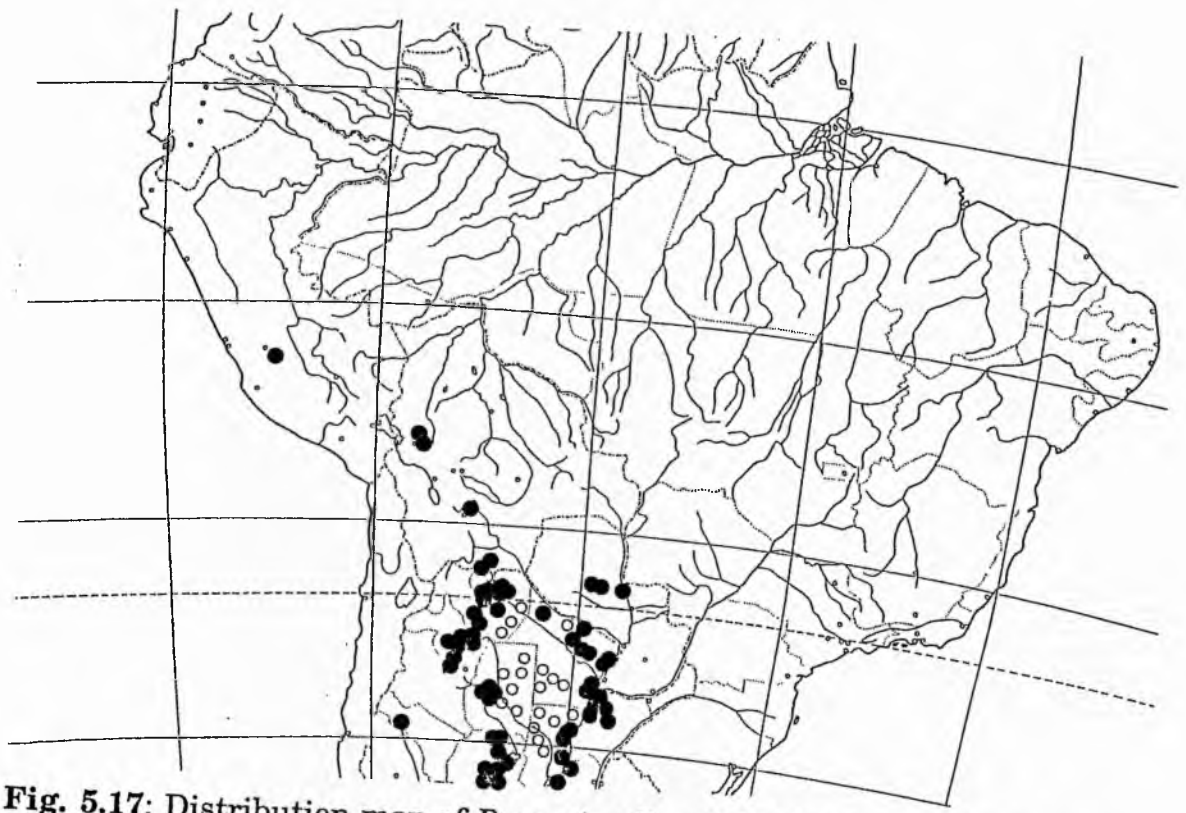




**Fig. 5.15:** Distribution map of *Prosopis affinis* . Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.

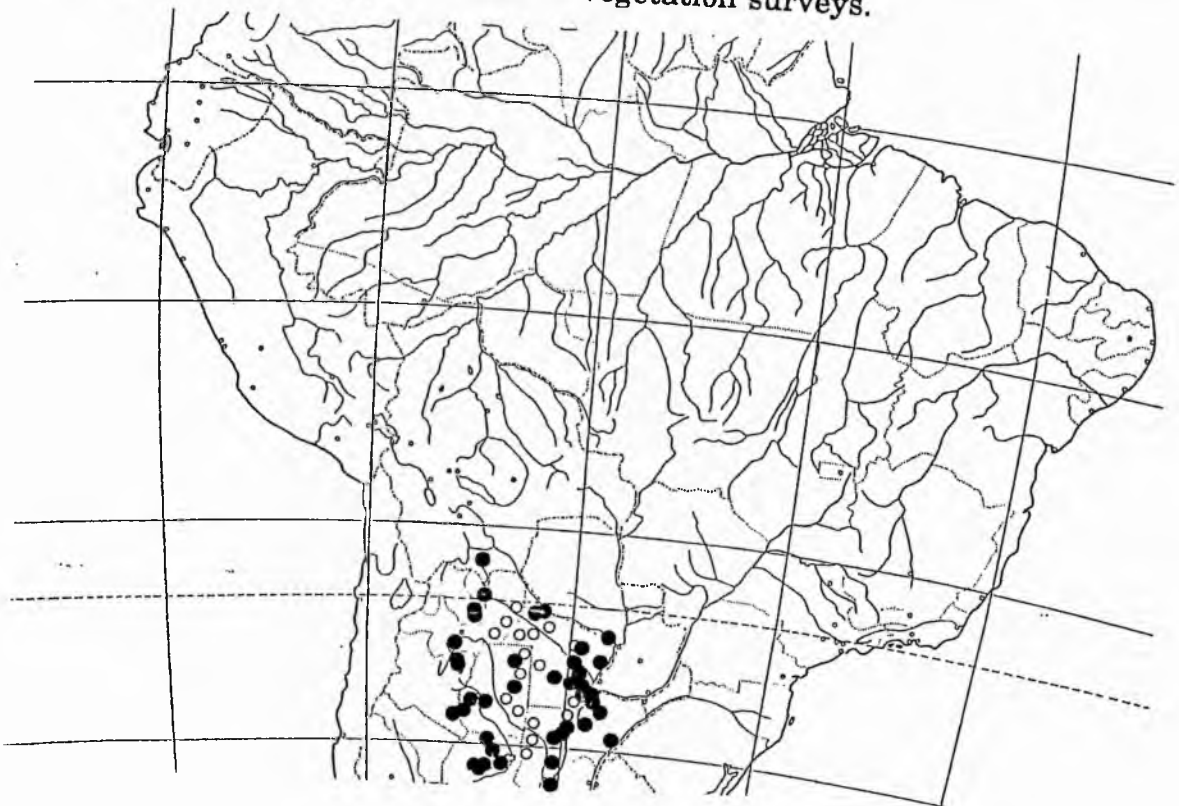
**Fig. 5.16:** Distribution map of *Geoffroea decorticans* . Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.

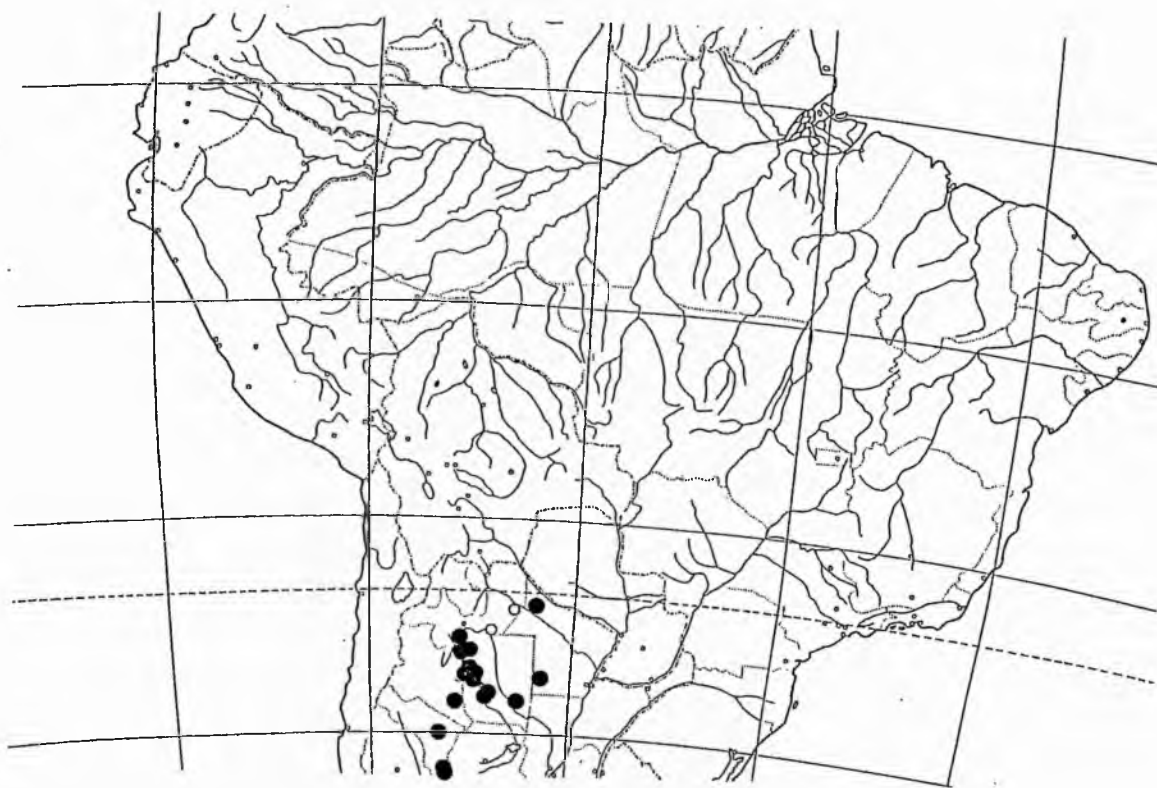




**Fig. 5.17:** Distribution map of *Prosopis alba*. Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.

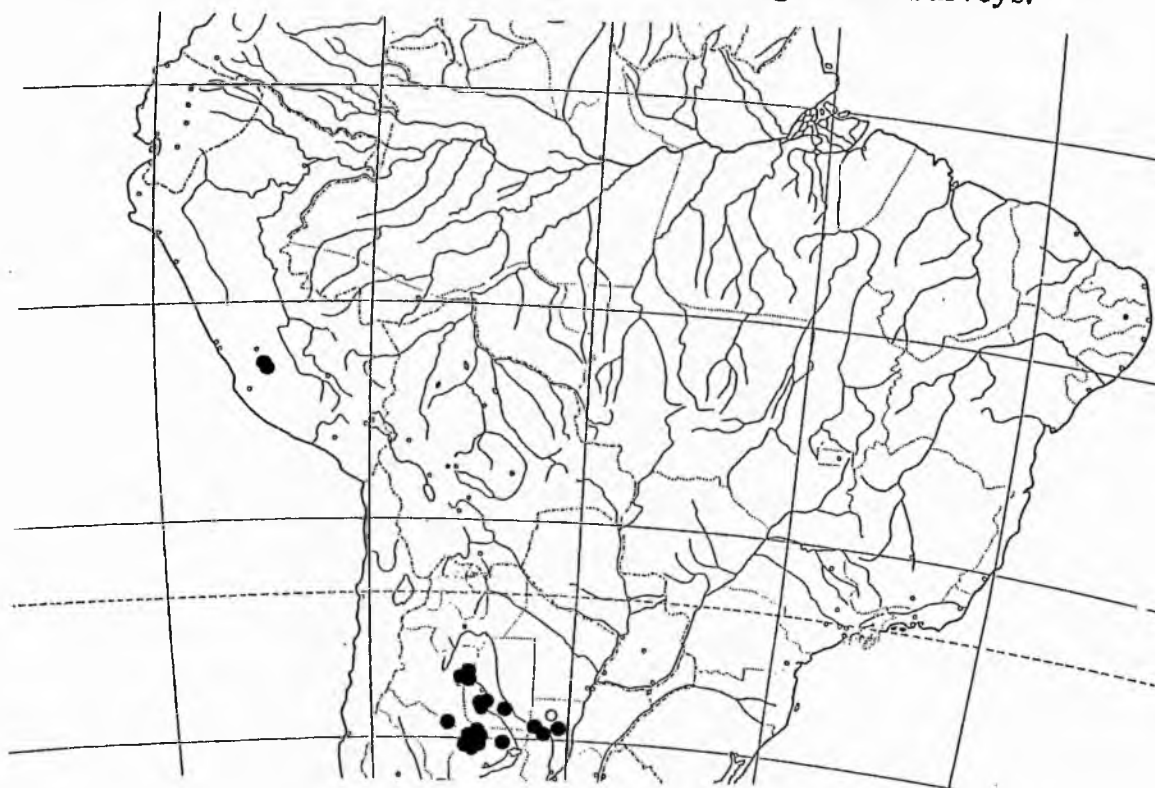
**Fig. 5.18:** Distribution map of *Prosopis nigra*. Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.

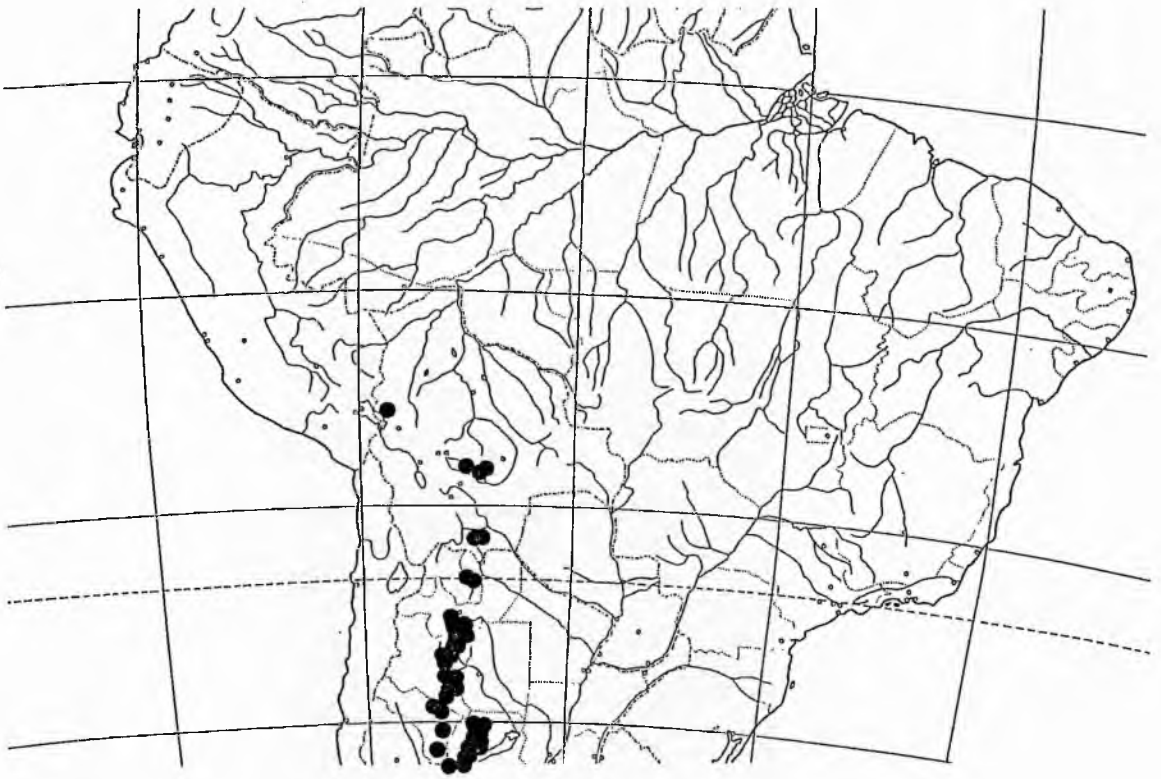




**Fig. 5.19:** Distribution map of *Prosopis sericantha*. Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.

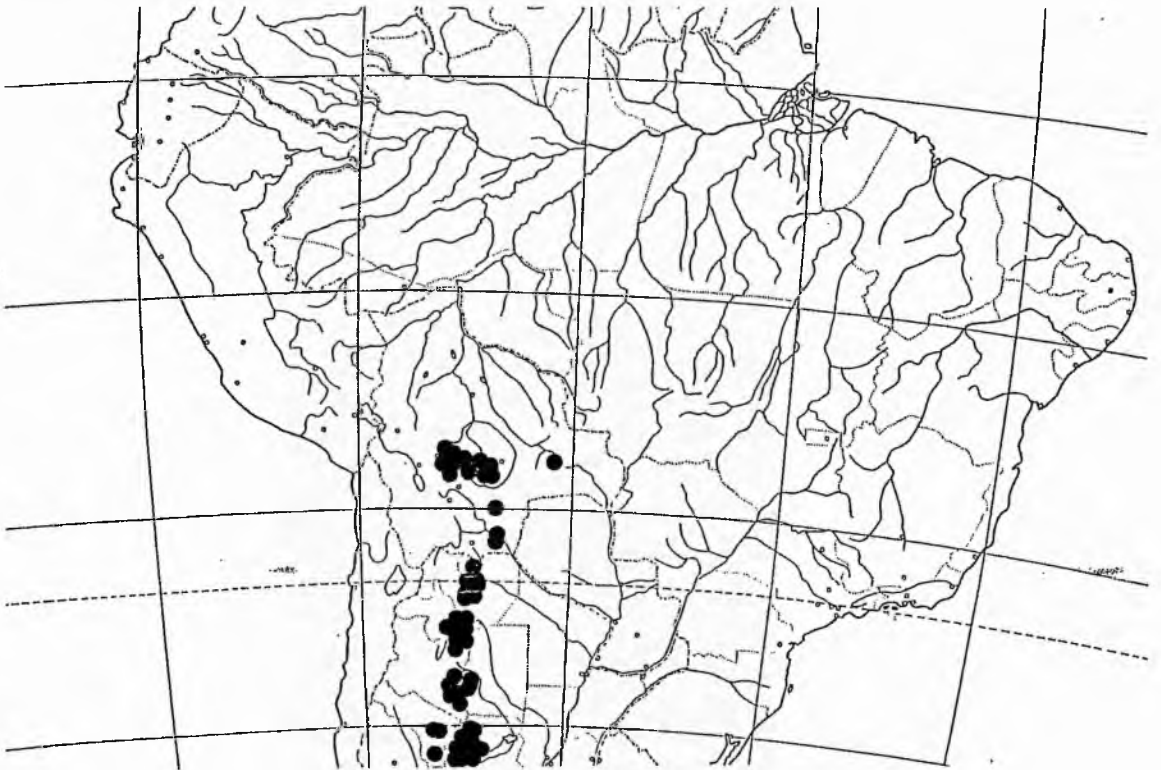
**Fig. 5.20:** Distribution map of *Prosopis reptans*. Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.

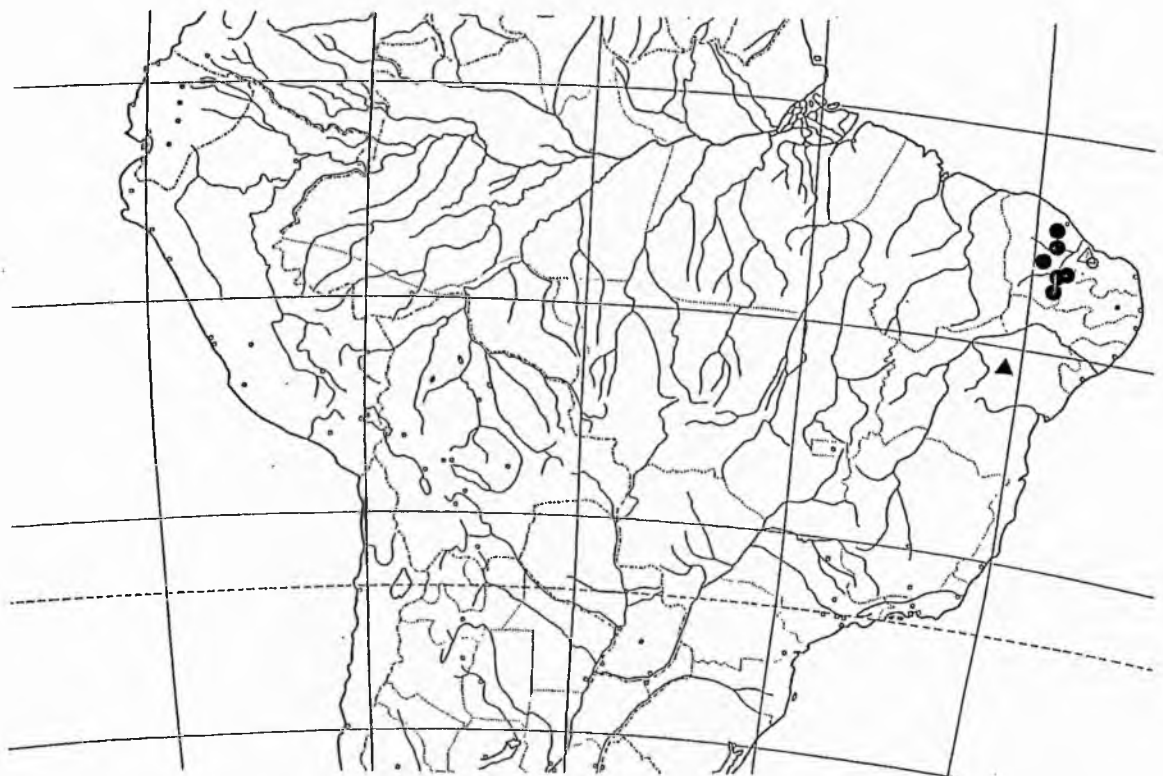




**Fig. 5.21:** Distribution map of *Lythraea ternifolia*.

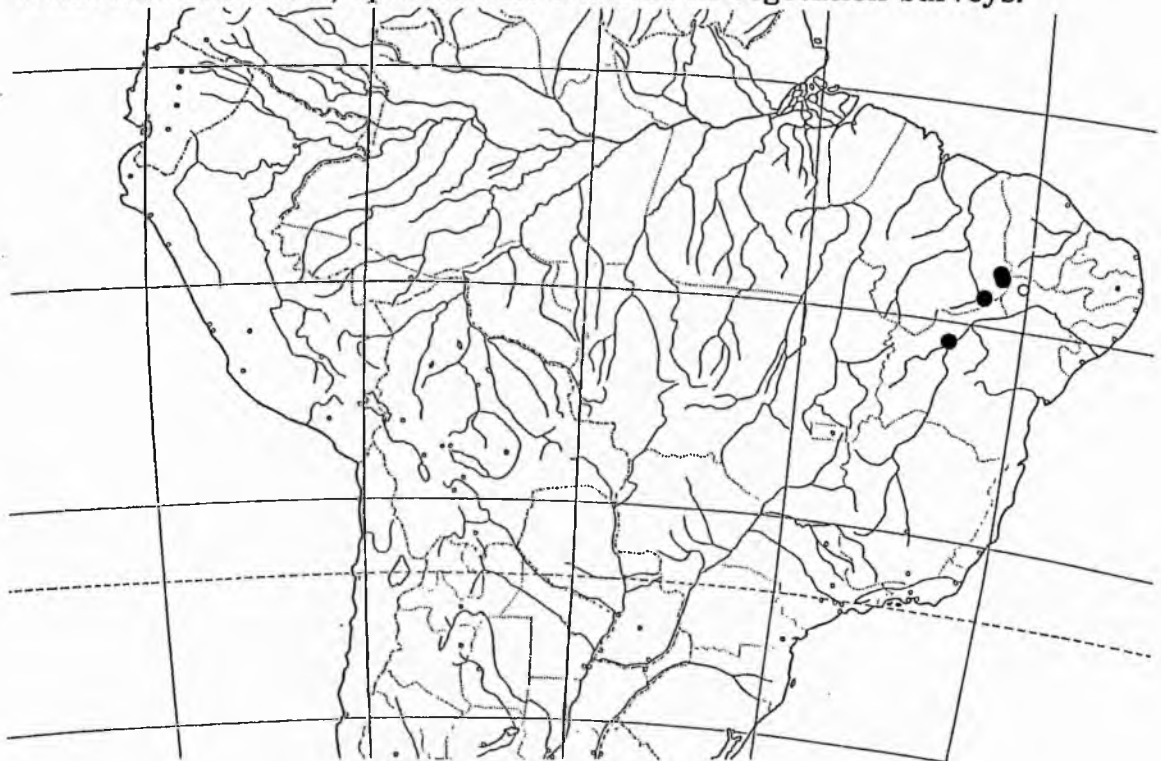
**Fig. 5.22:** Distribution map of *Schinopsis haenkeana*.

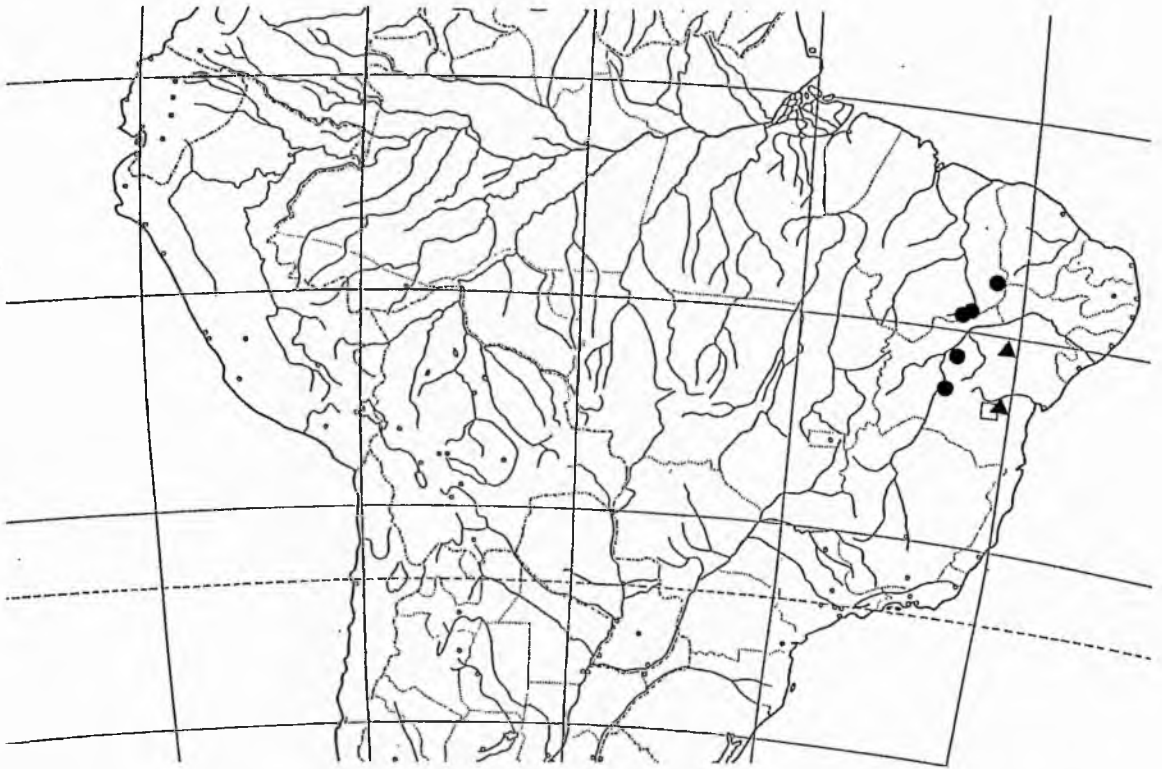




**Fig. 5.23:** Distribution map of *Auxemma oncocalyx* (circles) and *A. glazioviana* (triangles). Solid black dots/triangles: herbarium exsiccata; open circles/triangles: citations in vegetation surveys.

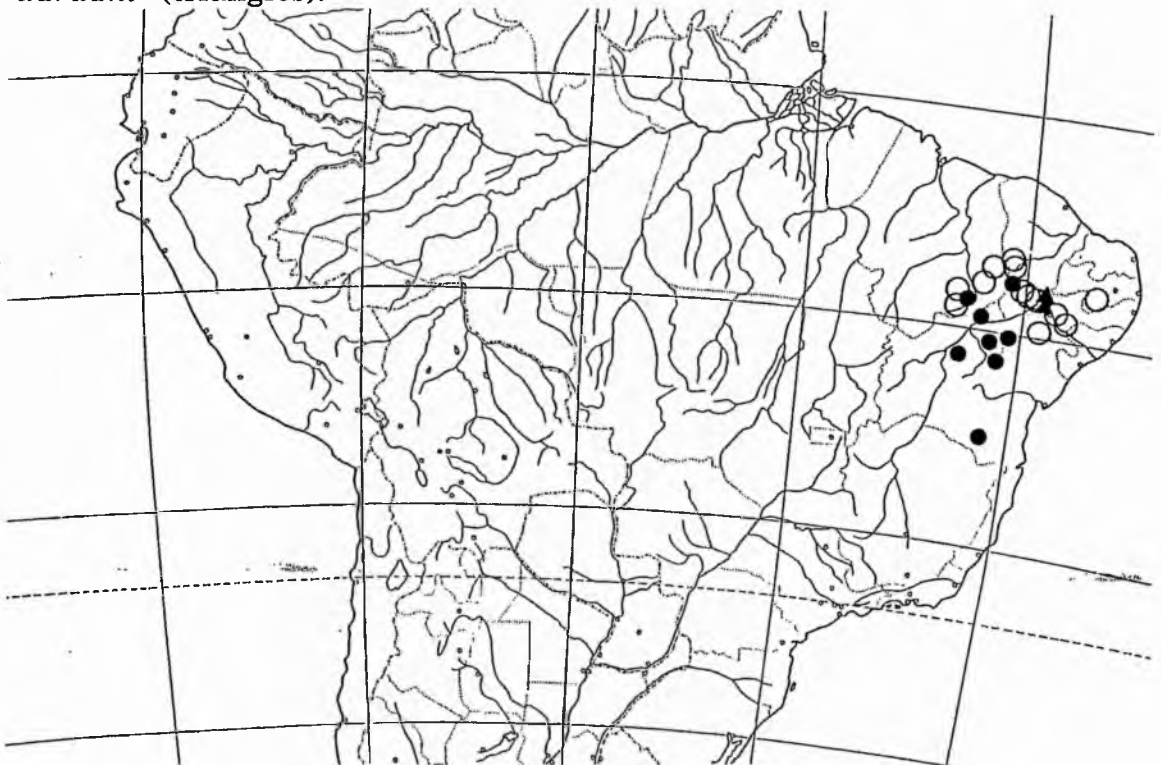
**Fig. 5.24:** Distribution map of *Fraunhoffera multiflora*. Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.

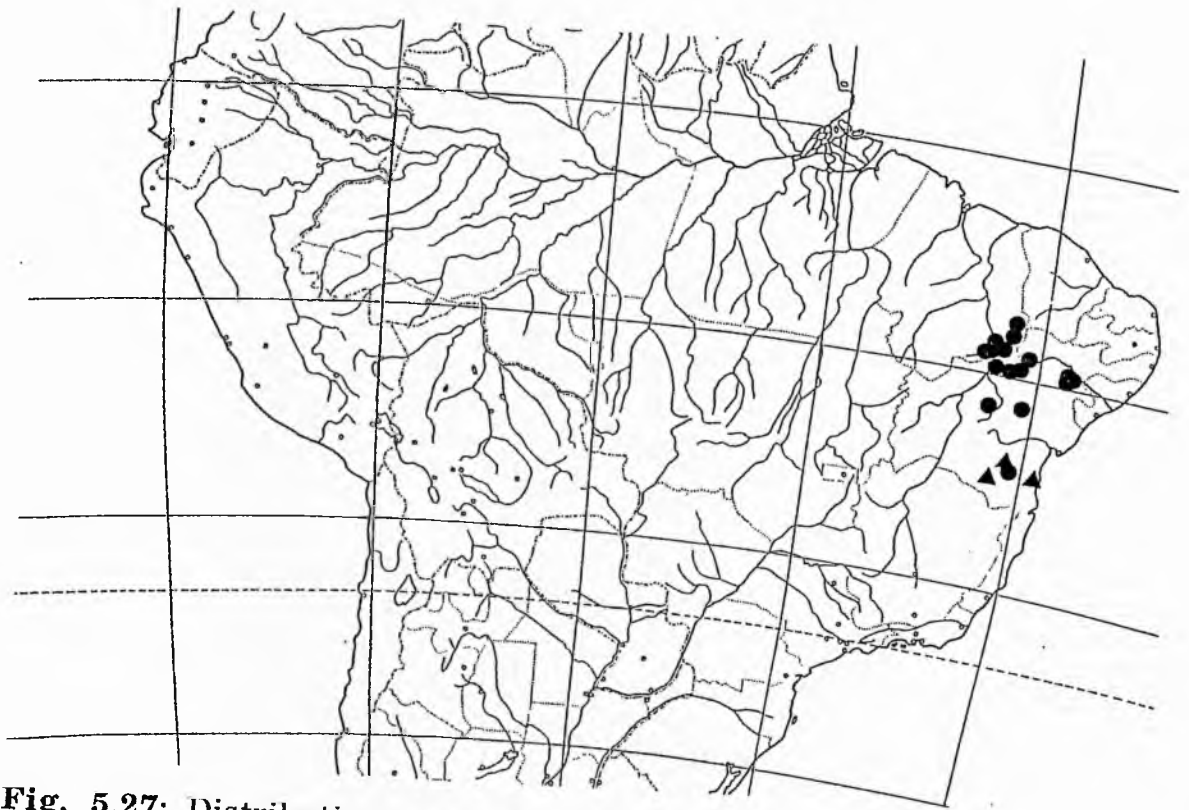




**Fig. 5.25:** Distribution map of *Bauhinia flexuosa* (dots), *B. estivana* (triangles) and *B. cattingae* (open square).

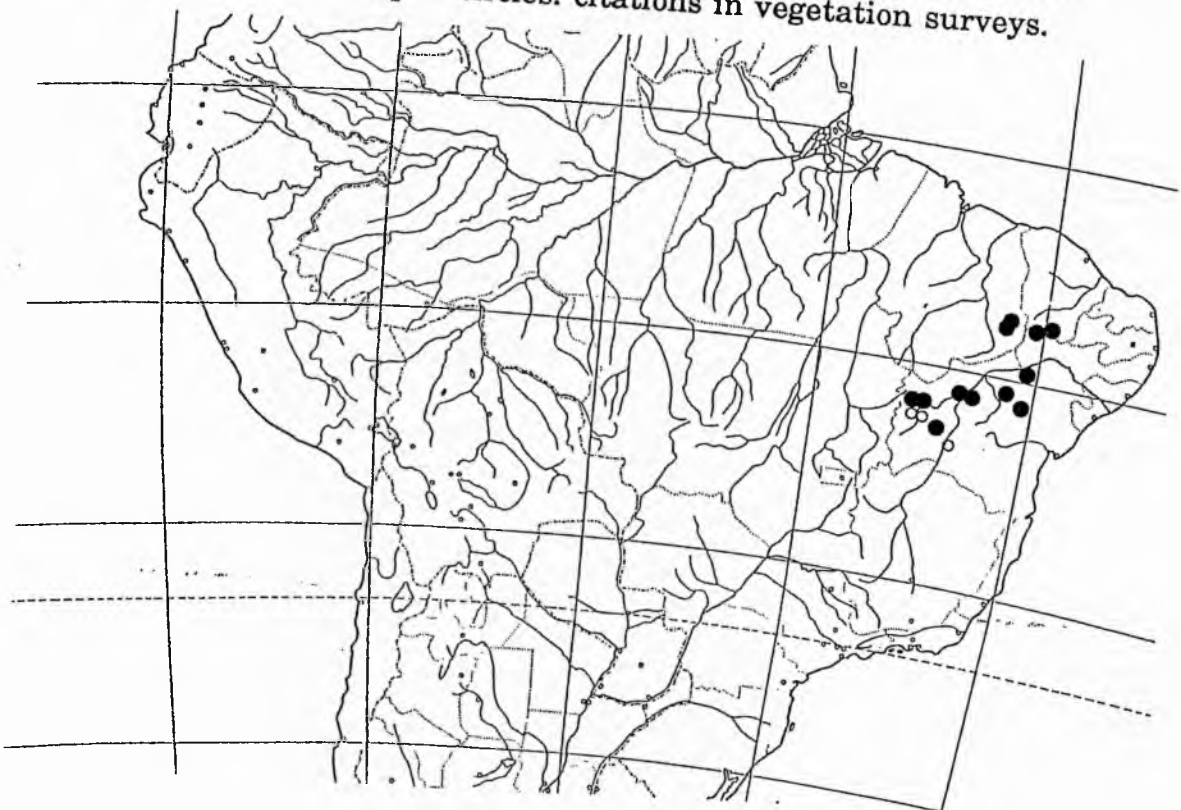
**Fig. 5.26:** Distribution map of *Cordia leucocephala* (solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys) and *C. dardani* (triangles).

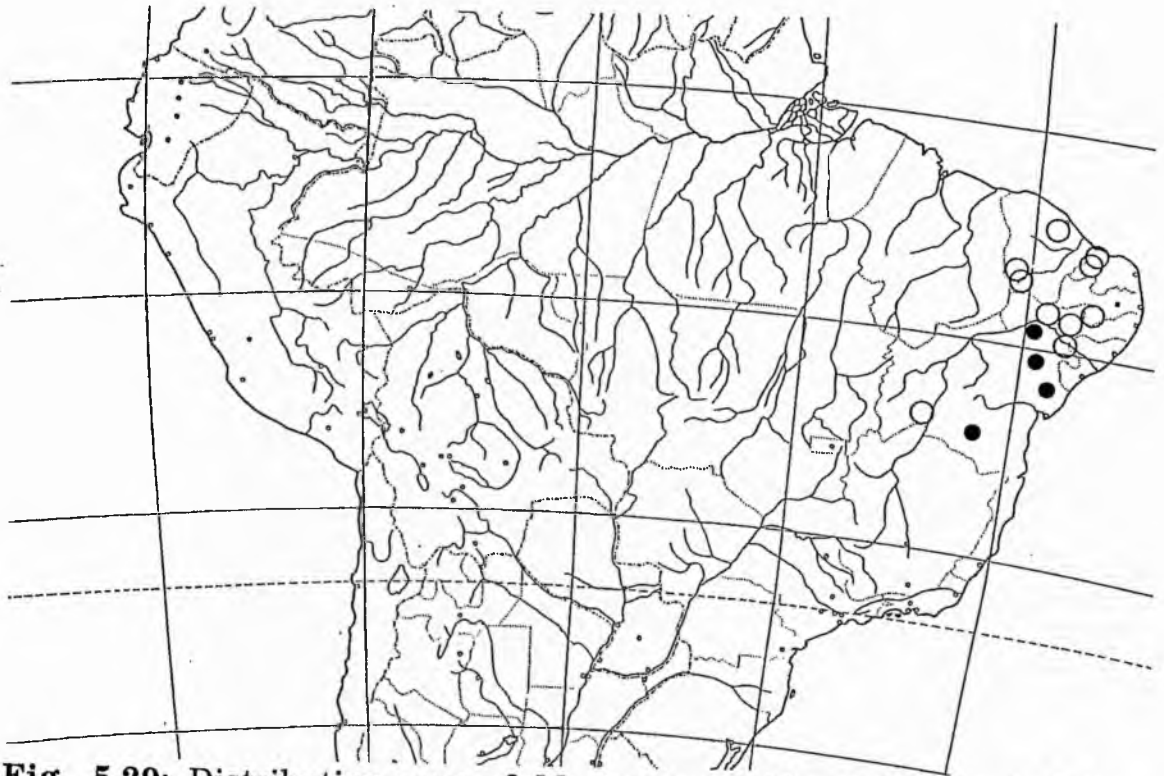




**Fig. 5.27:** Distribution map of *Cratylia mollis* (dots) and *C. nuda* (triangles).

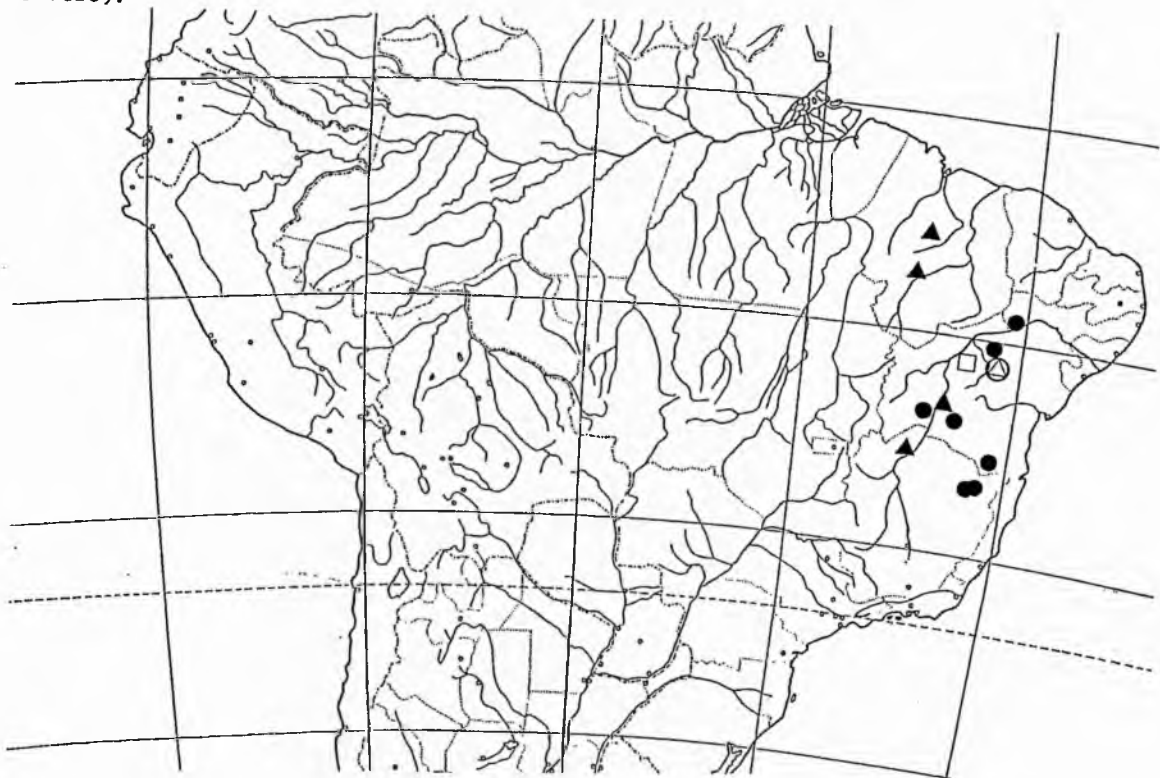
**Fig. 5.28:** Distribution map of *Hymenaea eriogyne*. Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.



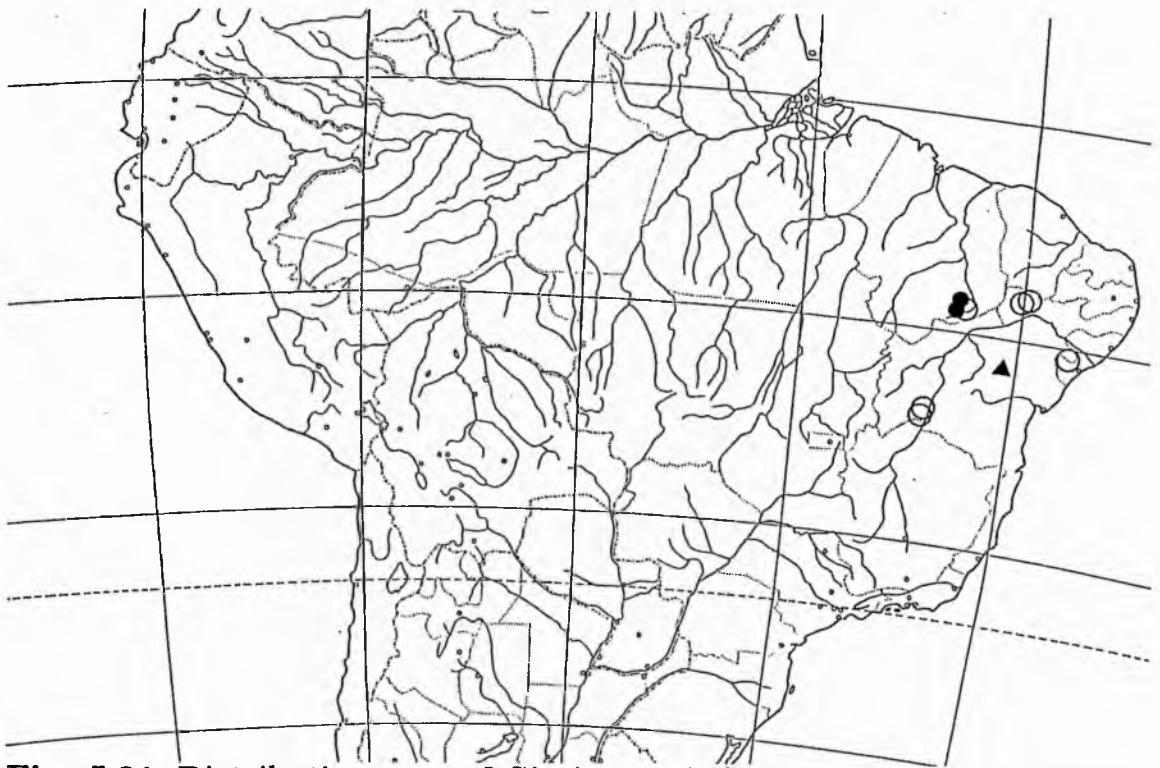


**Fig. 5.29:** Distribution map of *Maytenus rigida*. Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.

**Fig. 5.30:** Distribution map of *Mimosa adenophylla* (dots), *M. exalbescens* (triangles), *M. glaucula* (open square) and *M. morroënsis* (triangle in circle).

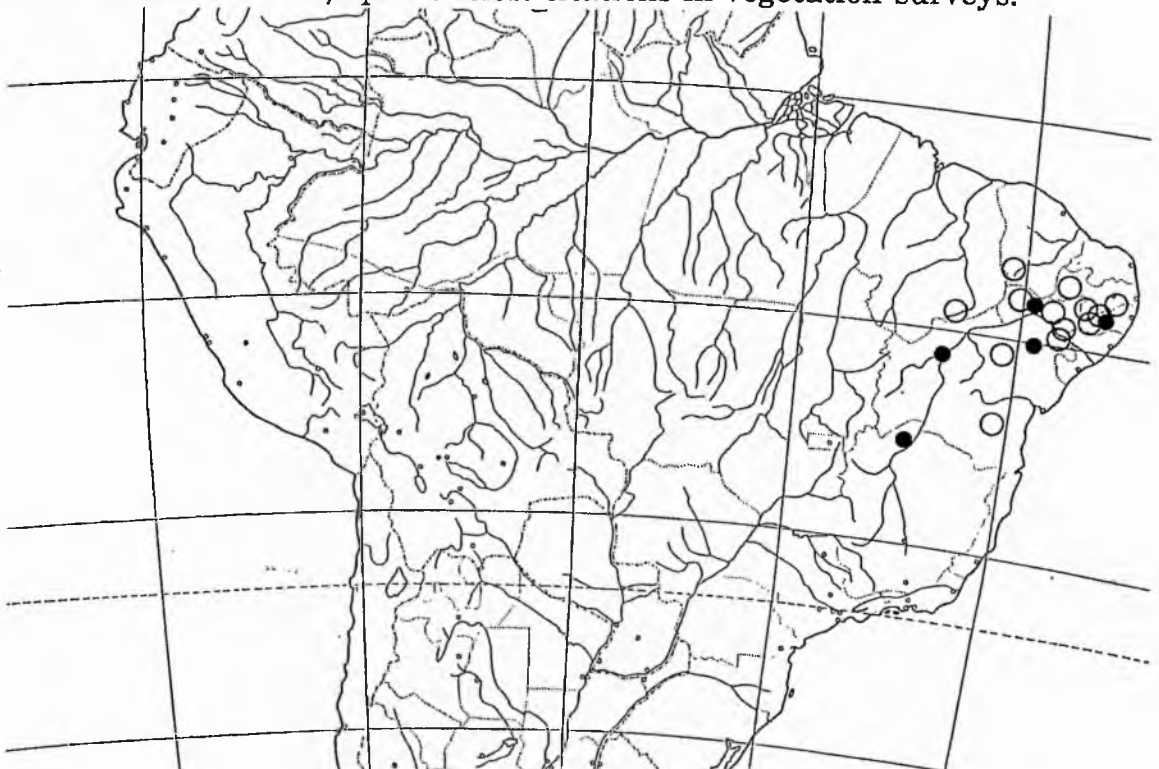


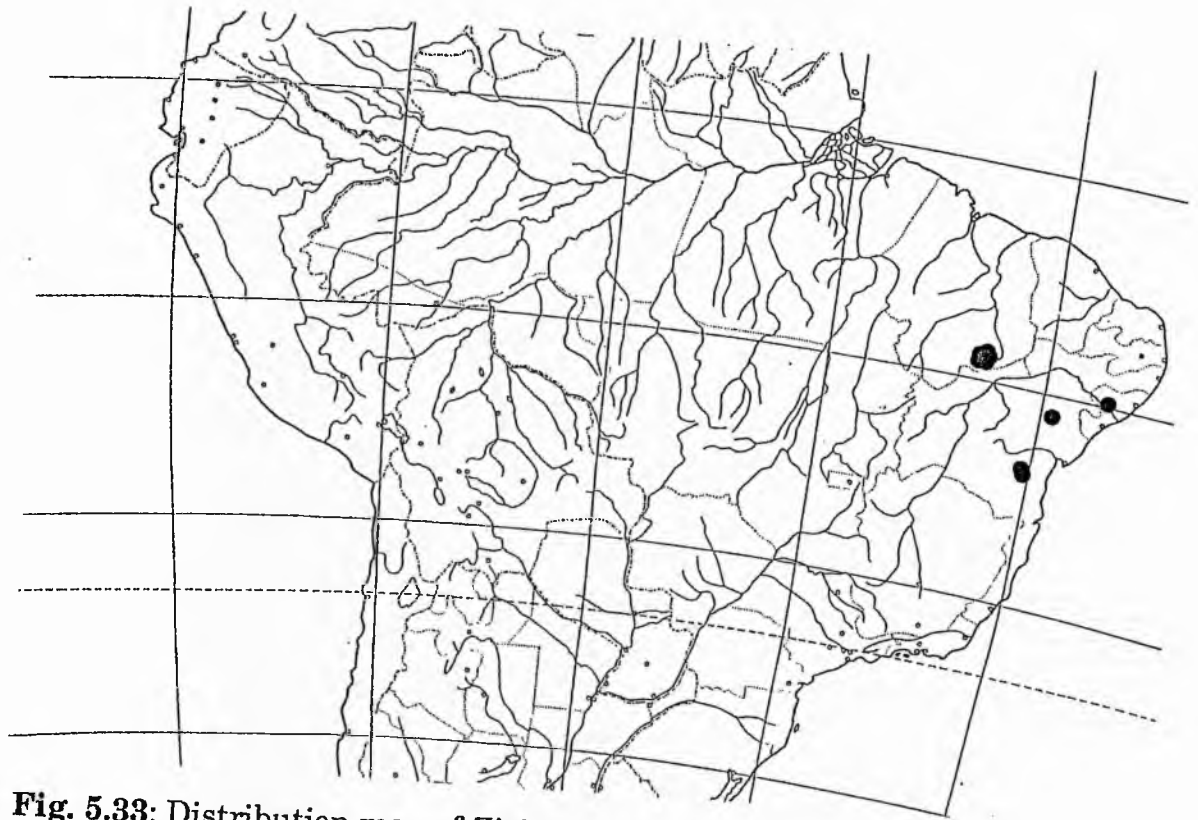




**Fig. 5.31:** Distribution map of *Simira* sp (solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys) and *Alseis involuta* (triangle).

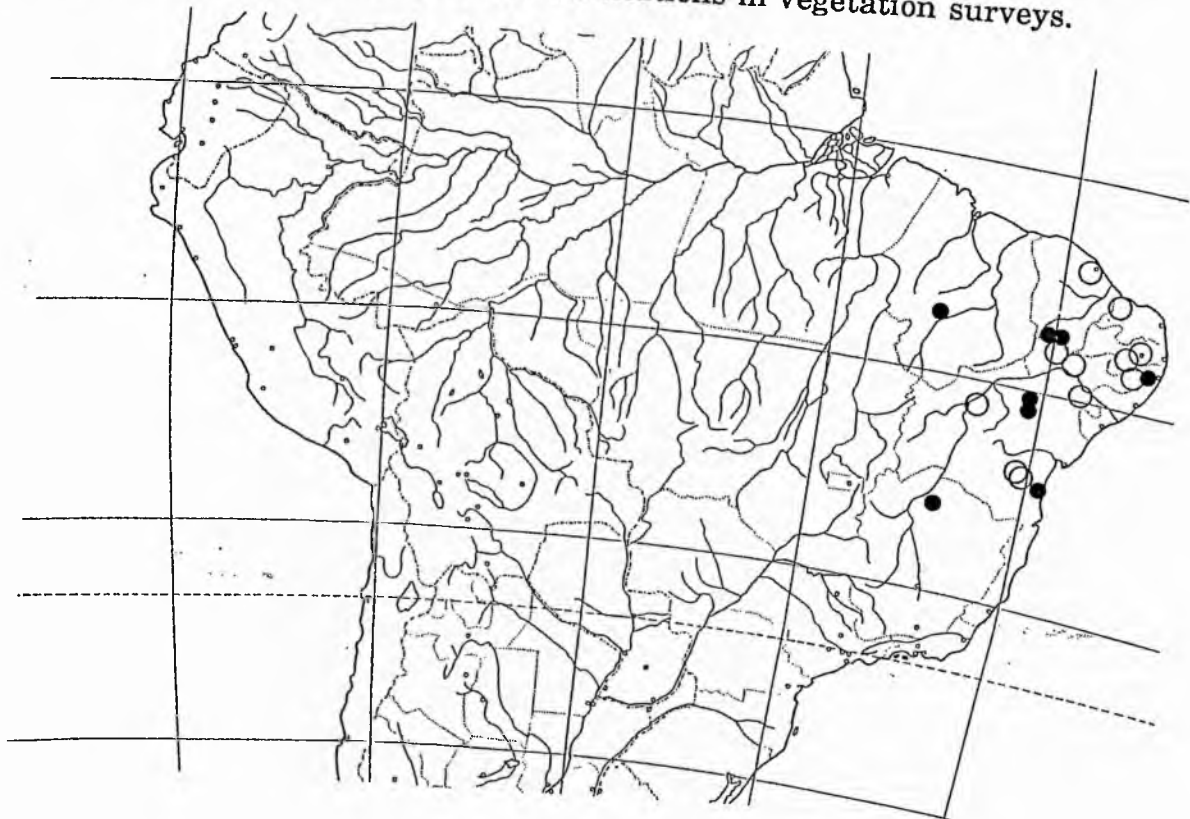
**Fig. 5.32:** Distribution map of *Spondias tuberosa*. Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.

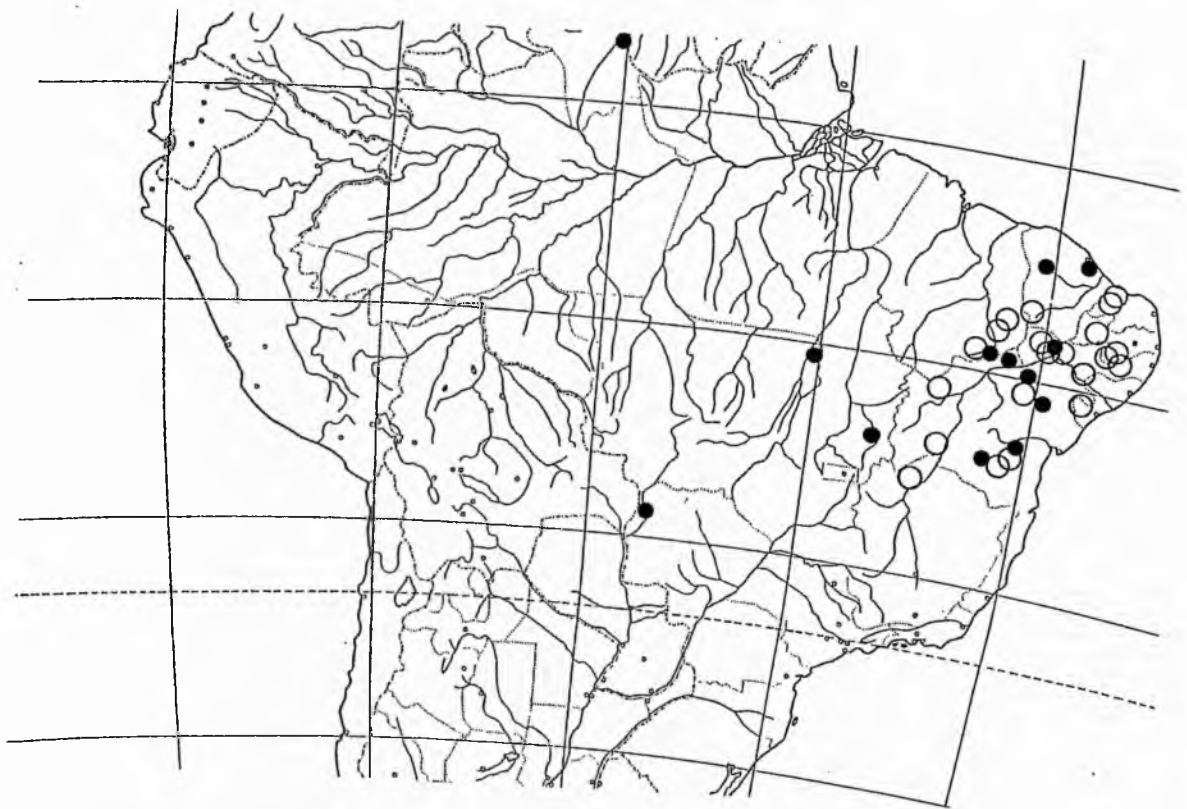




**Fig. 5.33:** Distribution map of *Ziziphus cotinifolia*.

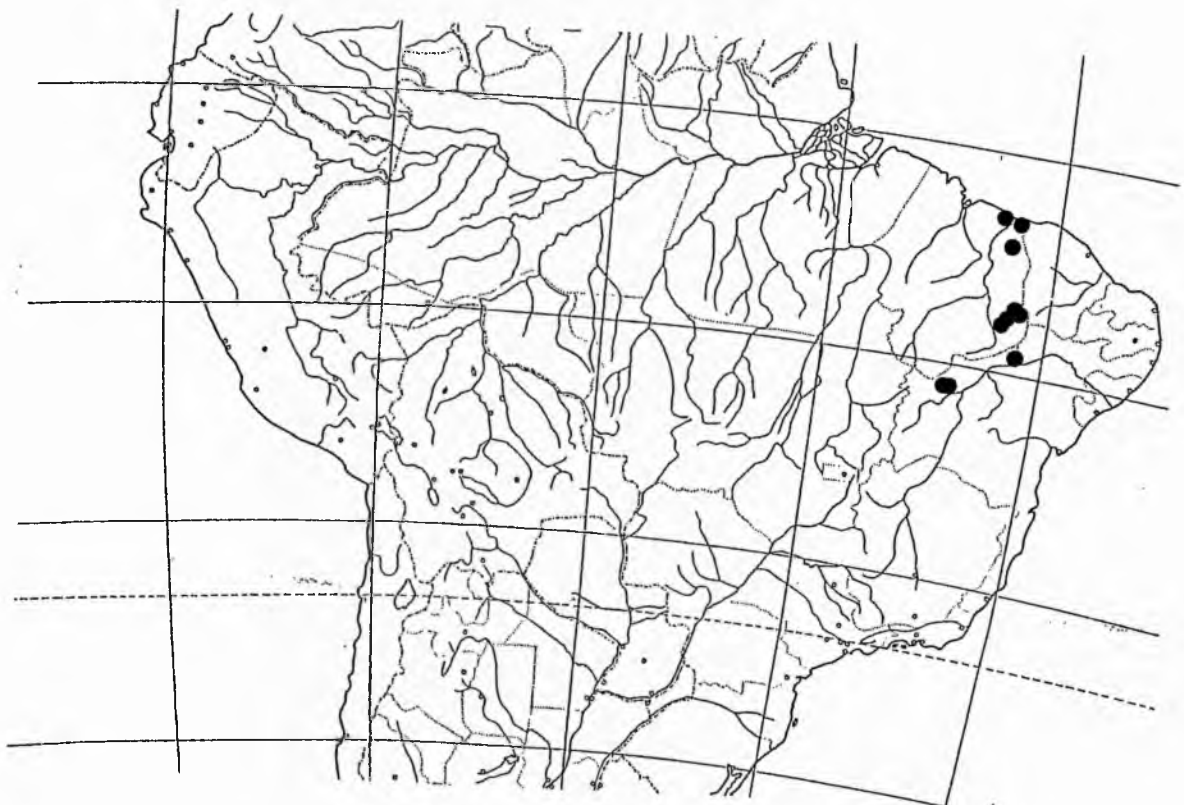
**Fig. 5.34:** Distribution map of *Ziziphus joazeiro*. Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.

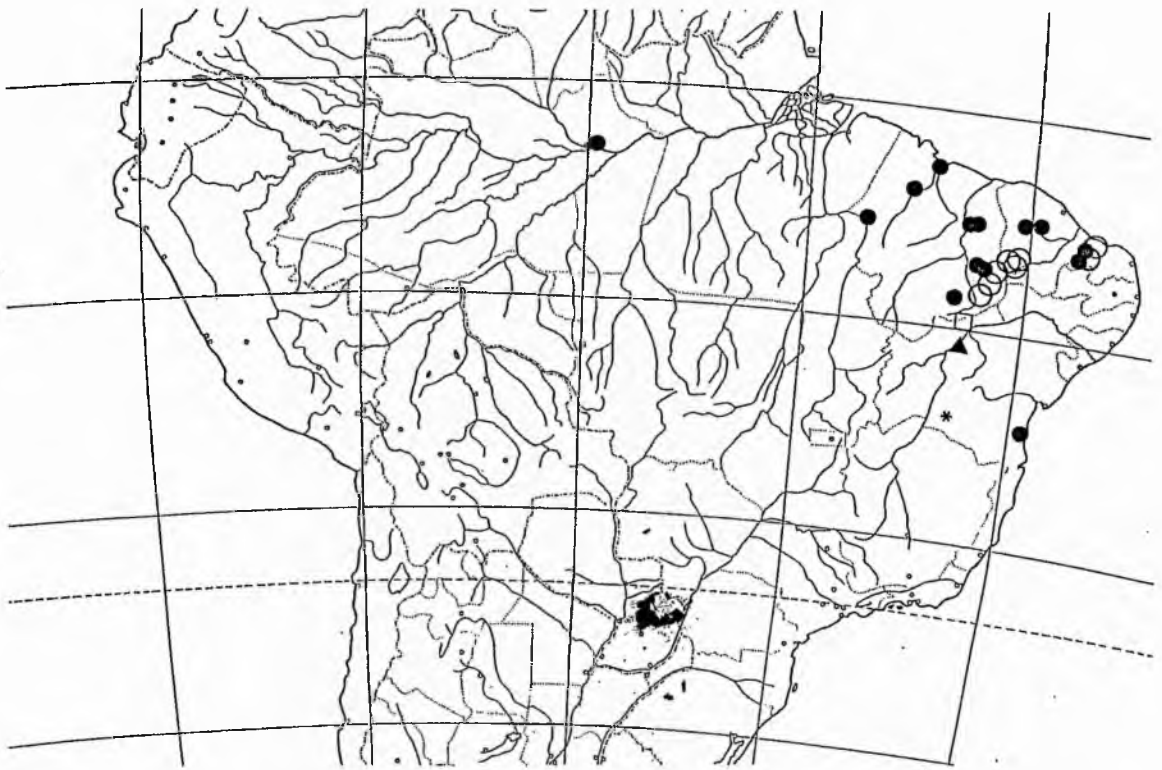




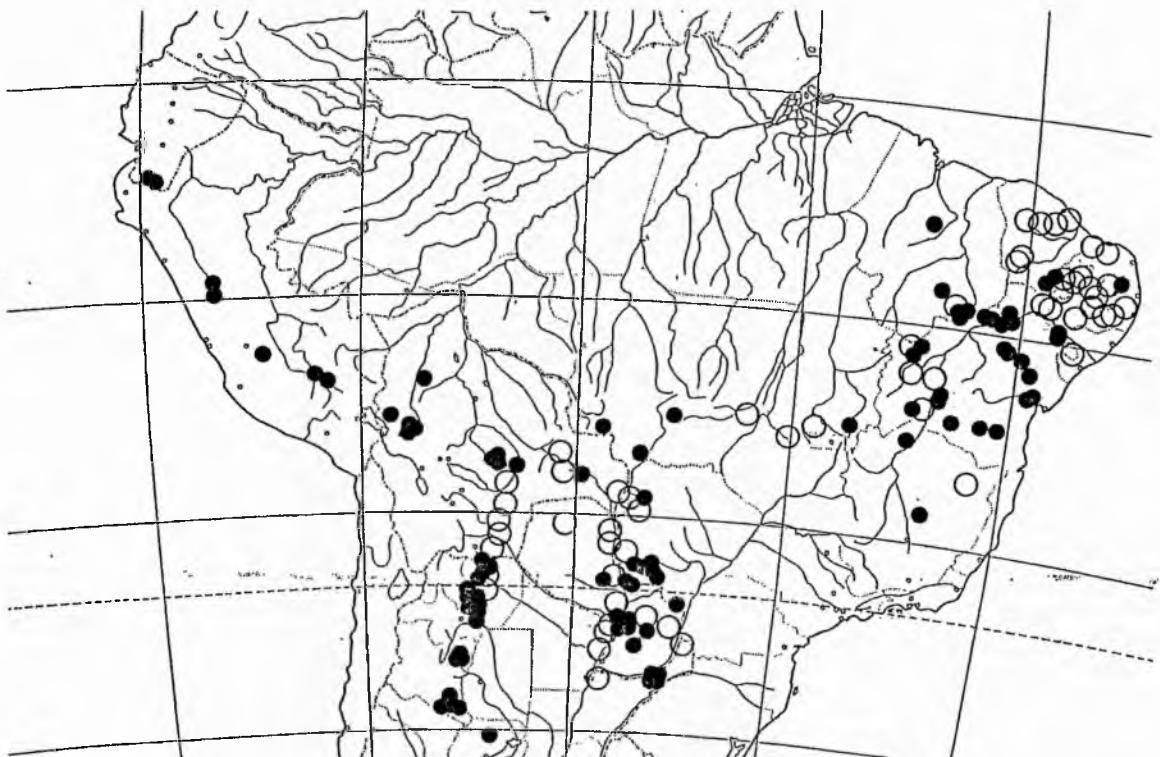
**Fig. 5.35:** Distribution map of *Commiphora leptophloeos*. Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.

**Fig. 5.36:** Distribution map of *Hymenaea velutina*.

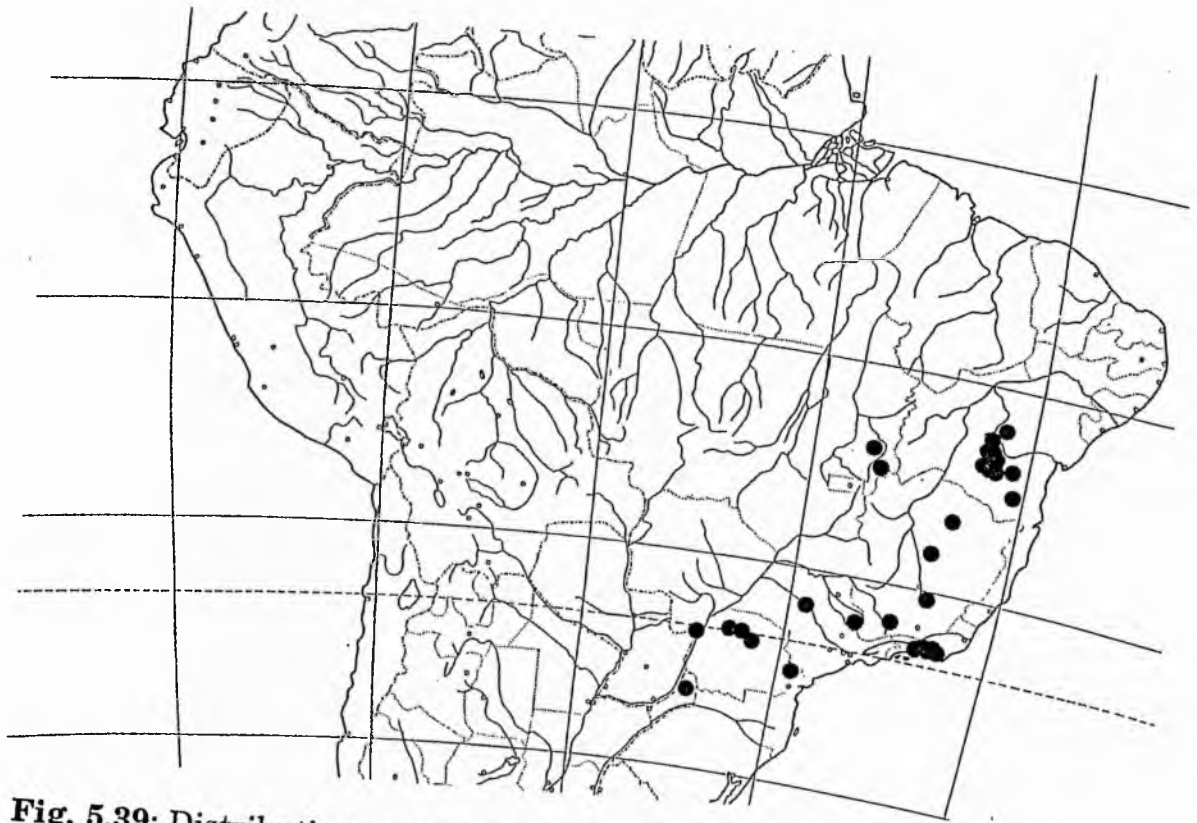




**Fig. 5.37:** Distribution map of *Mimosa caesalpiniiifolia* (solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys), *M. nothopteris* (open square), *M. xique-xiquensis* (triangle) and *M. coruscaesia* (asterisk).

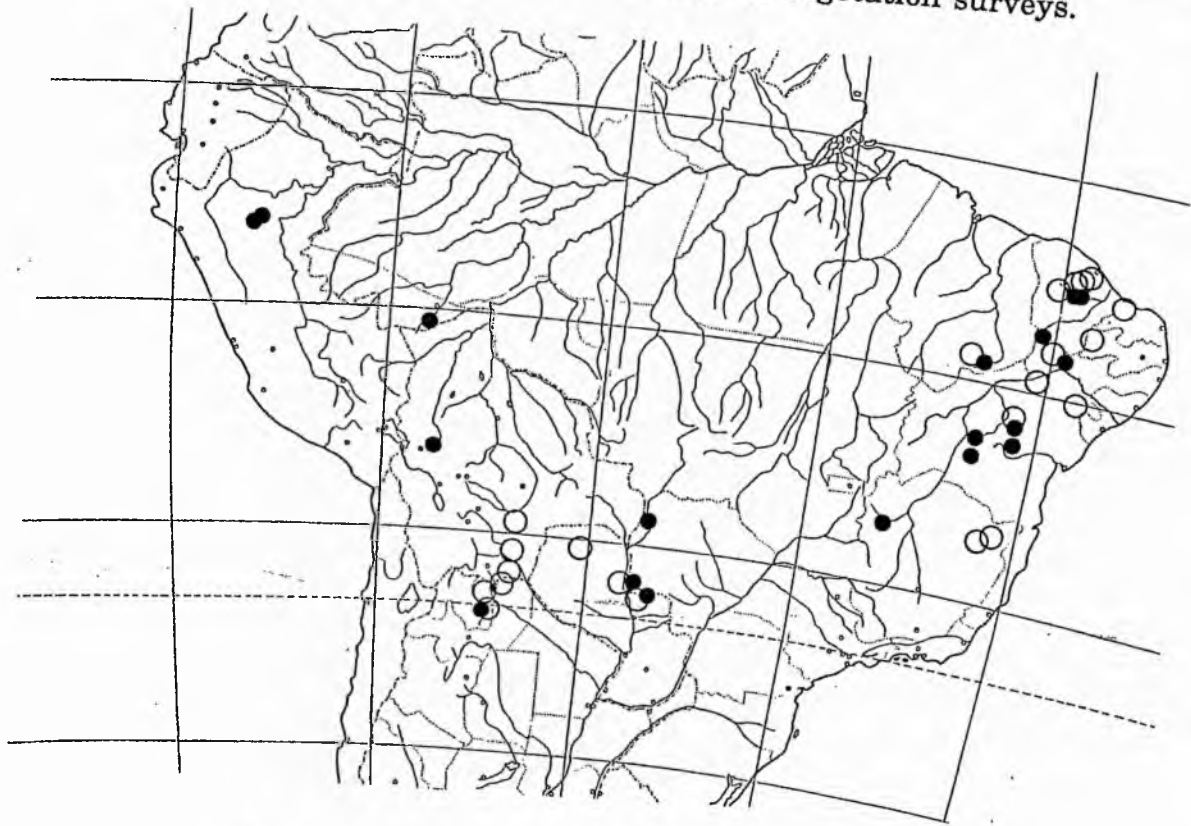


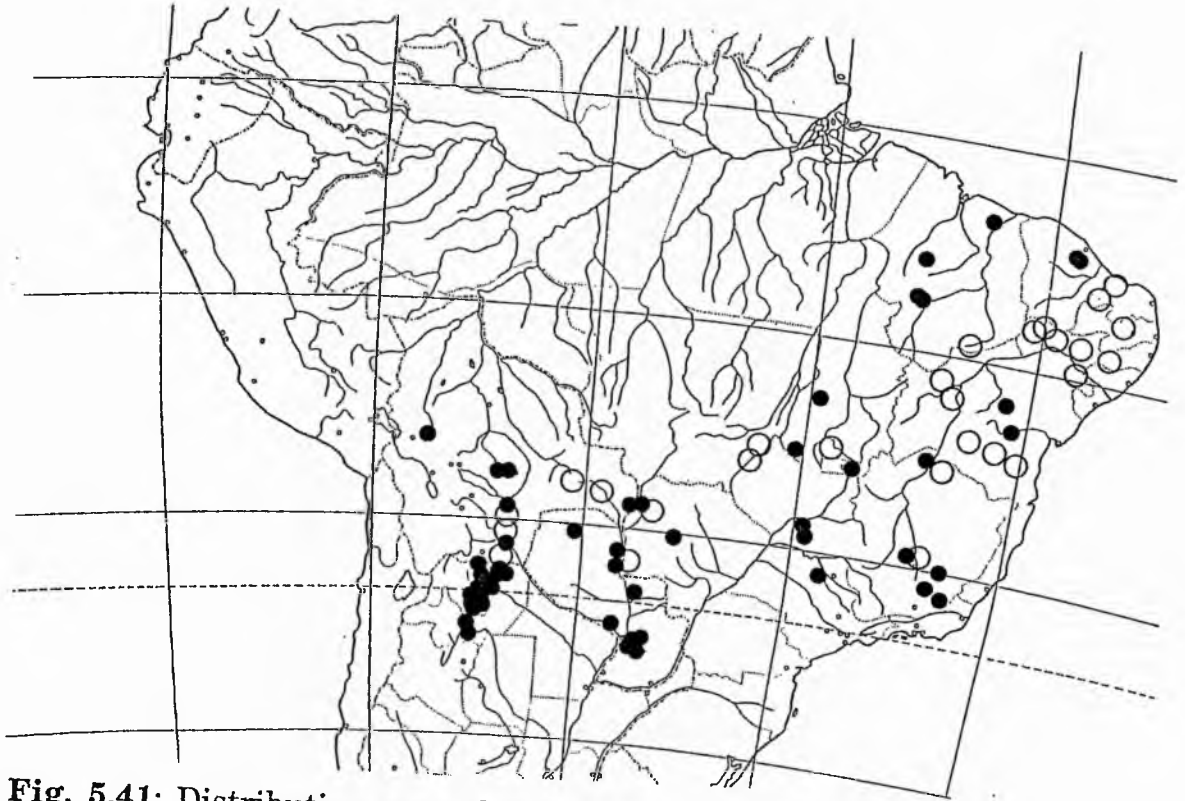
**Fig. 5.38:** Distribution map of *Anadenanthera colubrina* var. *cebil*. Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.



**Fig. 5.39:** Distribution map of *Anadenanthera colubrina* var. *colubrina*.

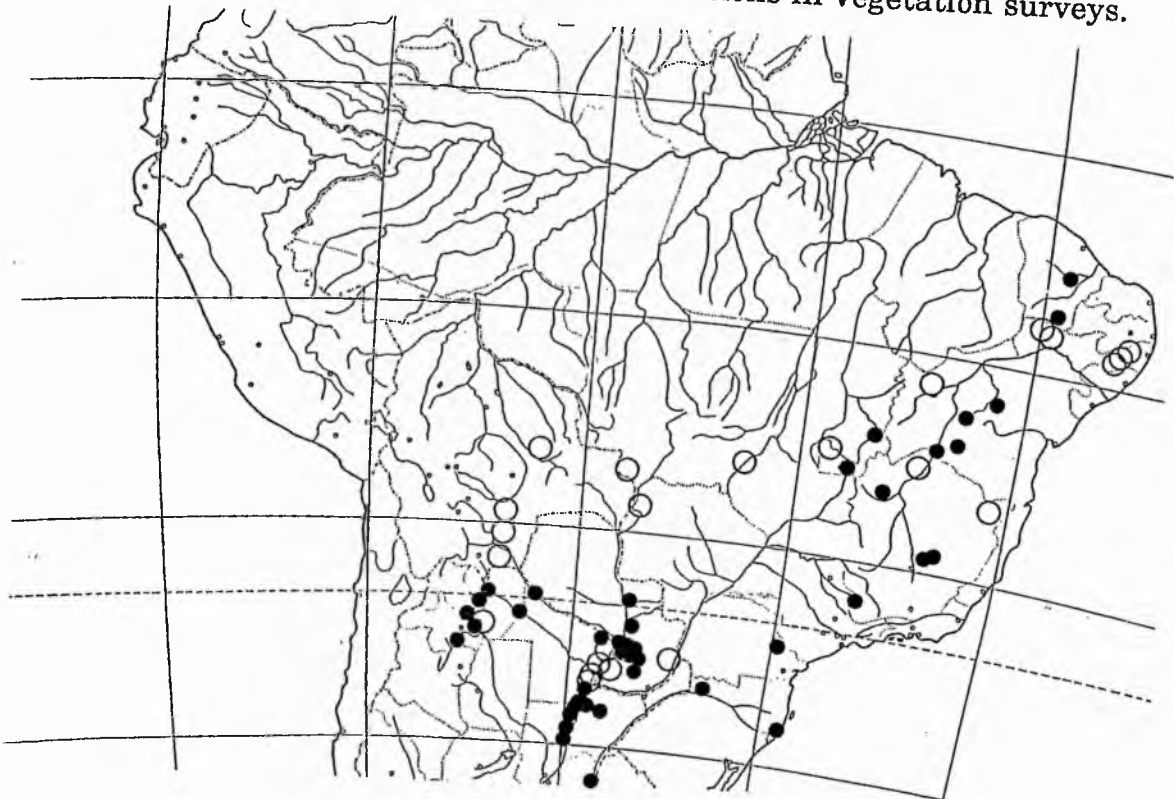
**Fig. 5.40:** Distribution map of *Amburana cearensis*. Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.

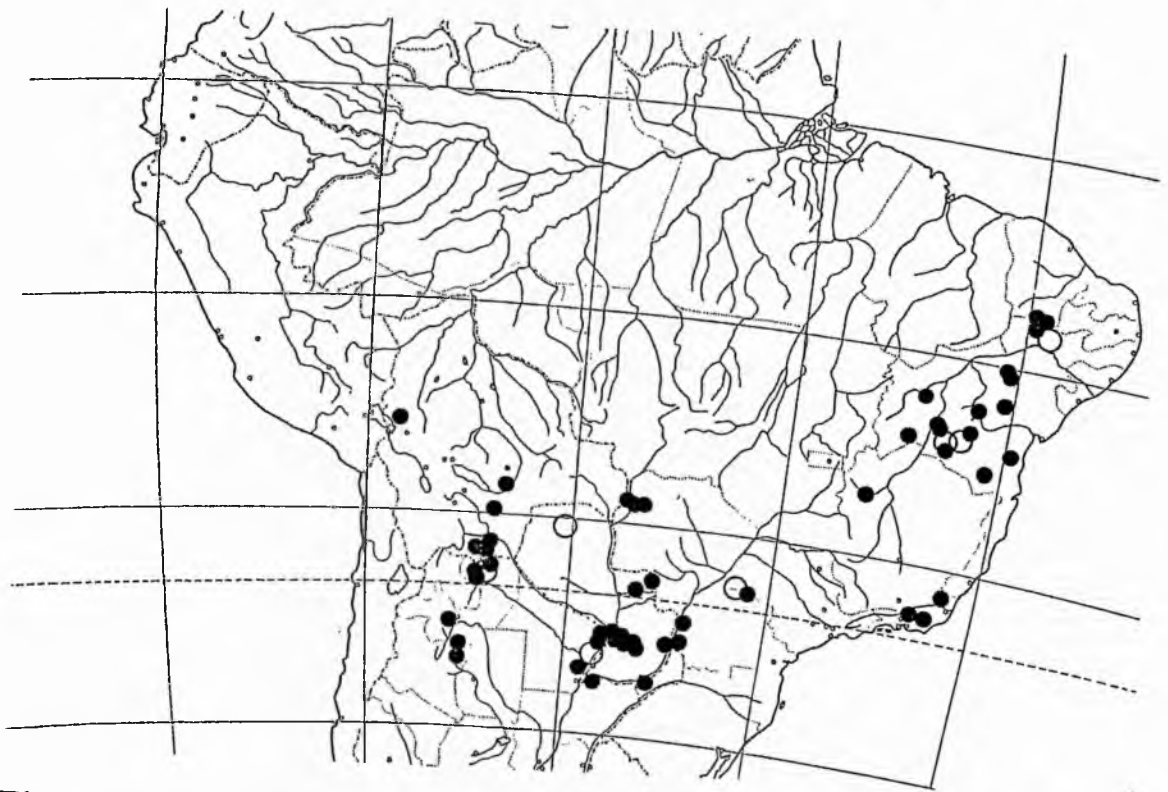




**Fig. 5.41:** Distribution map of *Astronium urundeuva*. Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.

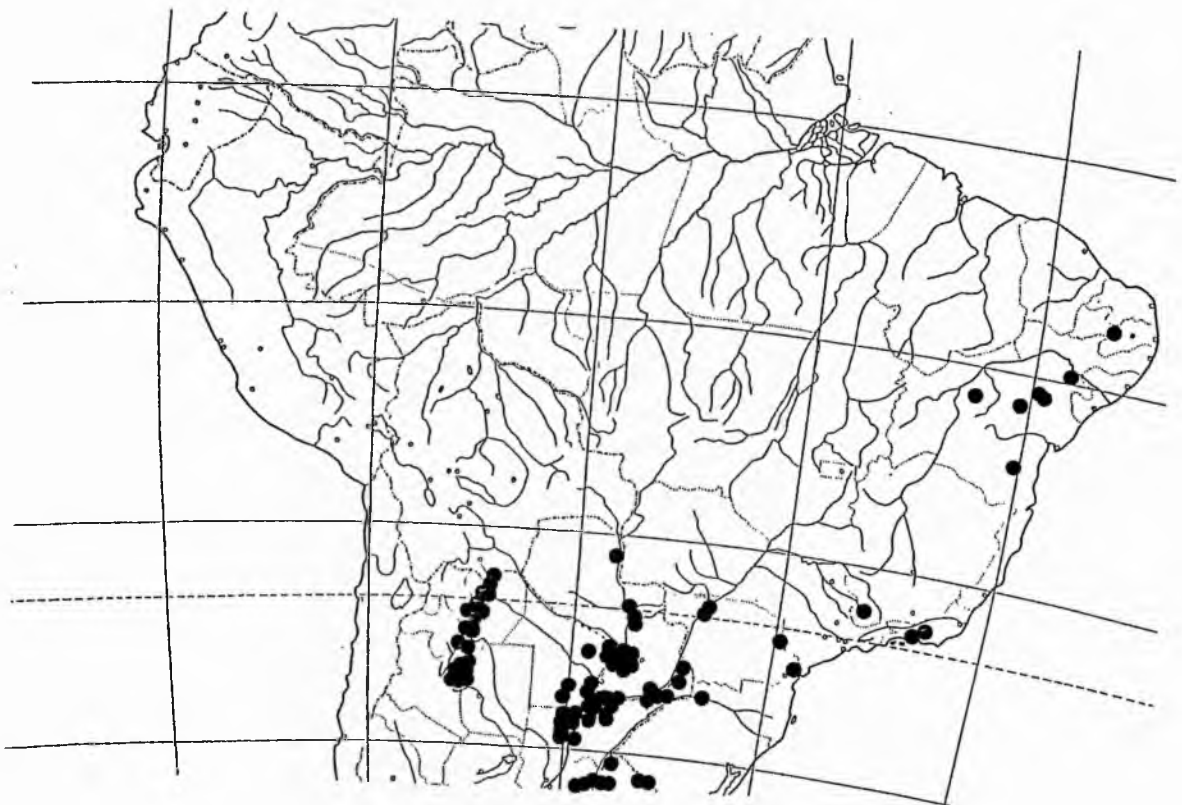
**Fig. 5.42:** Distribution map of *Enterolobium contortisiliquum*. Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.

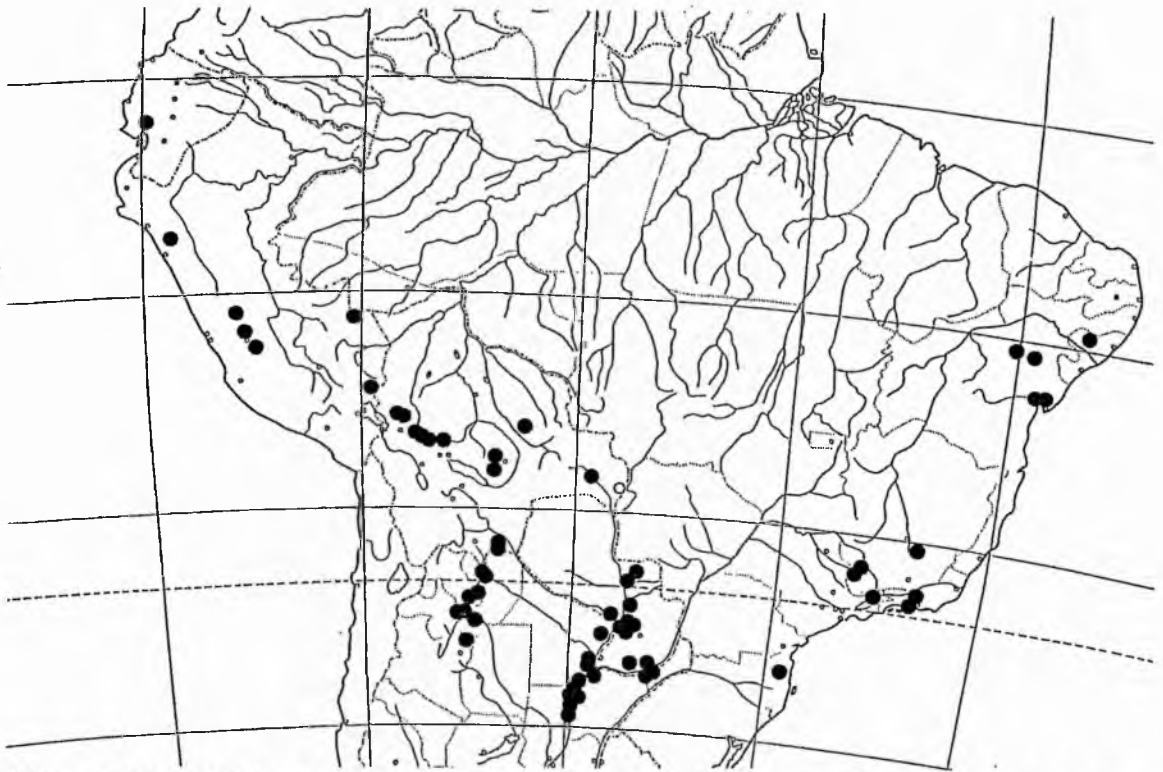




**Fig. 5.43:** Distribution map of *Pterogyne nitens* . Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.

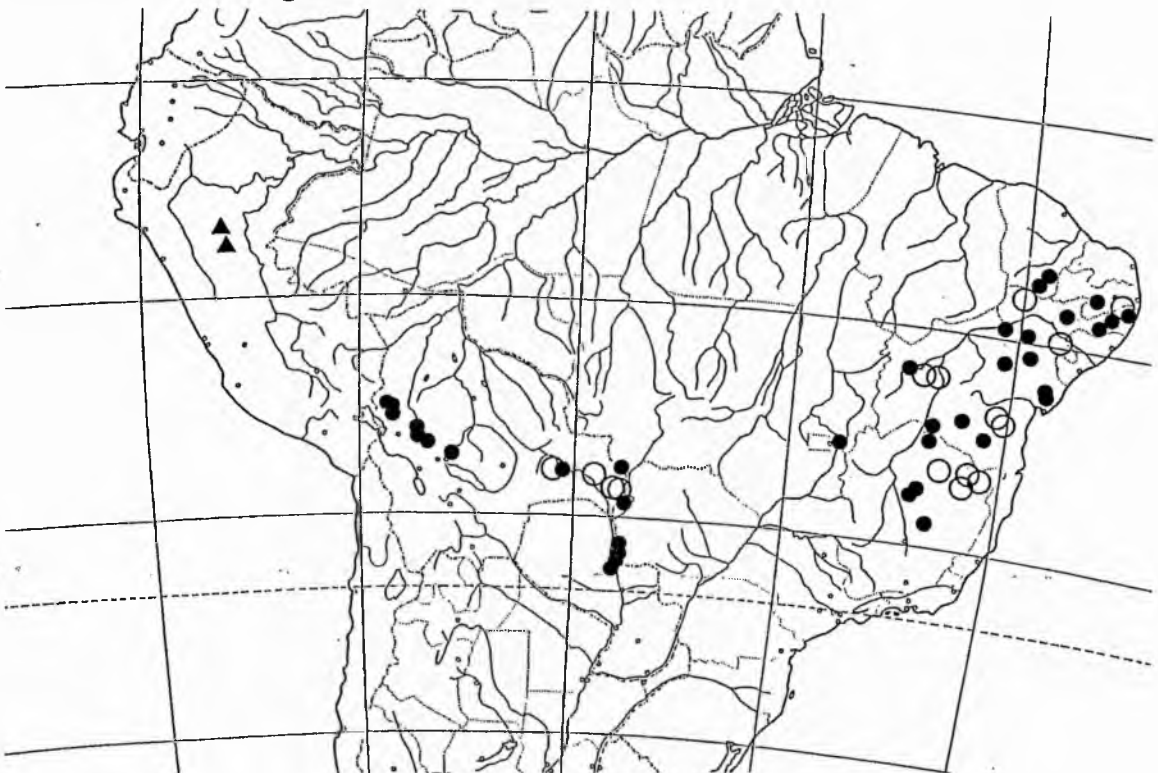
**Fig. 5.44:** Distribution map of *Ruprechtia laxiflora*.



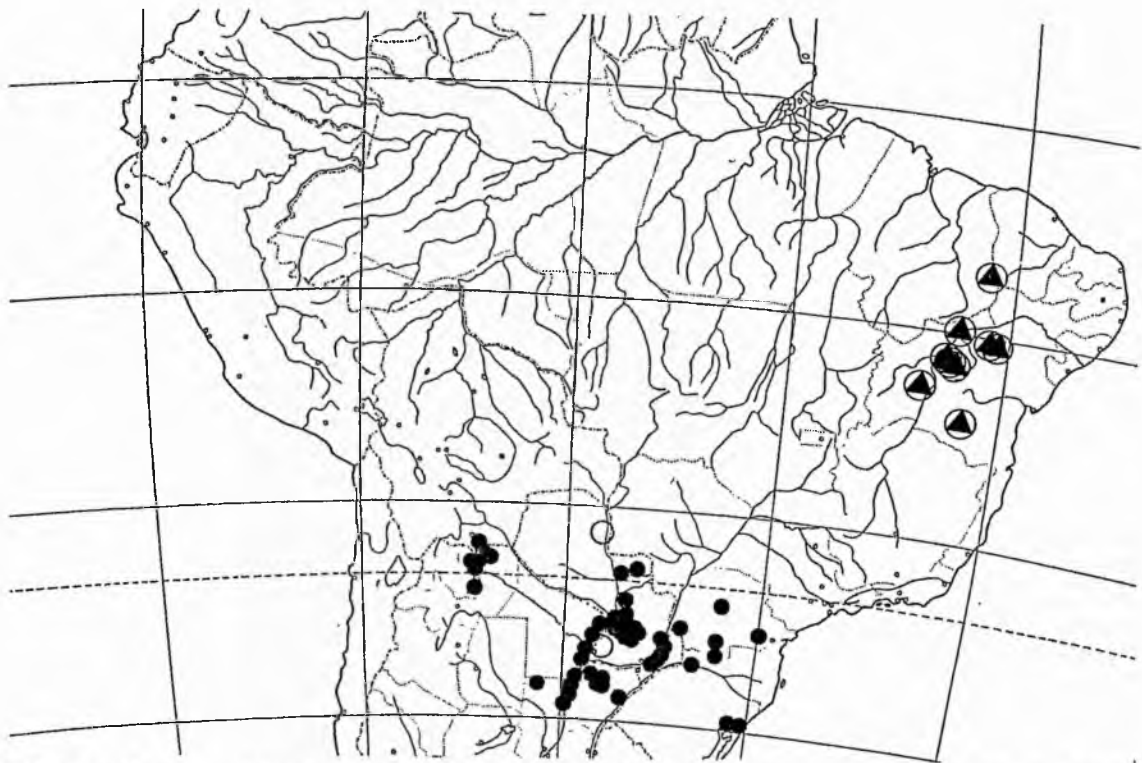


**Fig. 5.45:** Distribution map of *Celtis pubescens* . Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.

**Fig. 5.46:** Distribution map of *Schinopsis brasiliensis* (solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys) and *S. peruviana* (triangles).

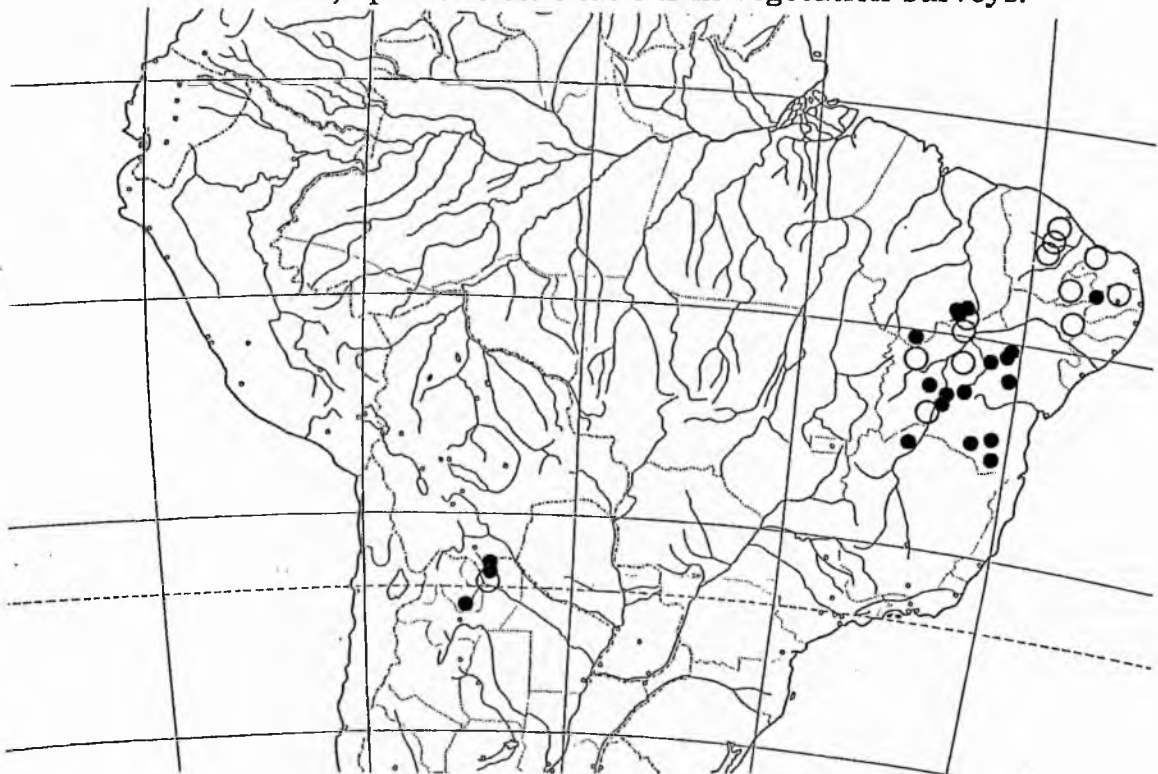


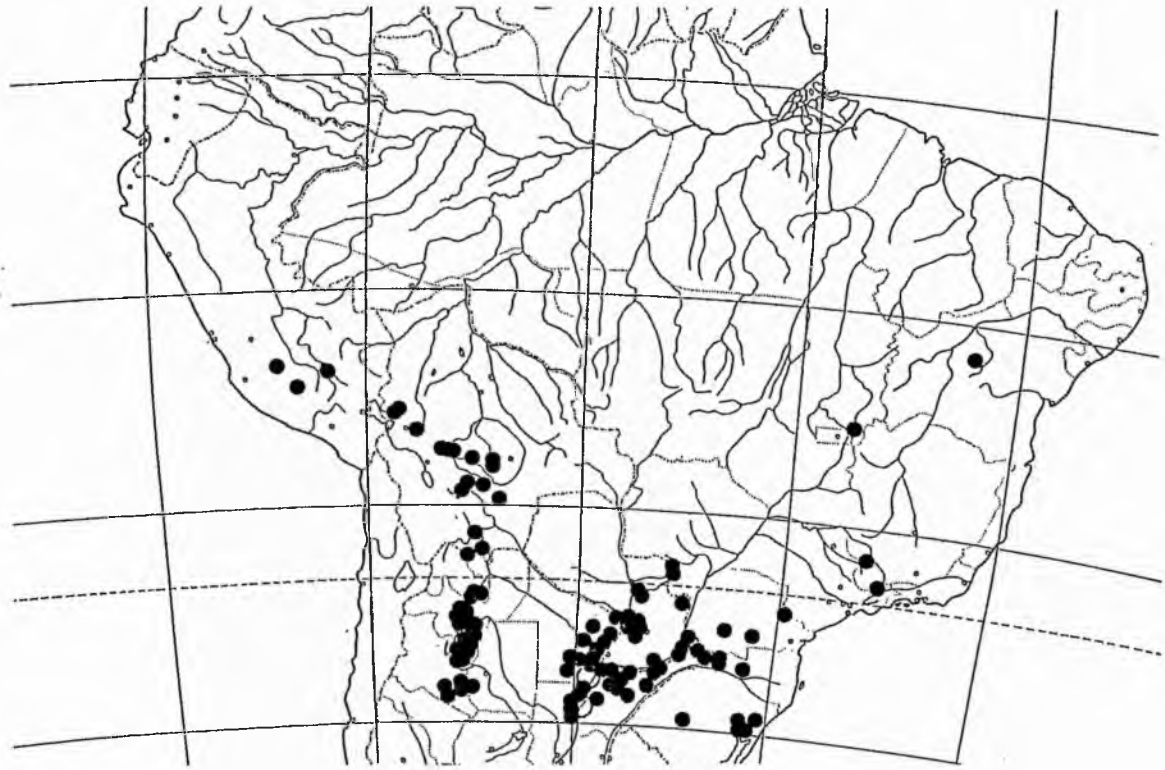




**Fig. 5.47:** Distribution map of *Patagonula bahiensis* (triangles in circles) and *P. americana* (solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys).

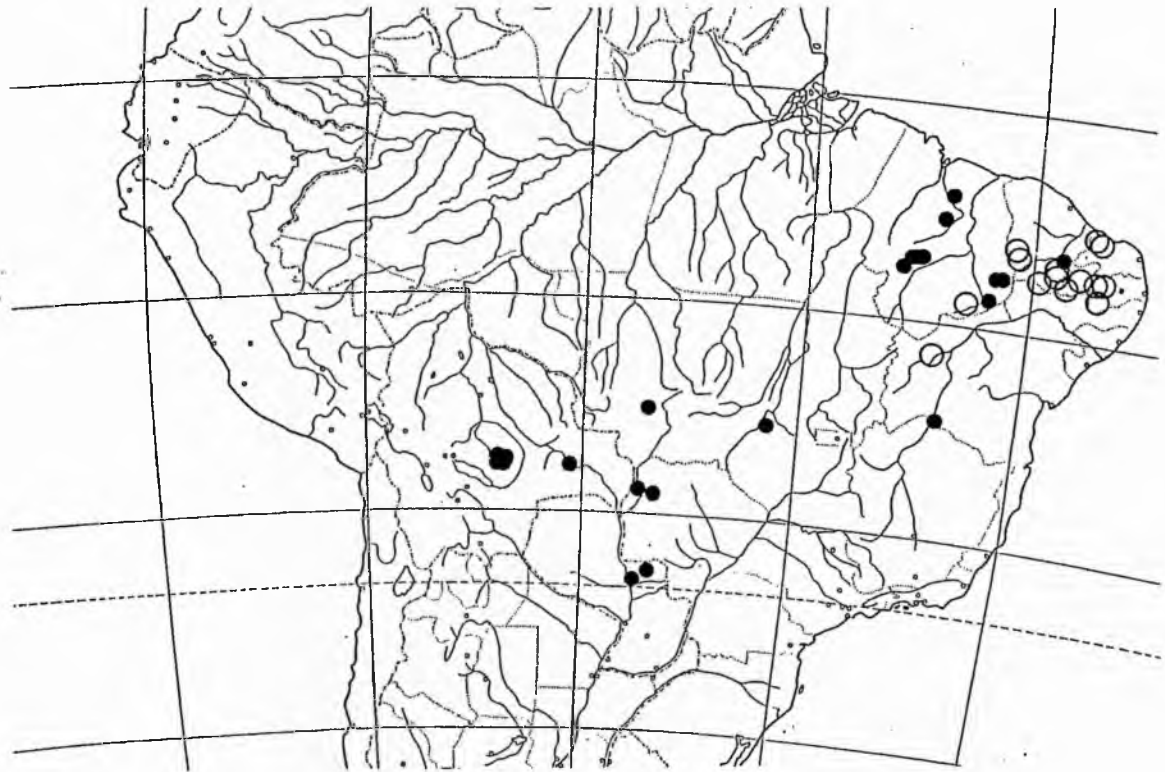
**Fig. 5.48:** Distribution map of *Piptadenia viridiflora*. Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.

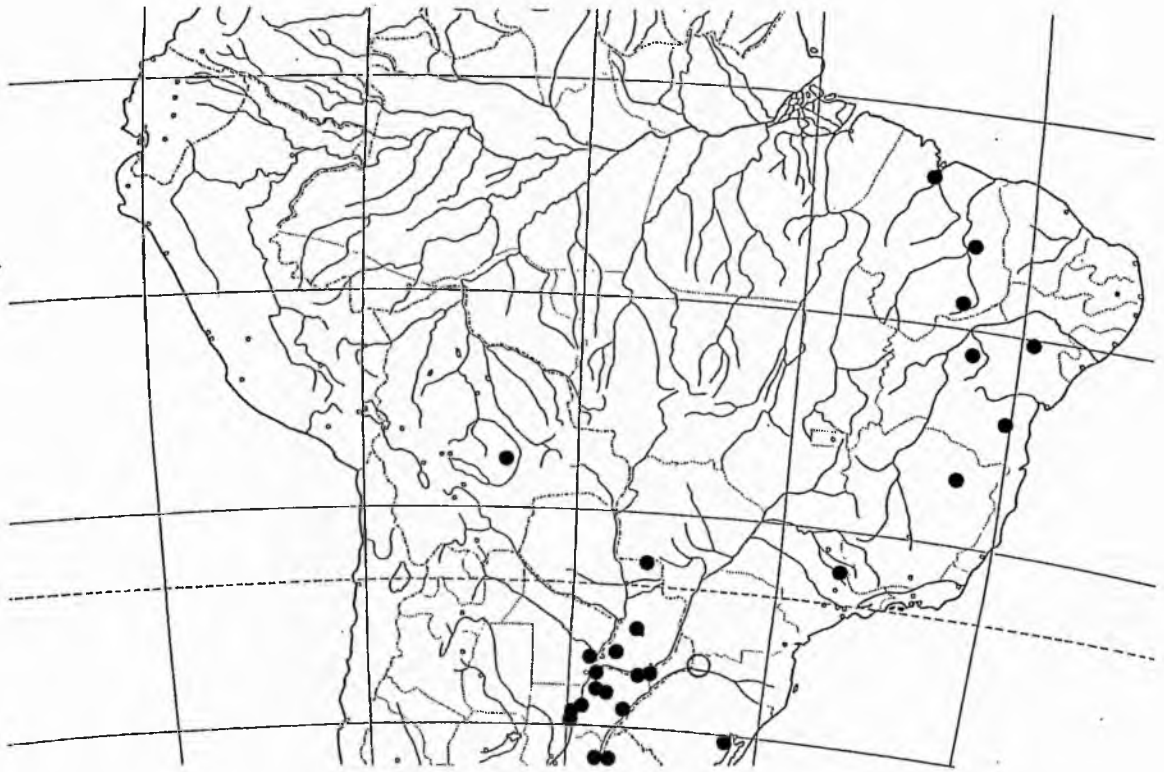




**Fig. 5.49:** Distribution map of *Carica quercifolia*.

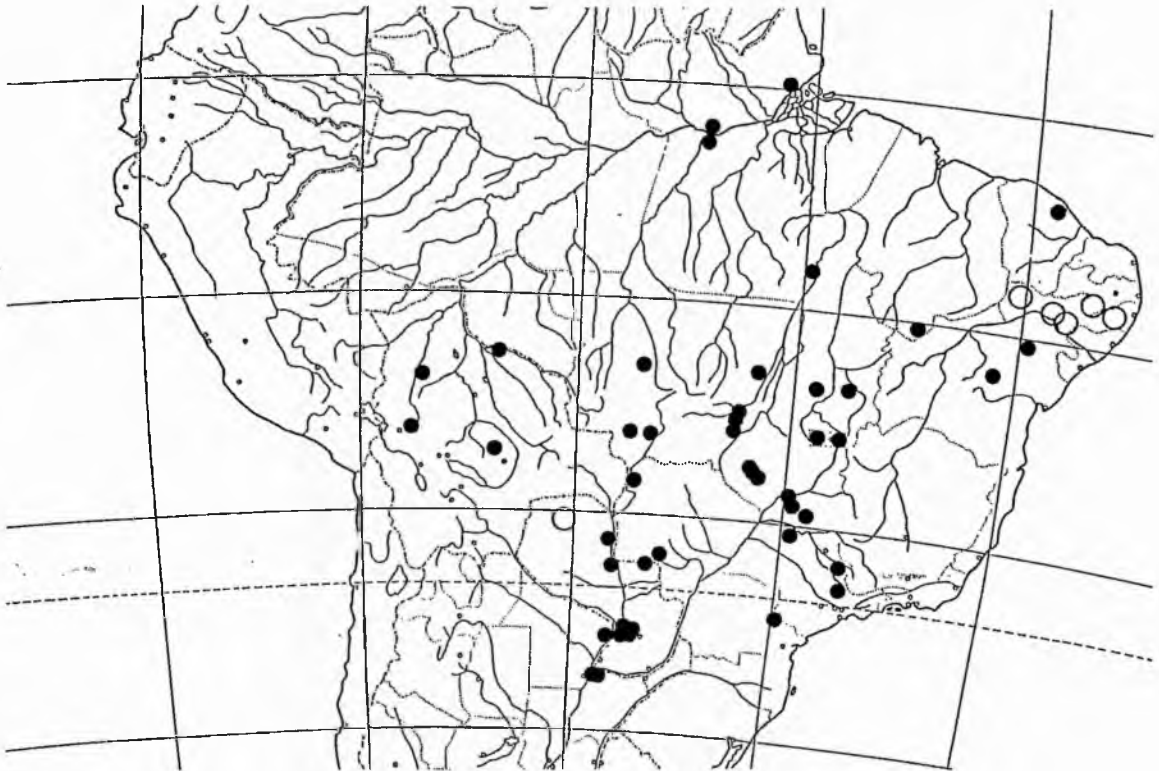
**Fig. 5.50:** Distribution map of *Combretum leprosum*. Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.

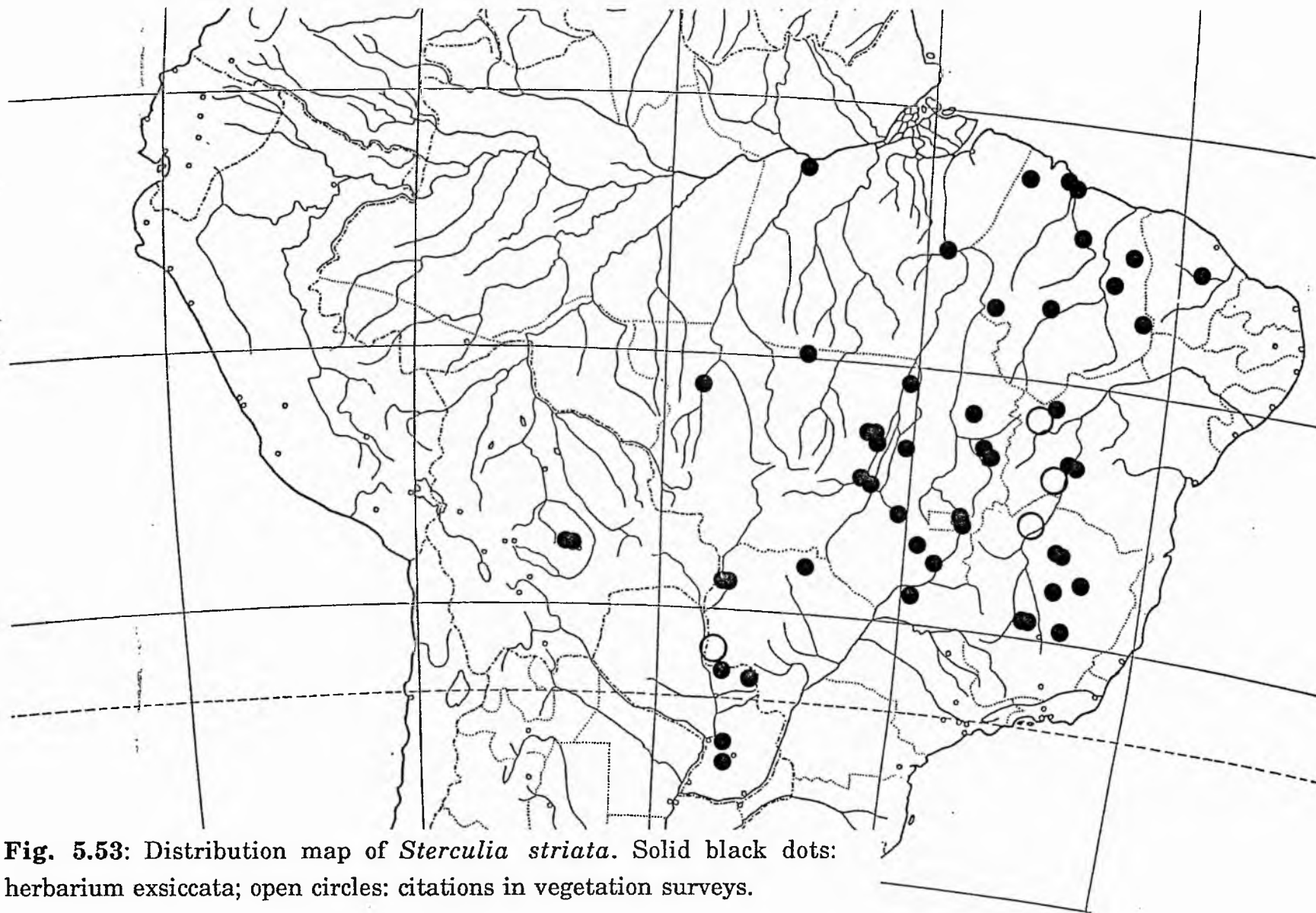




**Fig. 5.51:** Distribution map of *Pouteria gardneriana*. Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.

**Fig. 5.52:** Distribution map of *Tabebuia caraiba*. Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.





**Fig. 5.53:** Distribution map of *Sterculia striata*. Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.



**Fig. 5.54:** Distribution map of *Aspidosperma cuspa*.

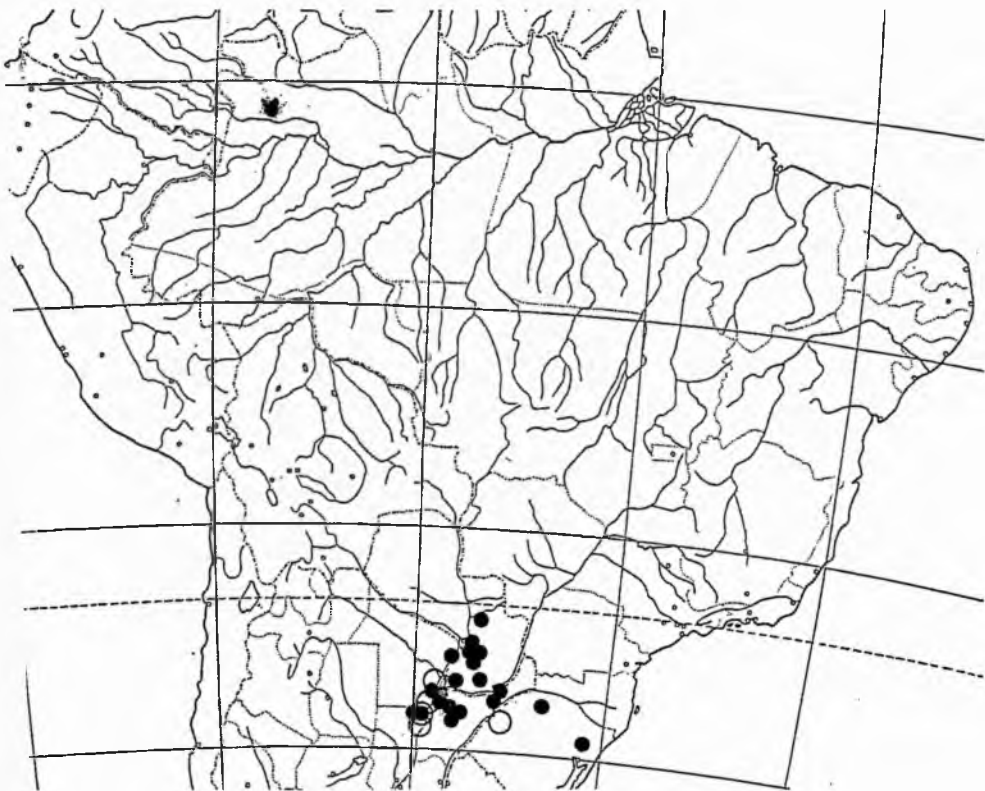


**Fig. 5.55:** Distribution map of *Aspidosperma polyneuron*.



Fig. 5.56: Distribution map of *Brunfelsia uniflora*.

**Fig. 5.57:** Distribution map of *Brunfelsia australis* . Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.





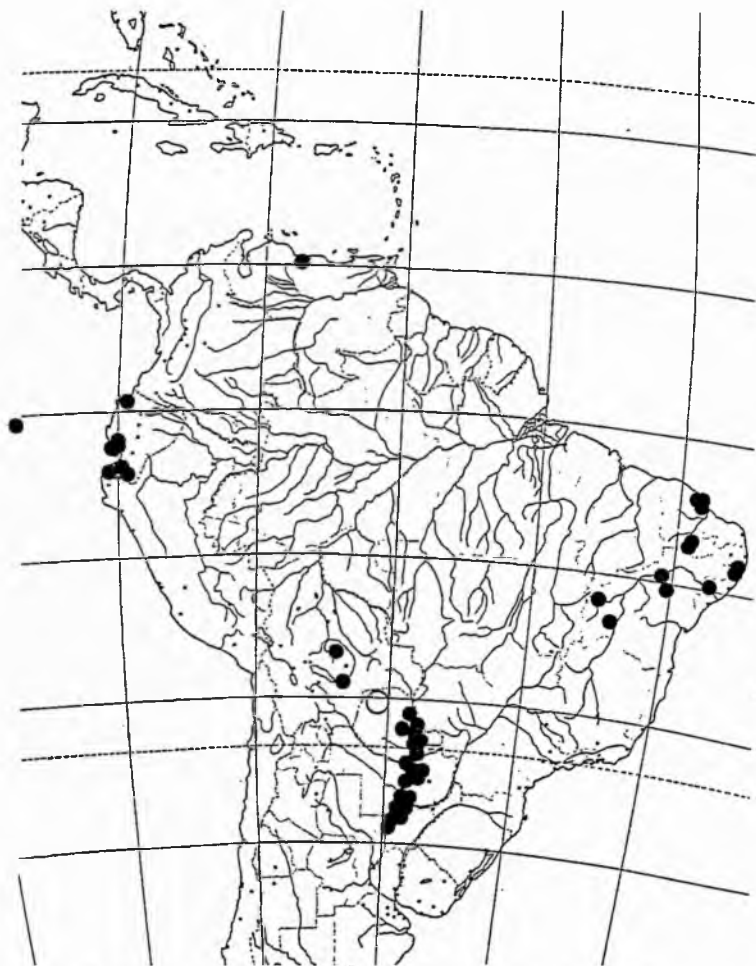


Fig. 5.58: Distribution map of the *Geoffroea striata/spinosa* complex. Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.

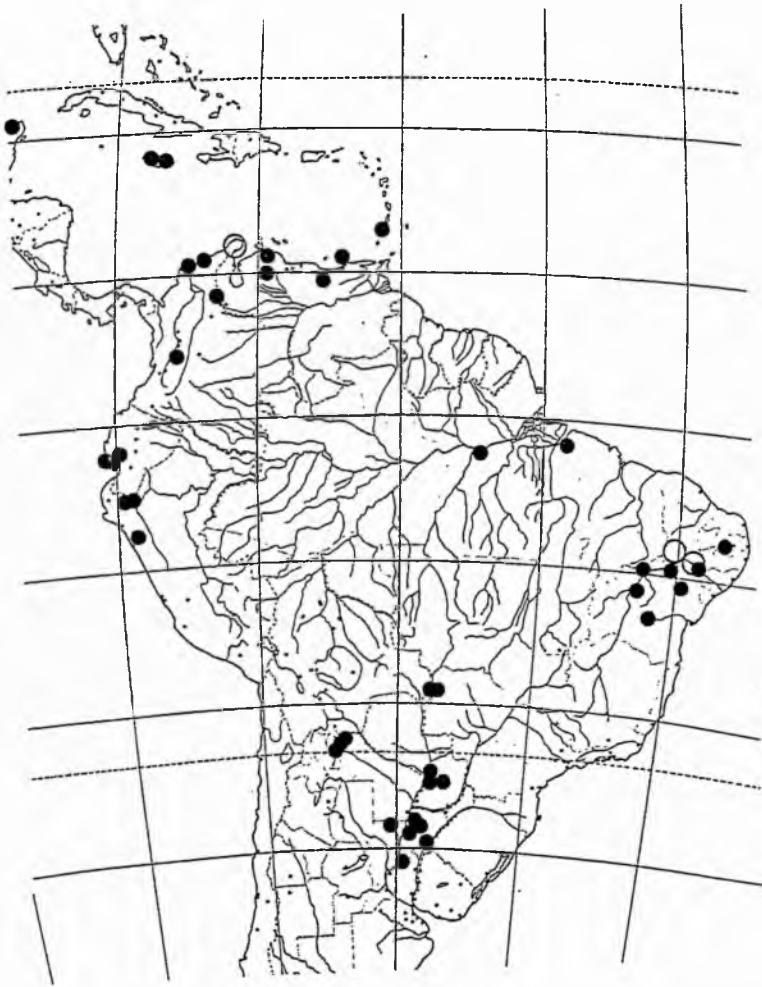


Fig. 5.59: Distribution map of *Ipomoea carnea* ssp. *fistulosa*. Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.

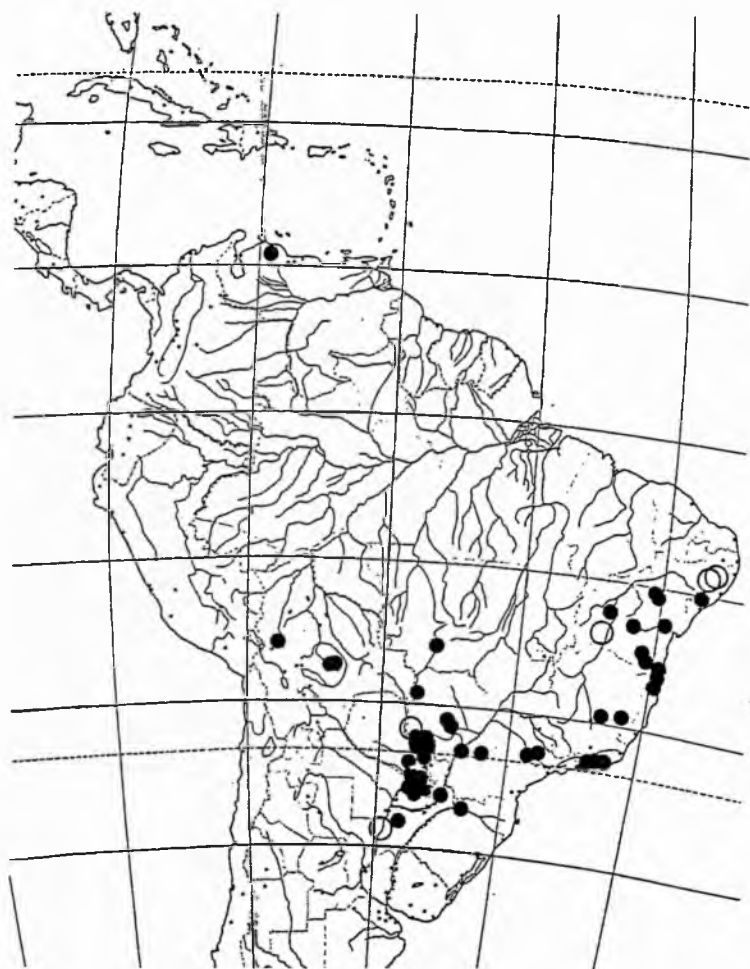


Fig. 5.60: Distribution map of *Peltophorum dubium*. Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.

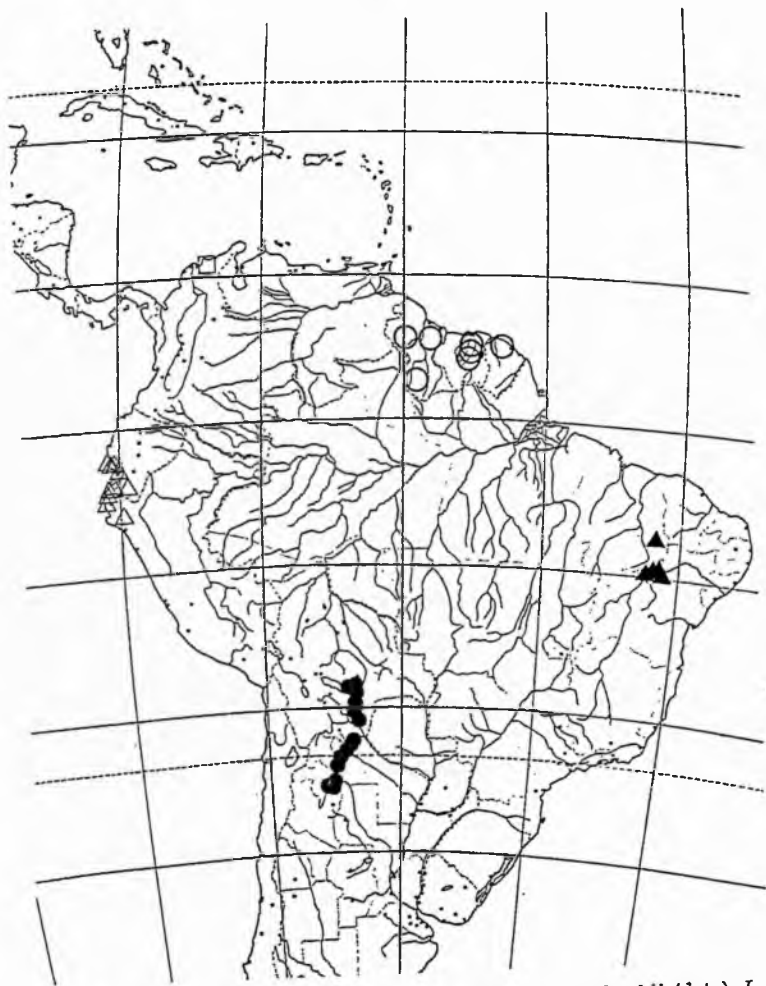


Fig. 5.61: Distribution map of *Loxopterigium grisebachii* (dots), *L. huasango* (open triangles), *L. gutierrezii* (open square), *L. sagotii* (open circles) and *L. gardneri* (solid black triangles).

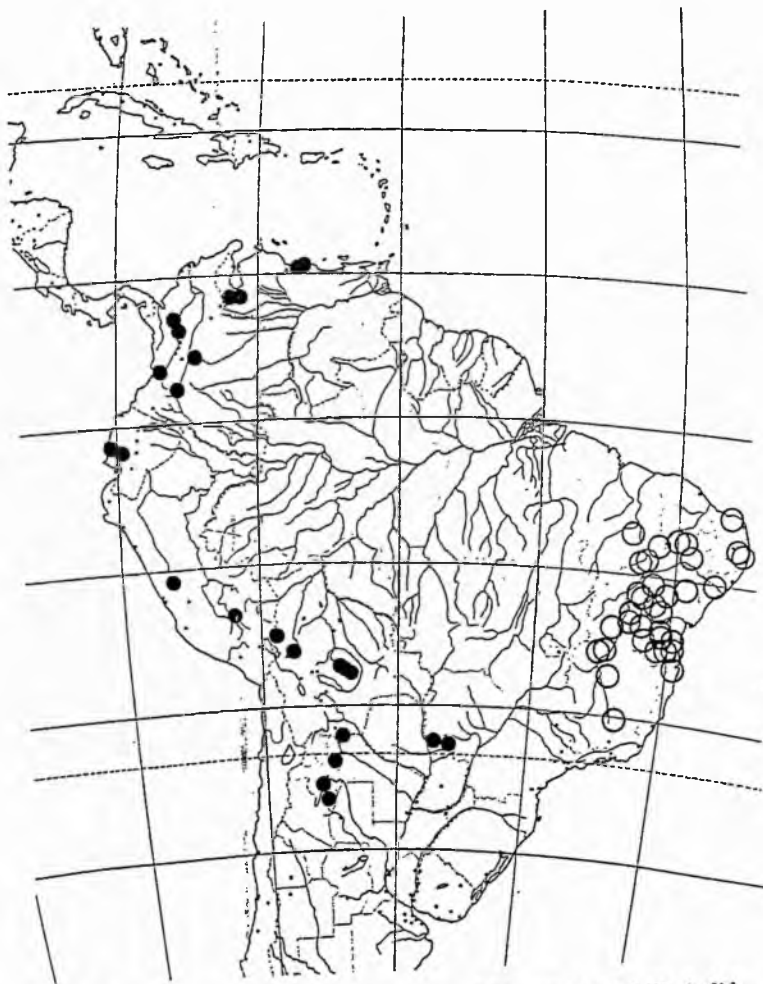


Fig. 5.62: Distribution map of *Senna spectabilis* var. *spectabilis* (solid black dots) and var. *excelsa* (open circles).

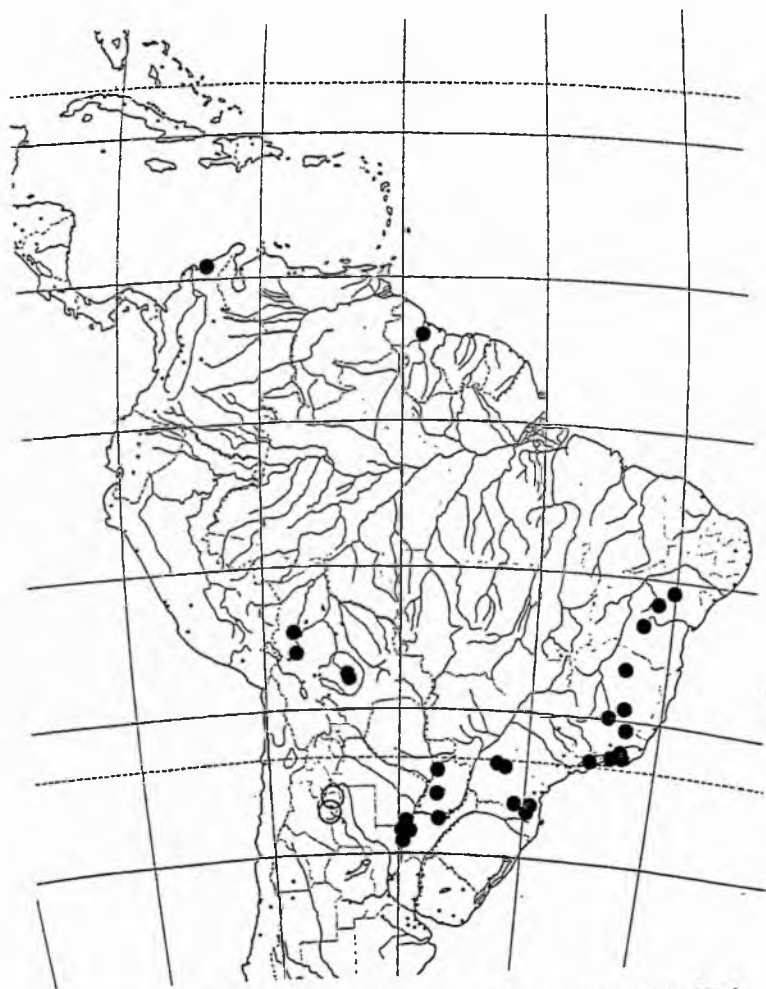


Fig. 5.63: Distribution map of *Solanum granuloso-leprosum*. Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.

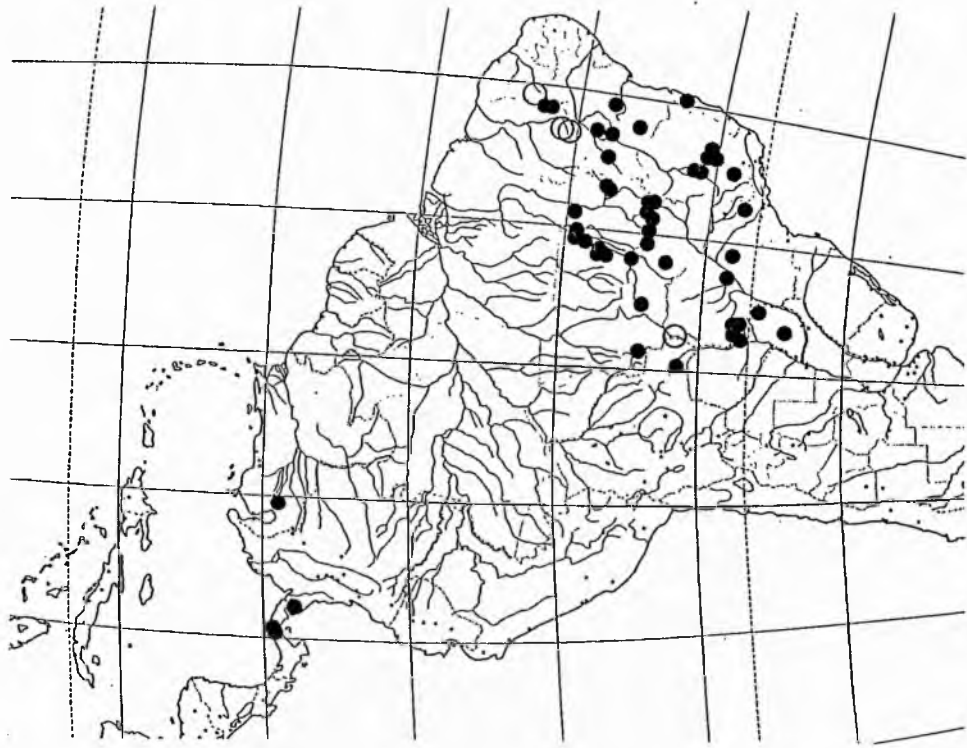


Fig. 5.64: Distribution map of the *Cordia alliodora/trichotoma* complex: *C. alliodora* (solid black dots); *C. alliodora?/trichotoma?* (open circles); *C. trichotoma* (solid black triangles: herbarium exsiccata, open triangles: citations in vegetation surveys).

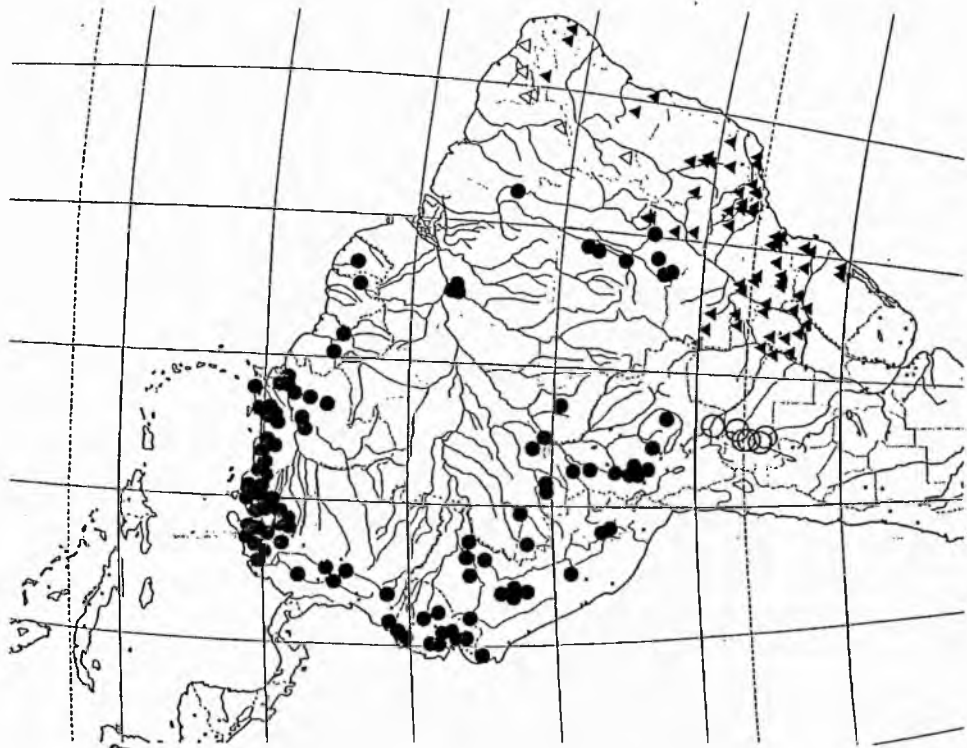


Fig. 5.65: Distribution map of *Platypodium elegans*. Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.

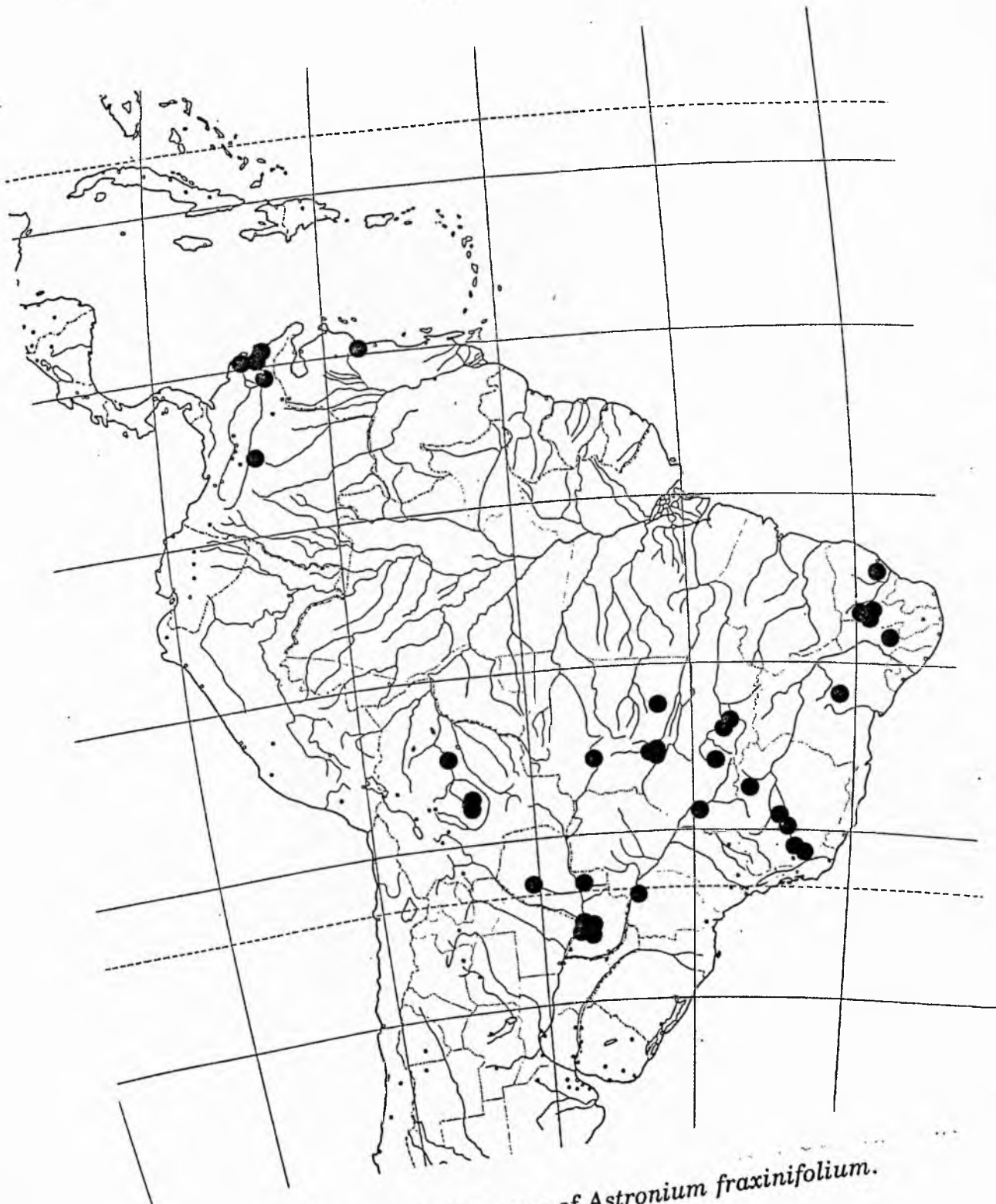
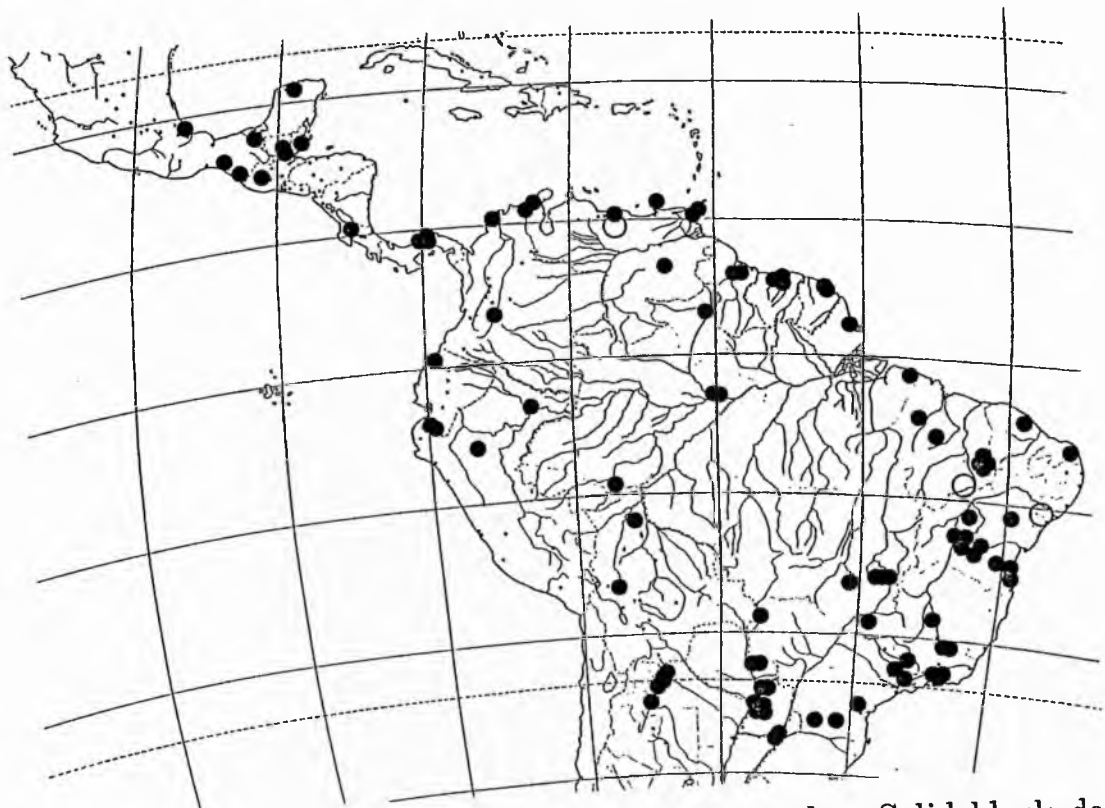


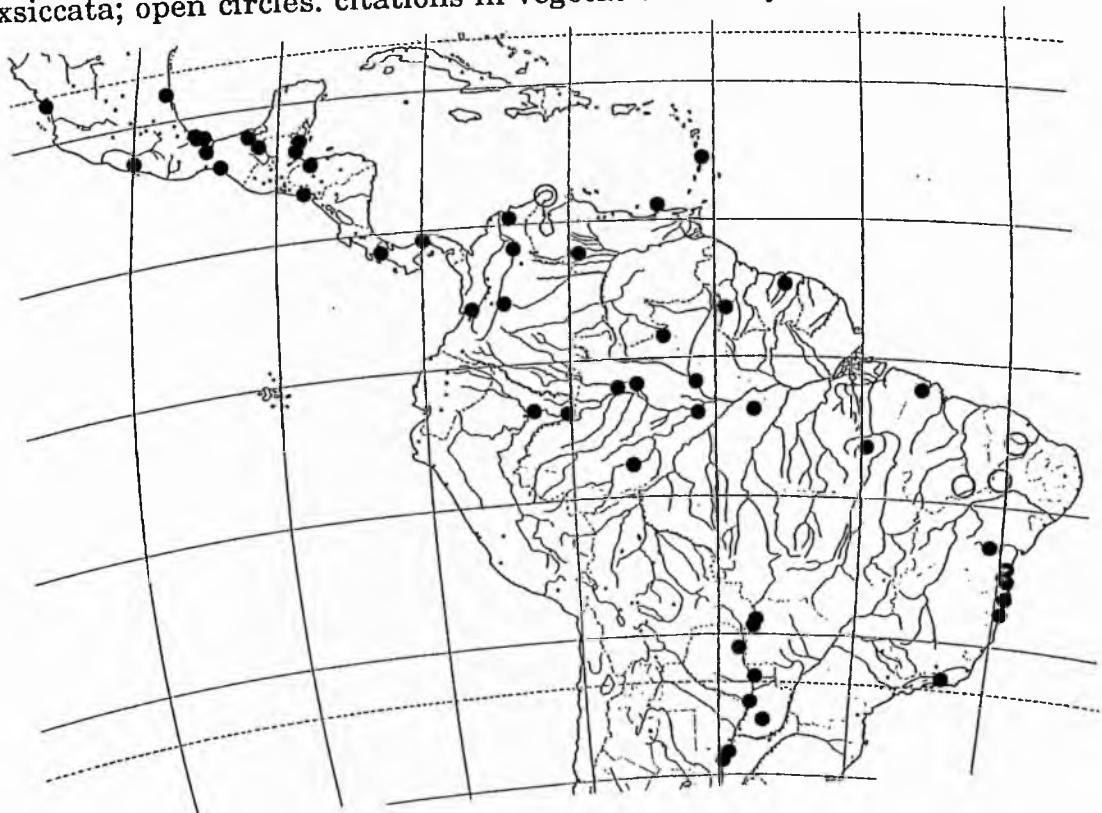
Fig. 5.66: Distribution map of *Astronium fraxinifolium*.





**Fig. 5.67:** Distribution map of *Coutarea hexandra*. Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.

**Fig. 5.68:** Distribution map of *Crateva tapia*. Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.



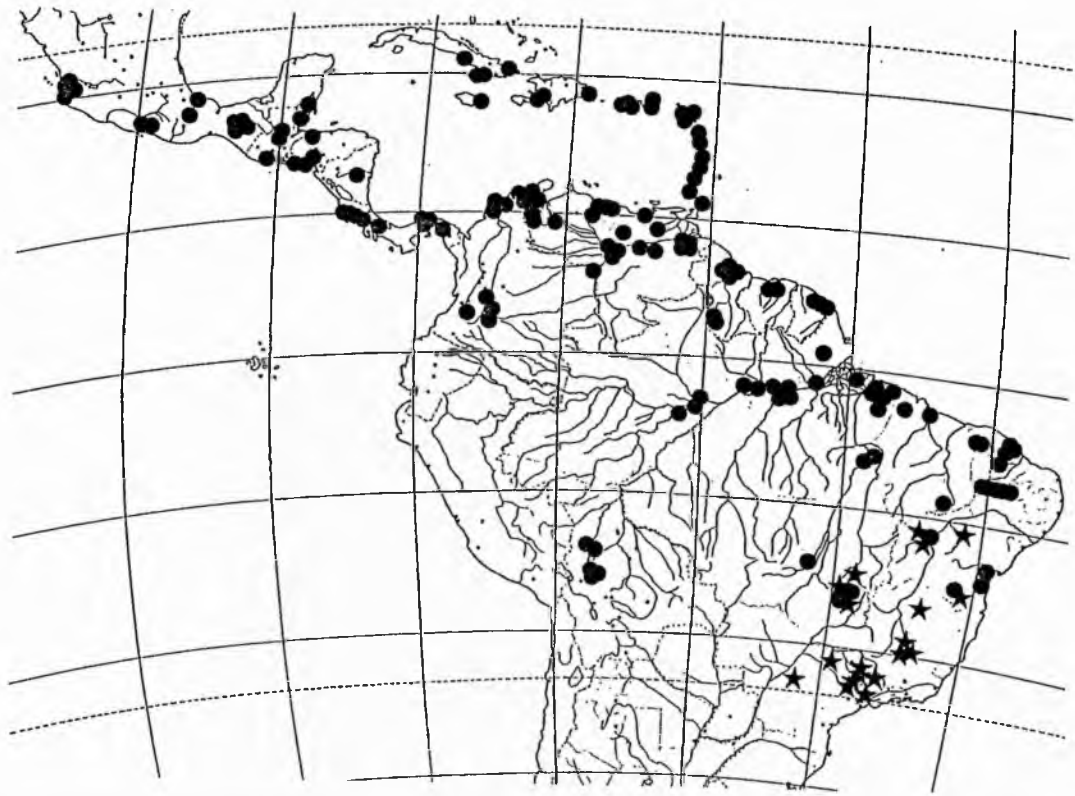
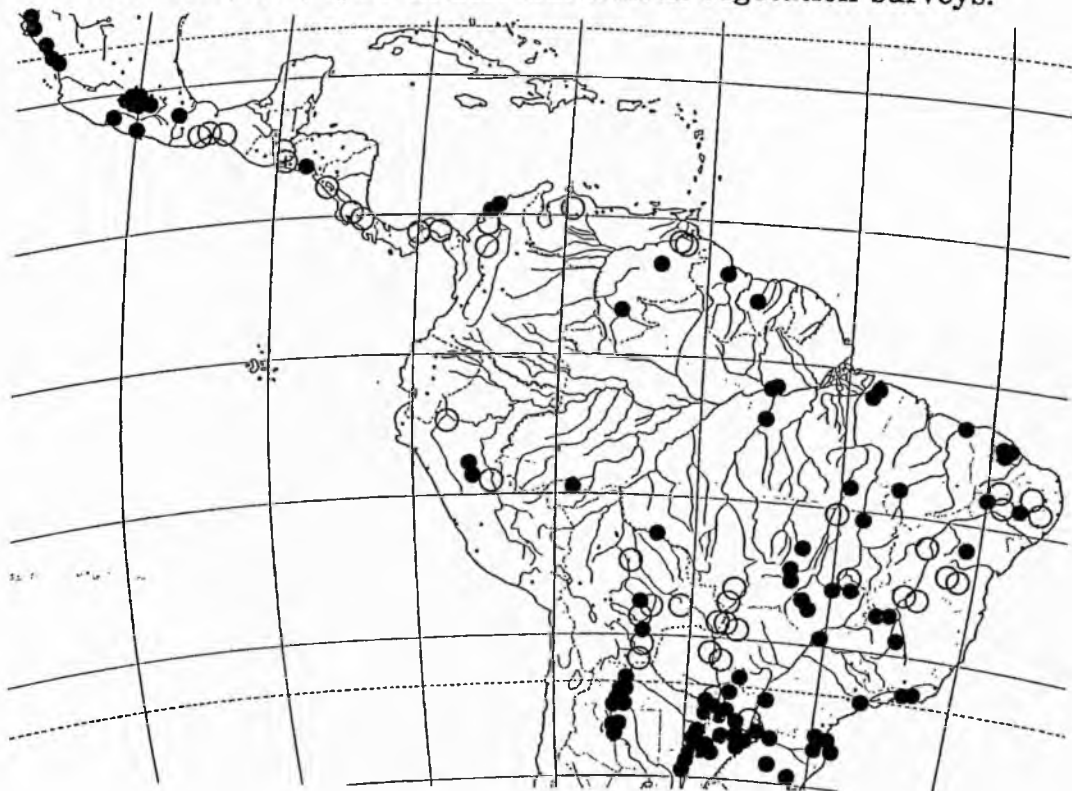


Fig. 5.69: Distribution map of *Hymenaea courbaril* var. *courbaril* (dots) and var. *stilbocarpa* (stars).

Fig. 5.70: Distribution map of *Tabebuia impetiginosa*. Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.



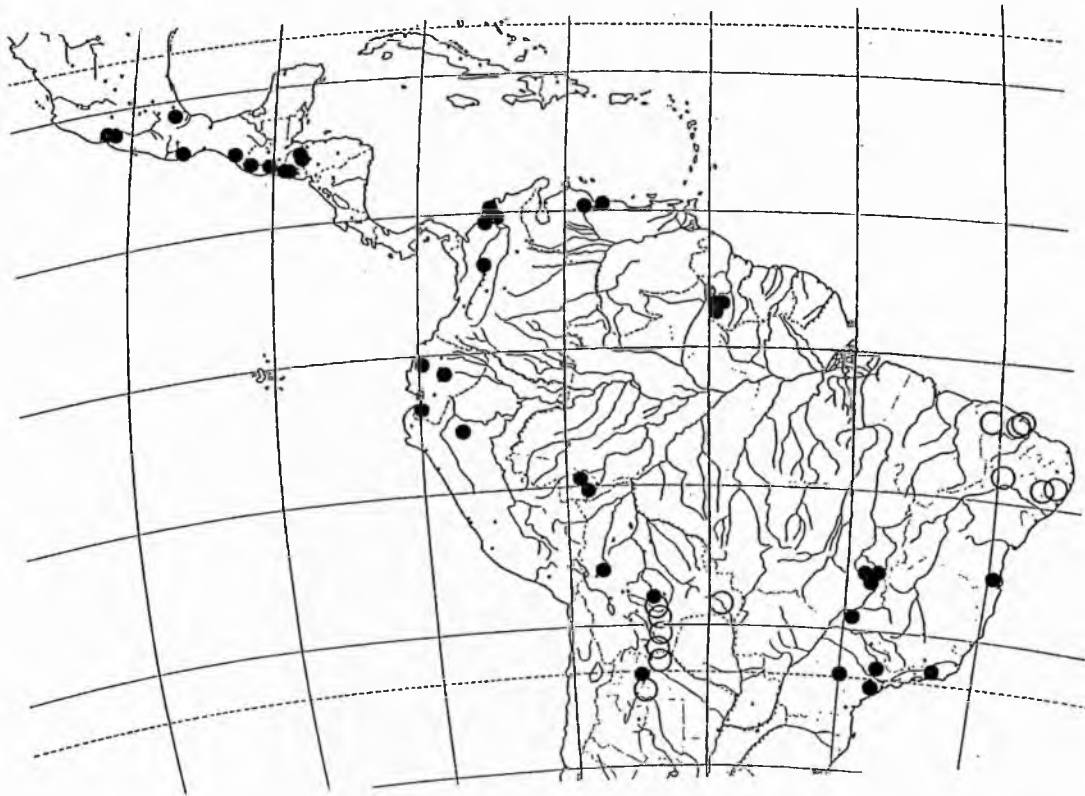
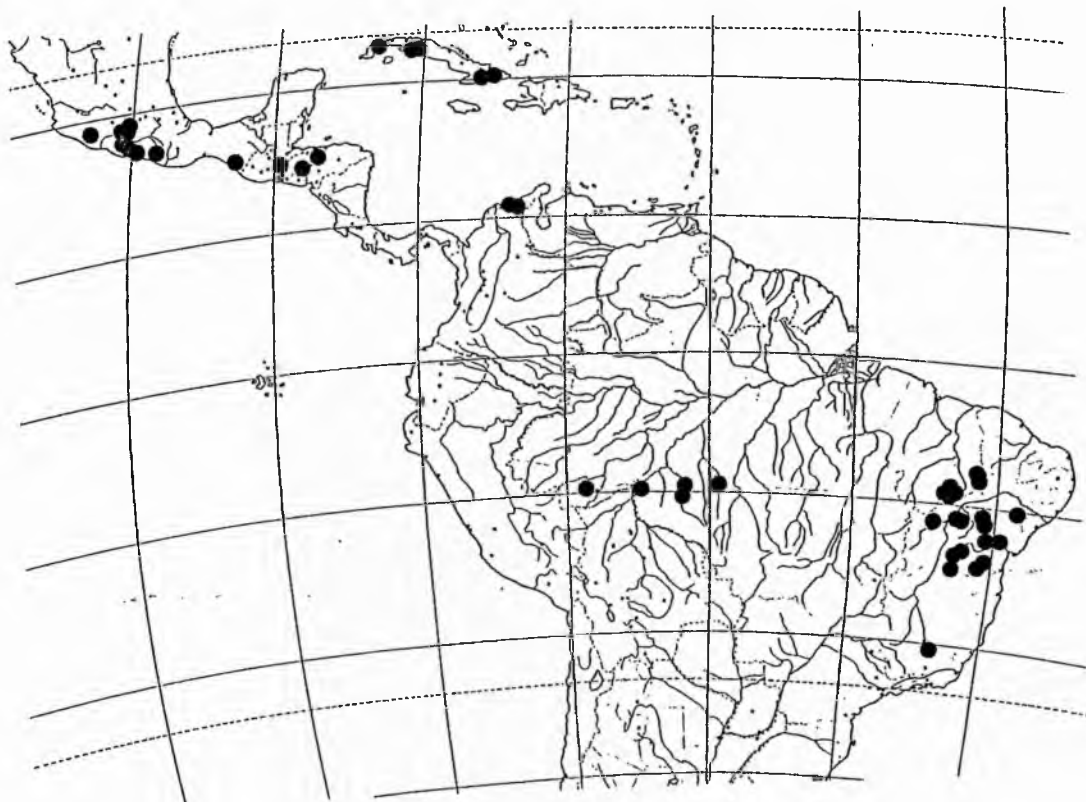
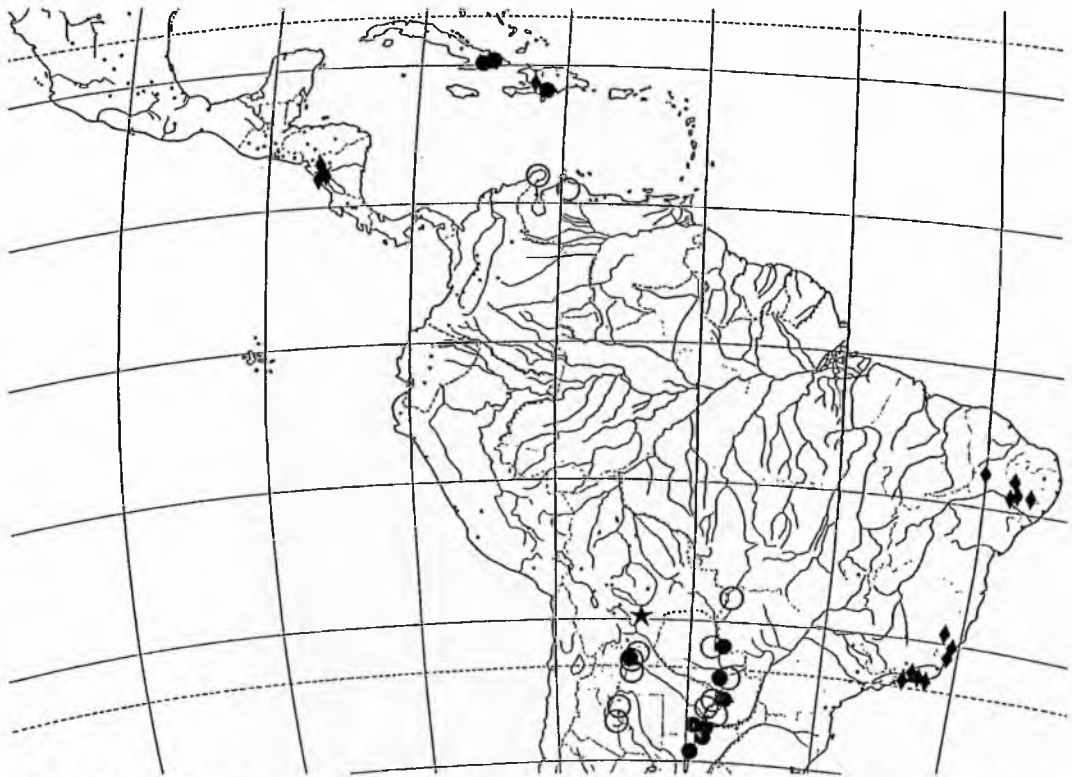


Fig. 5.71: Distribution map of *Myroxylon balsamum*. Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.

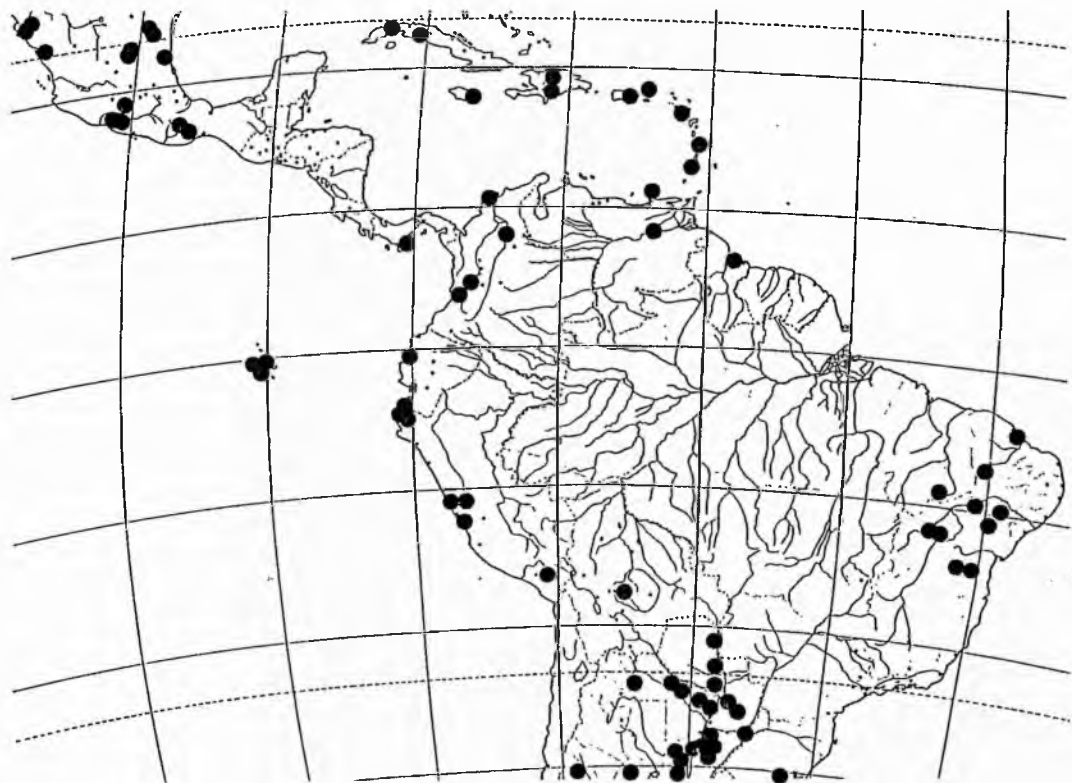
Fig. 5.72: Distribution map of *Poeppigia procera*.

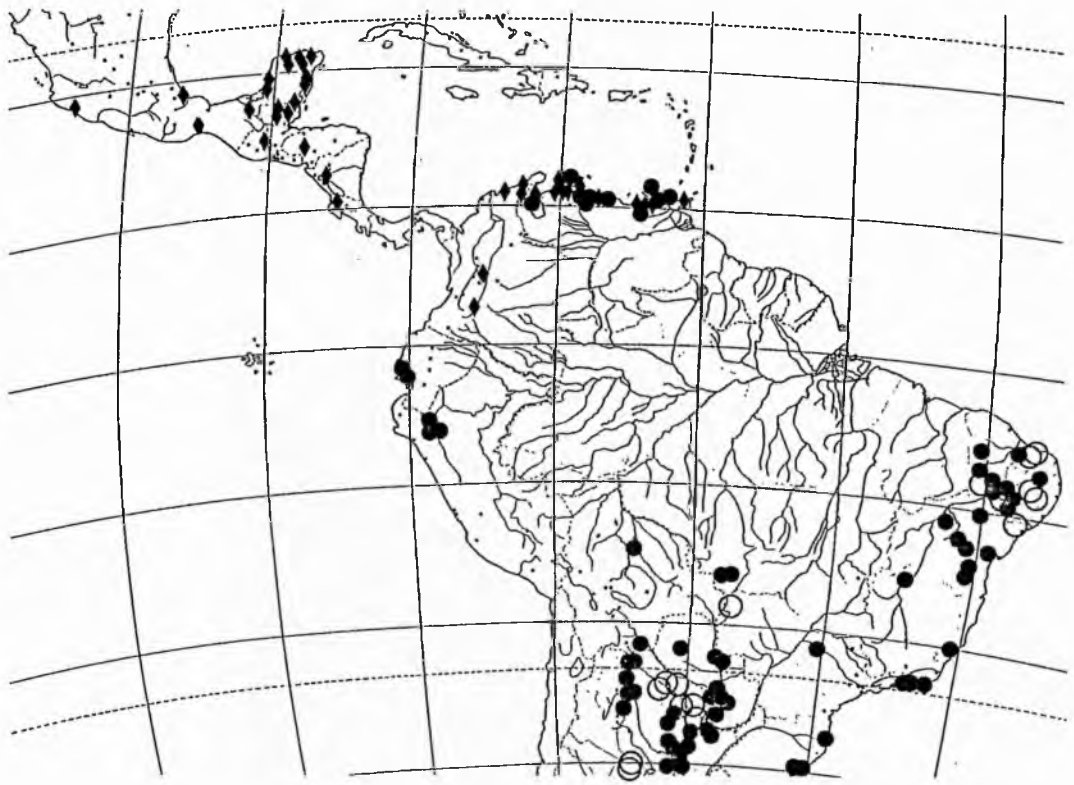




**Fig. 5.73:** Distribution map of *Phyllostylon rhamnoides* (solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys), *P. brasiliense* (diamonds) and *P. orthopterum* (star).

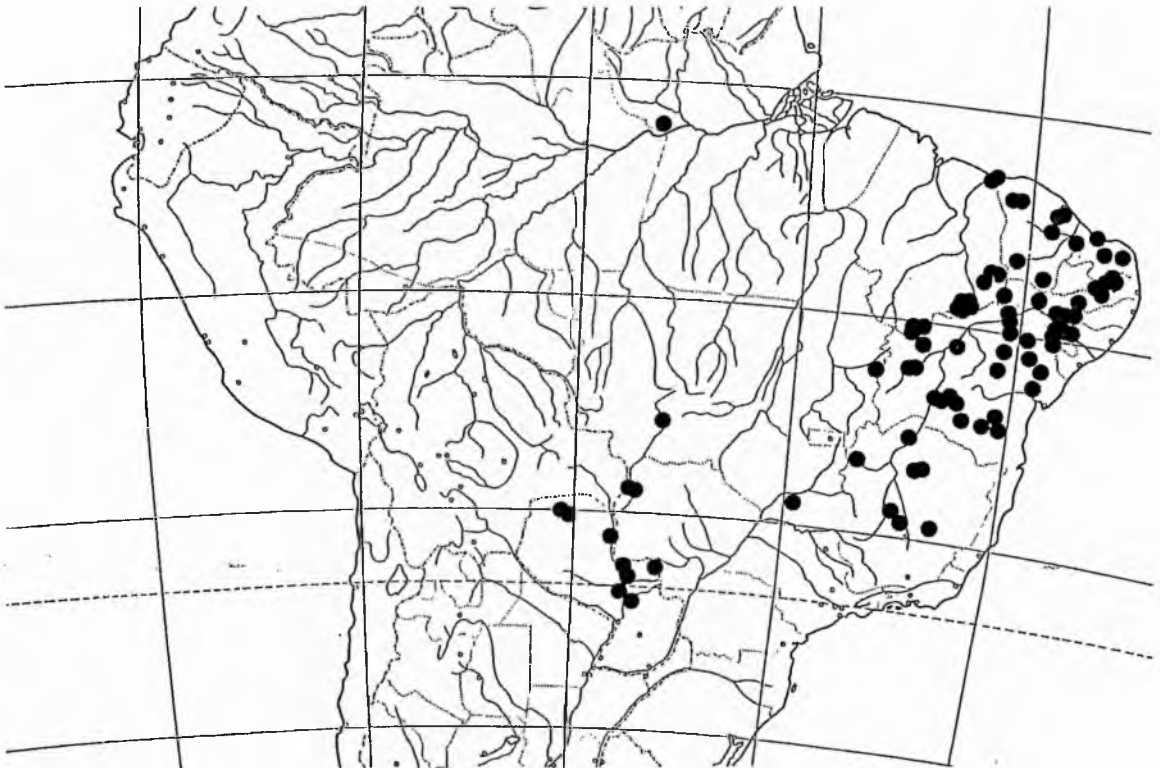
**Fig. 5.74:** Distribution map of *Parkinsonia aculeata*.

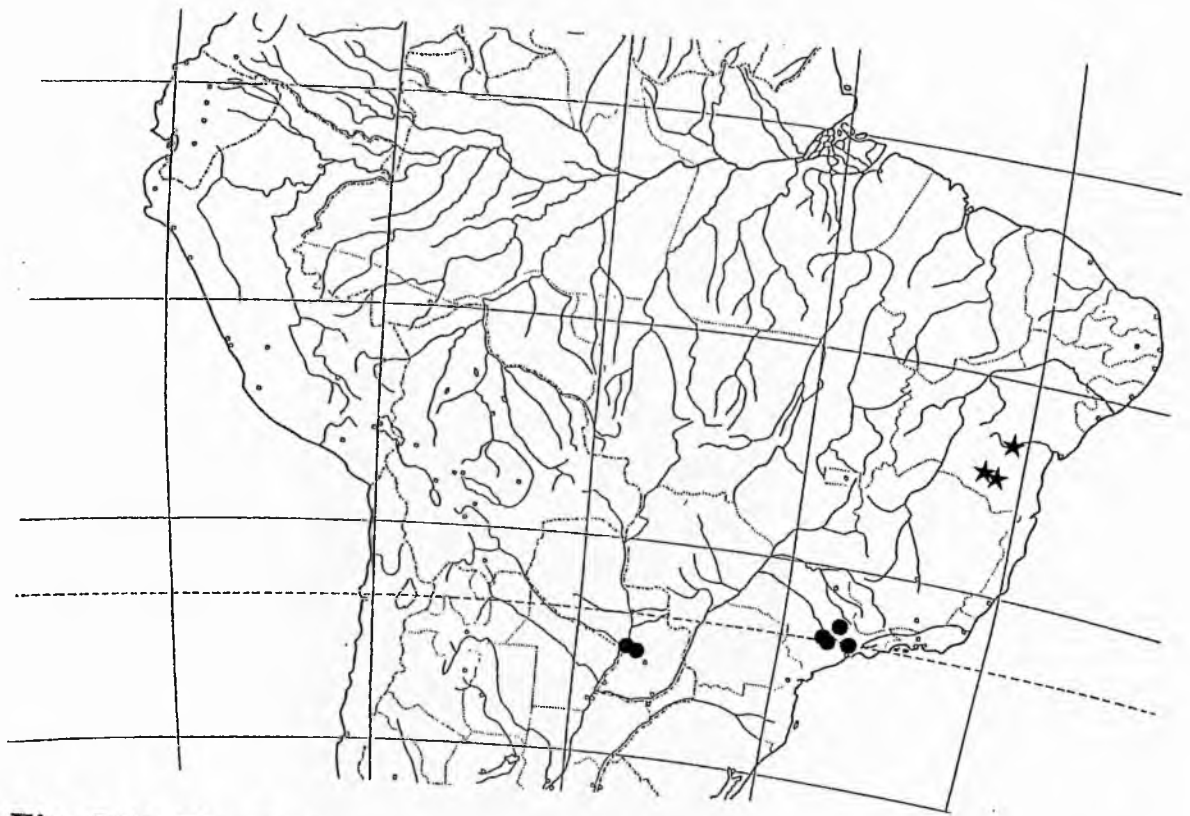




**Fig. 5.75:** Distribution map of *Sideroxylon obtusifolium* ssp. *obtusifolium* (solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys) and ssp. *buxifolium* (diamonds).

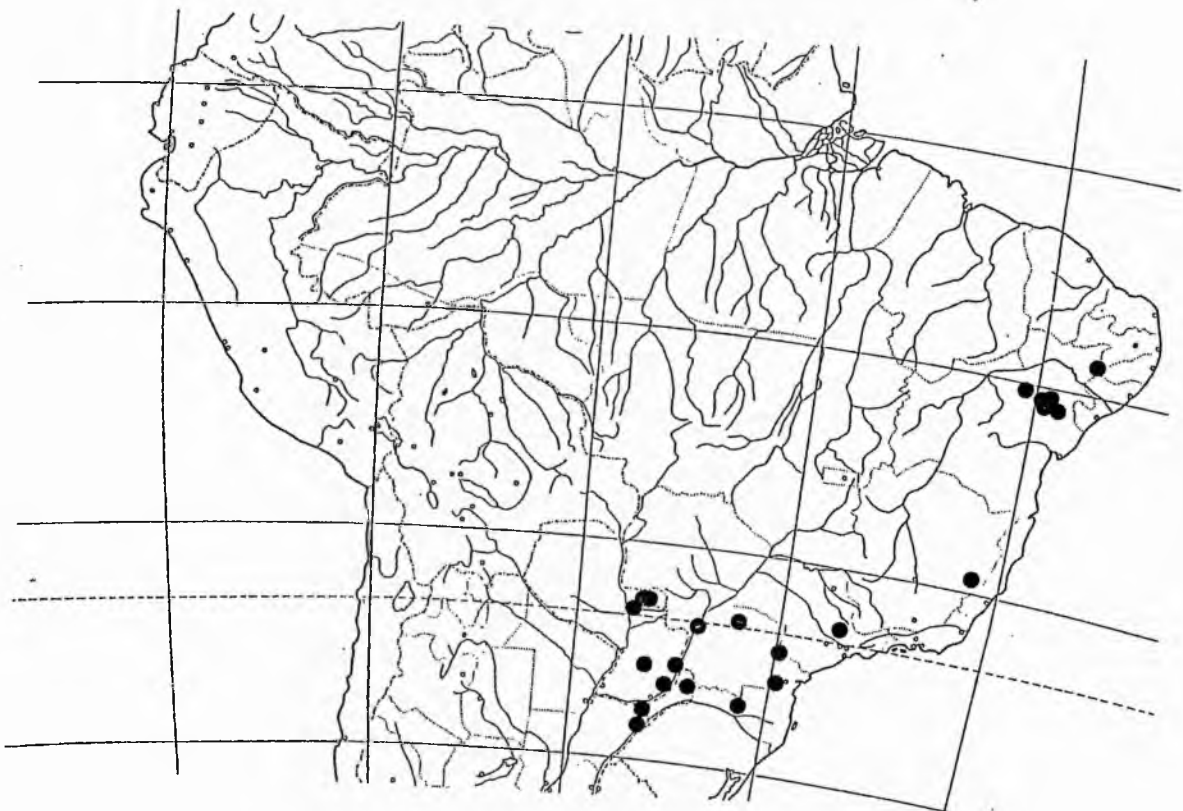
**Fig. 5.76:** Distribution map of *Aspidosperma pyriformis*.

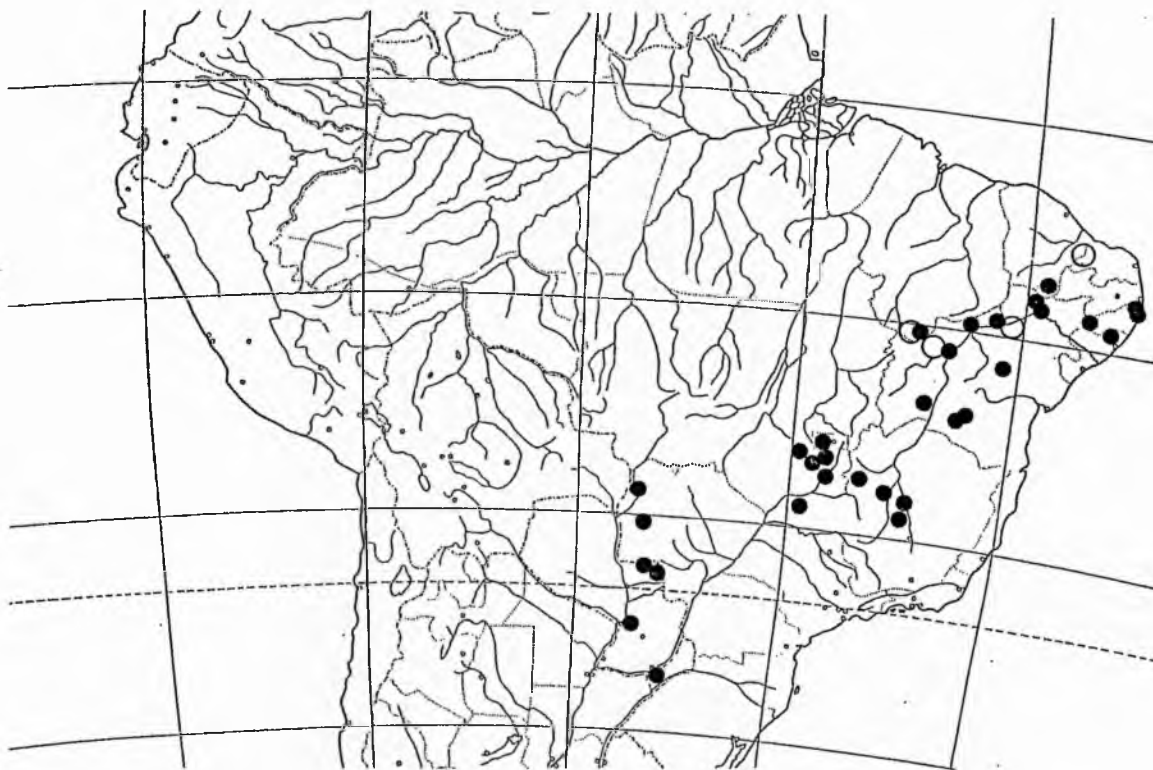




**Fig. 5.77:** Distribution map of *Aspidosperma riedelii* ssp. *riedelii* (dots) and ssp. *oliganthum* (stars).

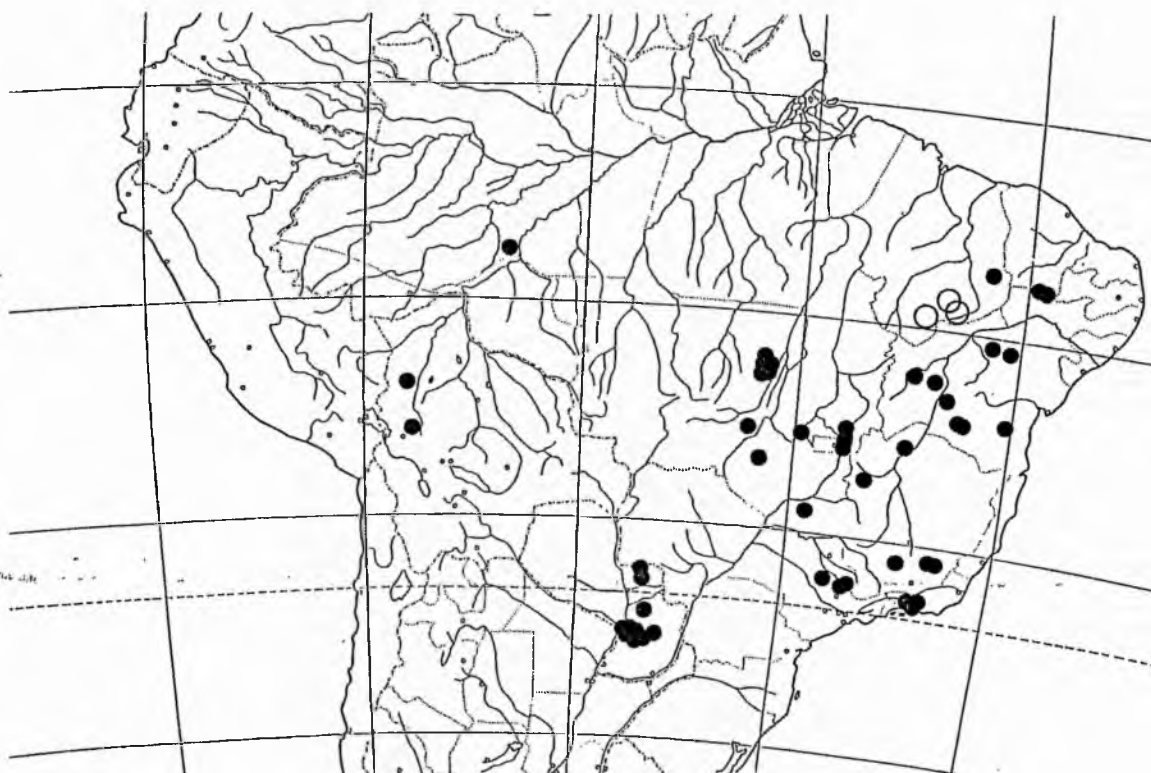
**Fig. 5.78:** Distribution map of *Balfourodendron riedelianum*.





**Fig. 5.79:** Distribution map of *Hymenaea martiana*. Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.

**Fig. 5.80:** Distribution map of *Machaerium acutifolium*. Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.



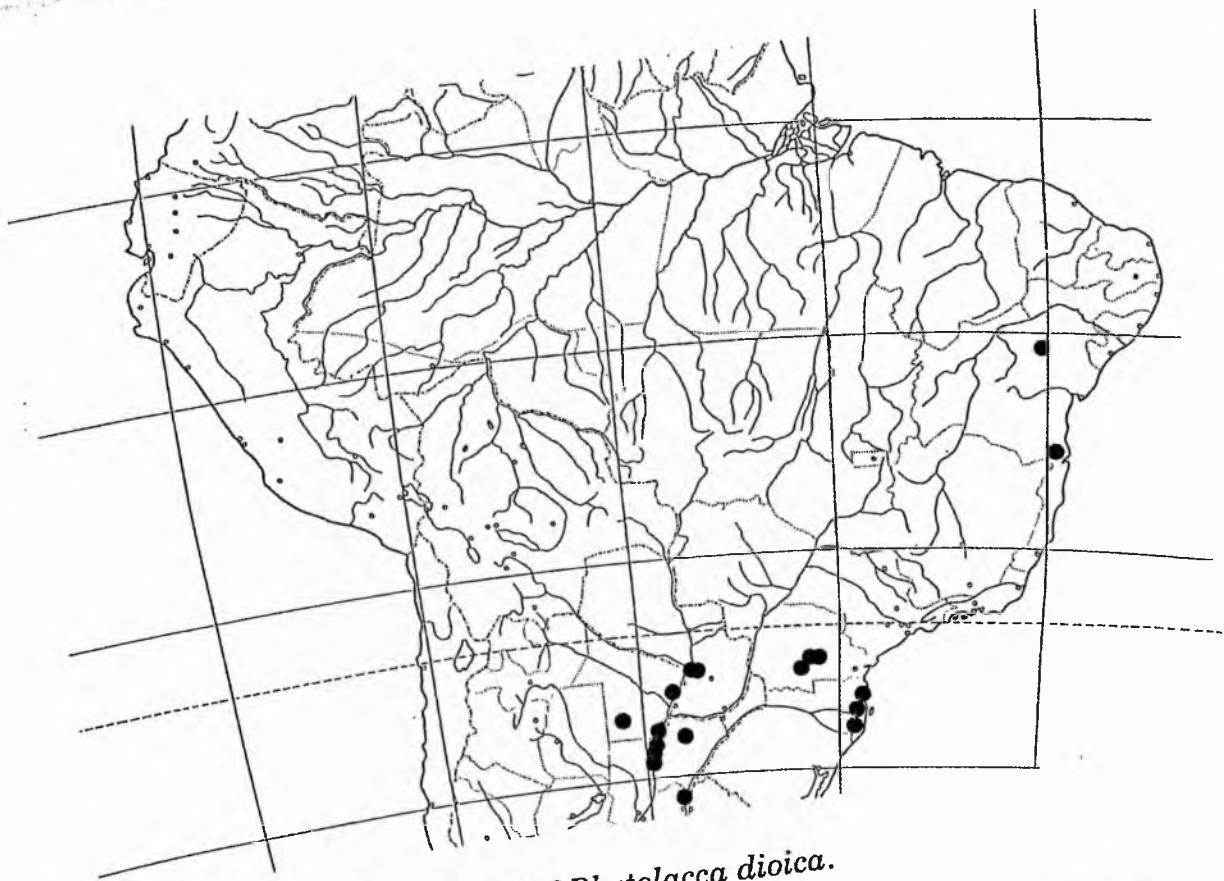
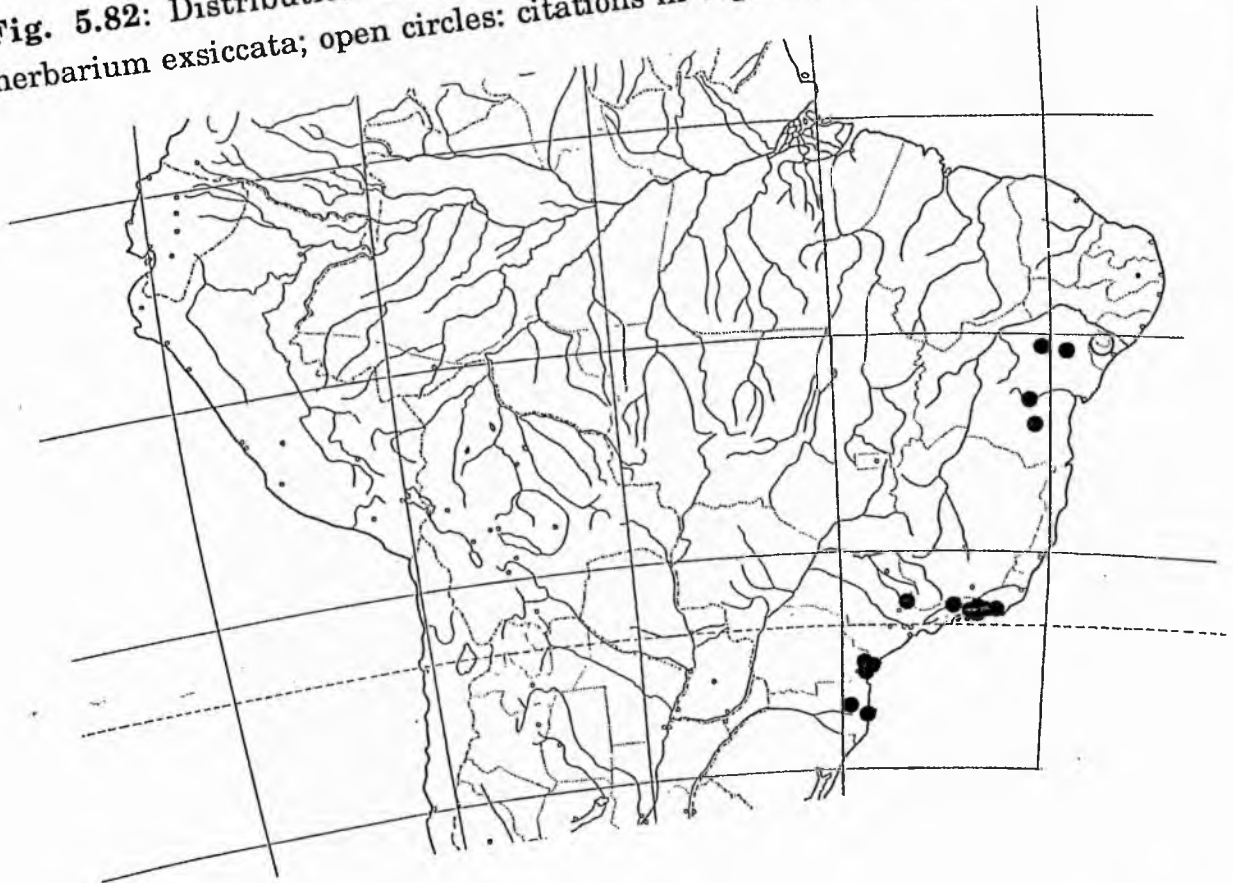
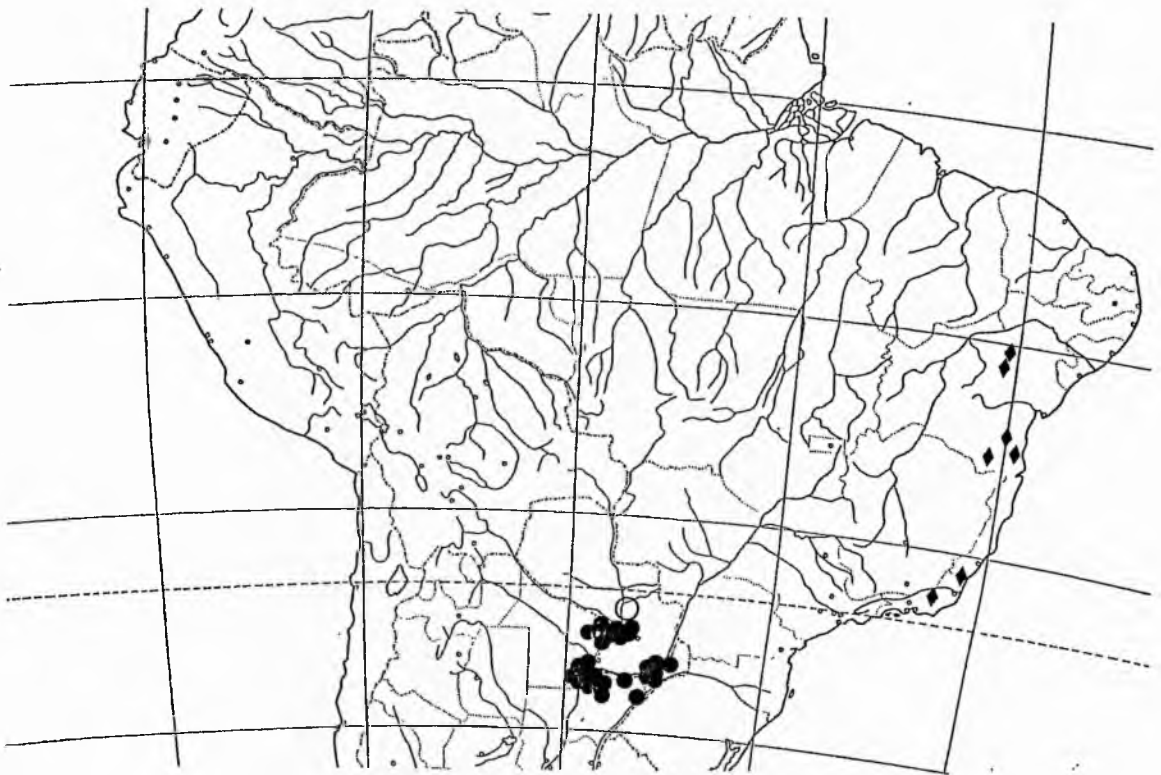


Fig. 5.81: Distribution map of *Phytolacca dioica*.

Fig. 5.82: Distribution map of *Alseis floribunda*. Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.

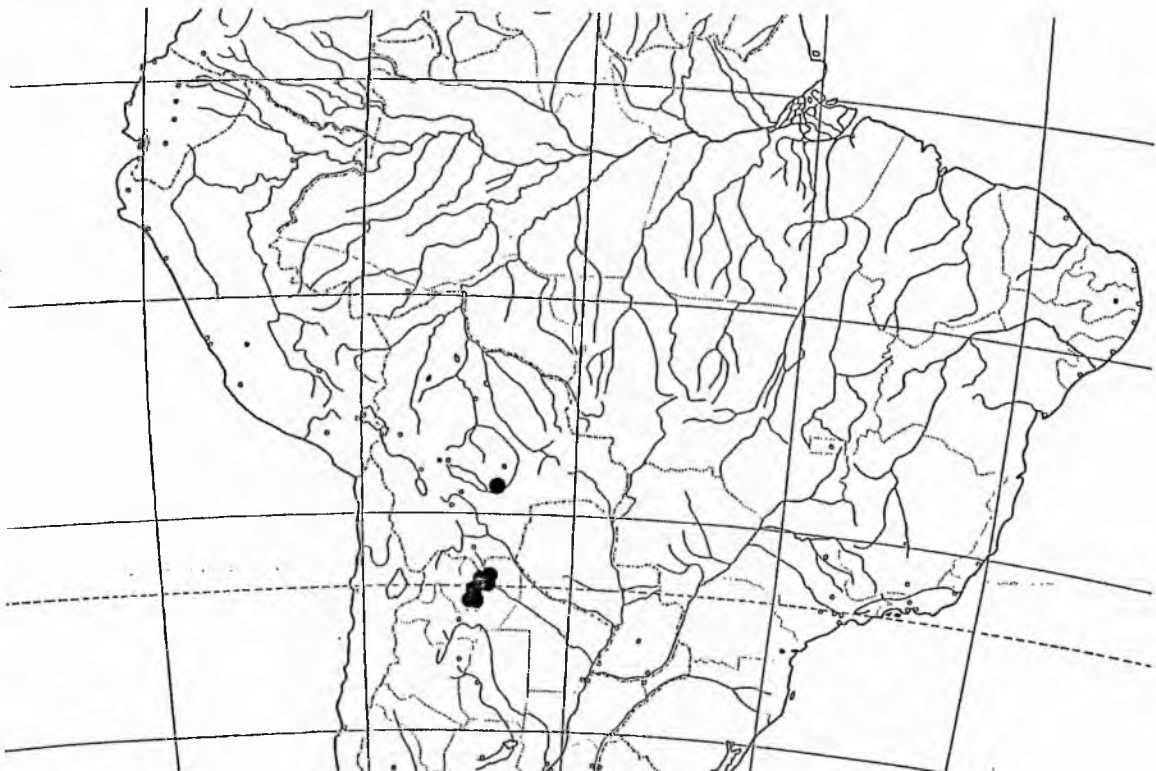






**Fig. 5.83:** Distribution map of *Astronium balansae* (solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys) and *A. concinnum* (diamonds).

**Fig. 5.84:** Distribution map of *Athyana weinmannifolia*.



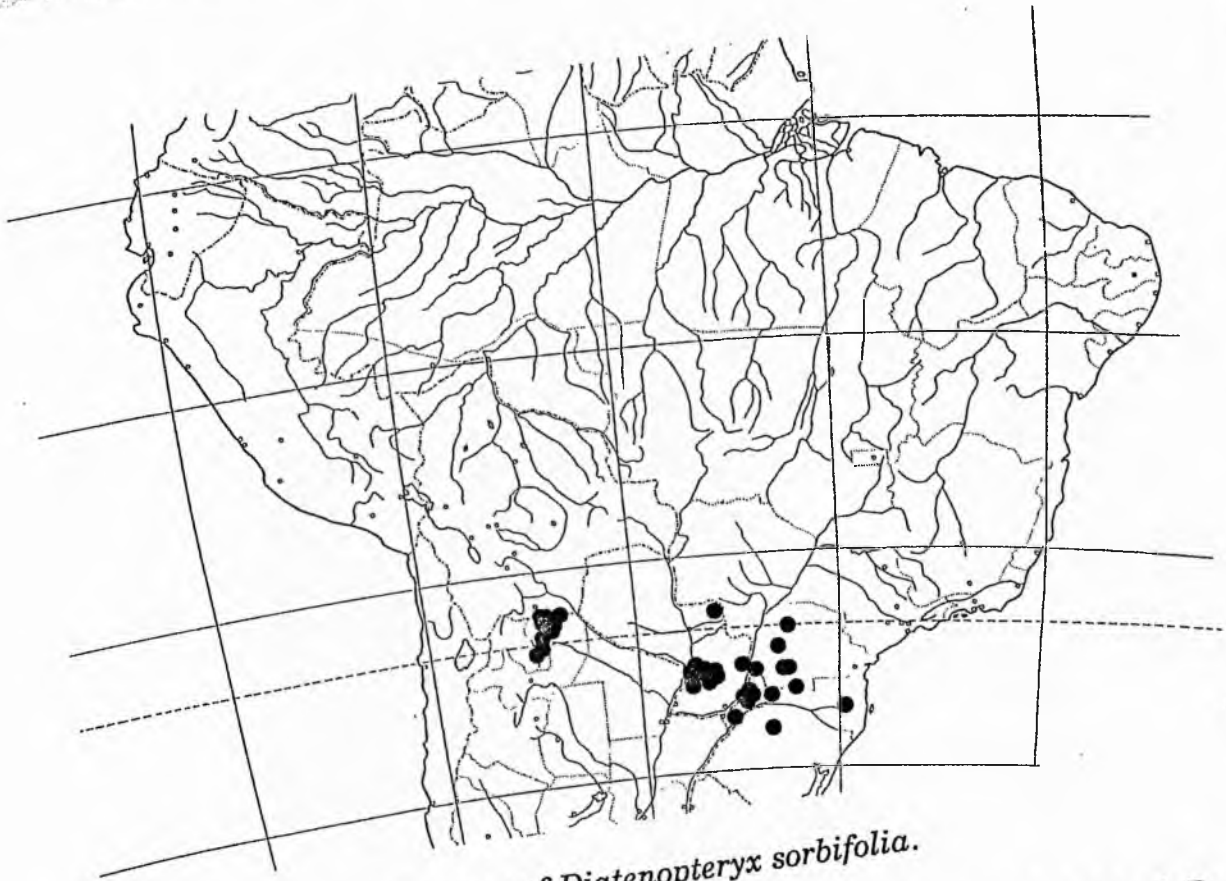
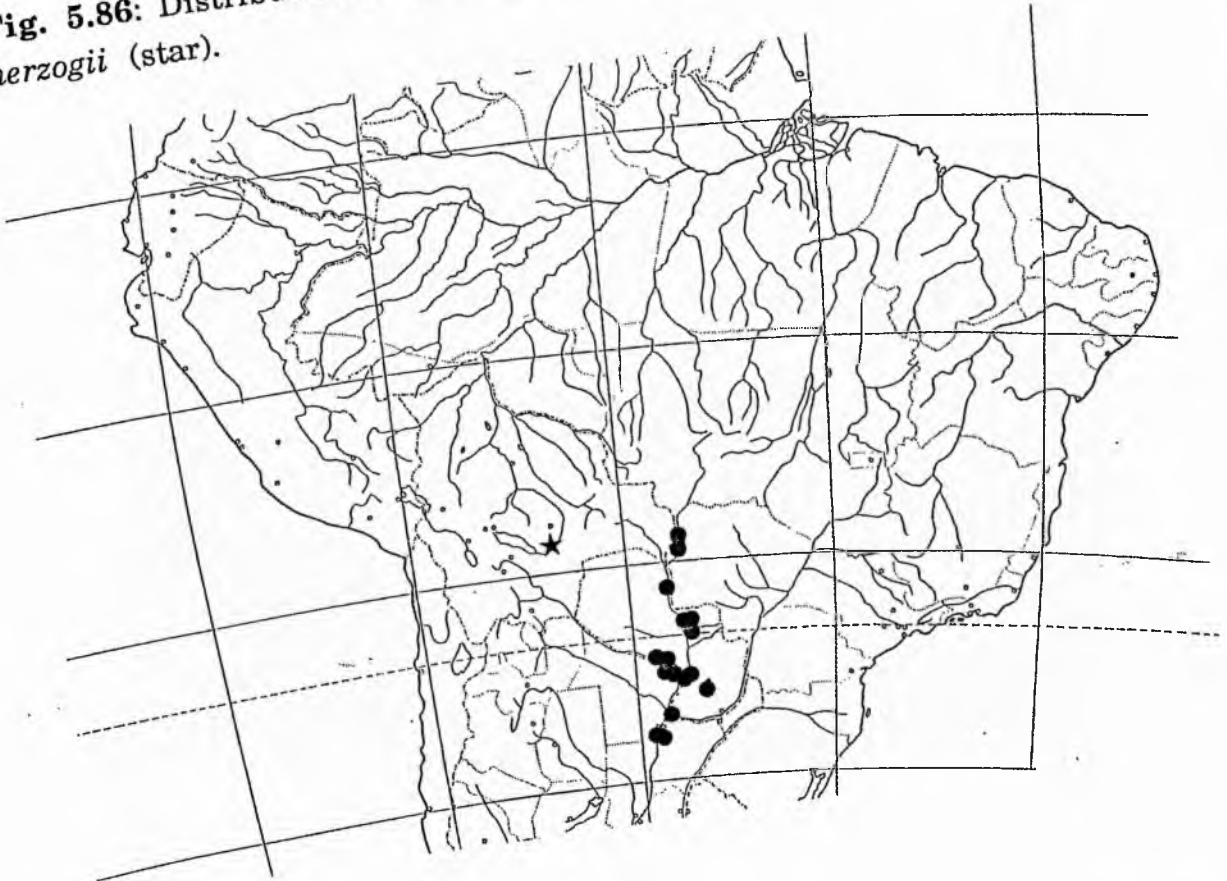
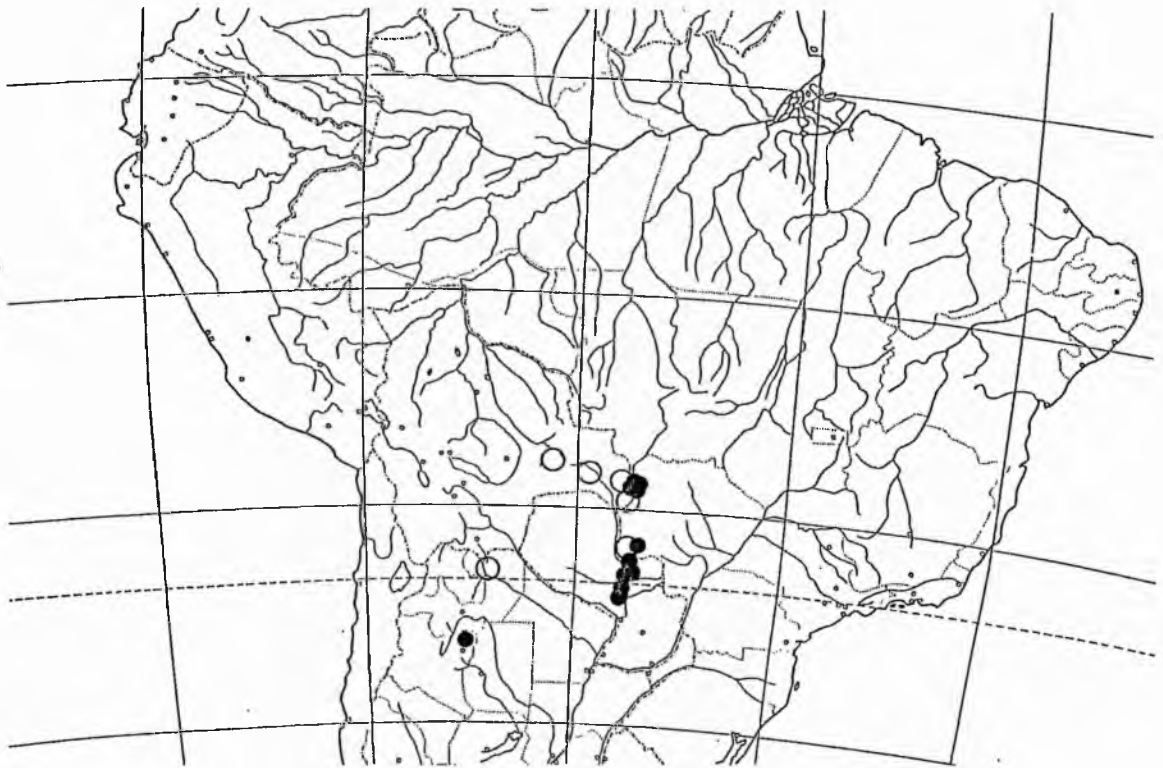


Fig. 5.85: Distribution map of *Diatenopteryx sorbifolia*.

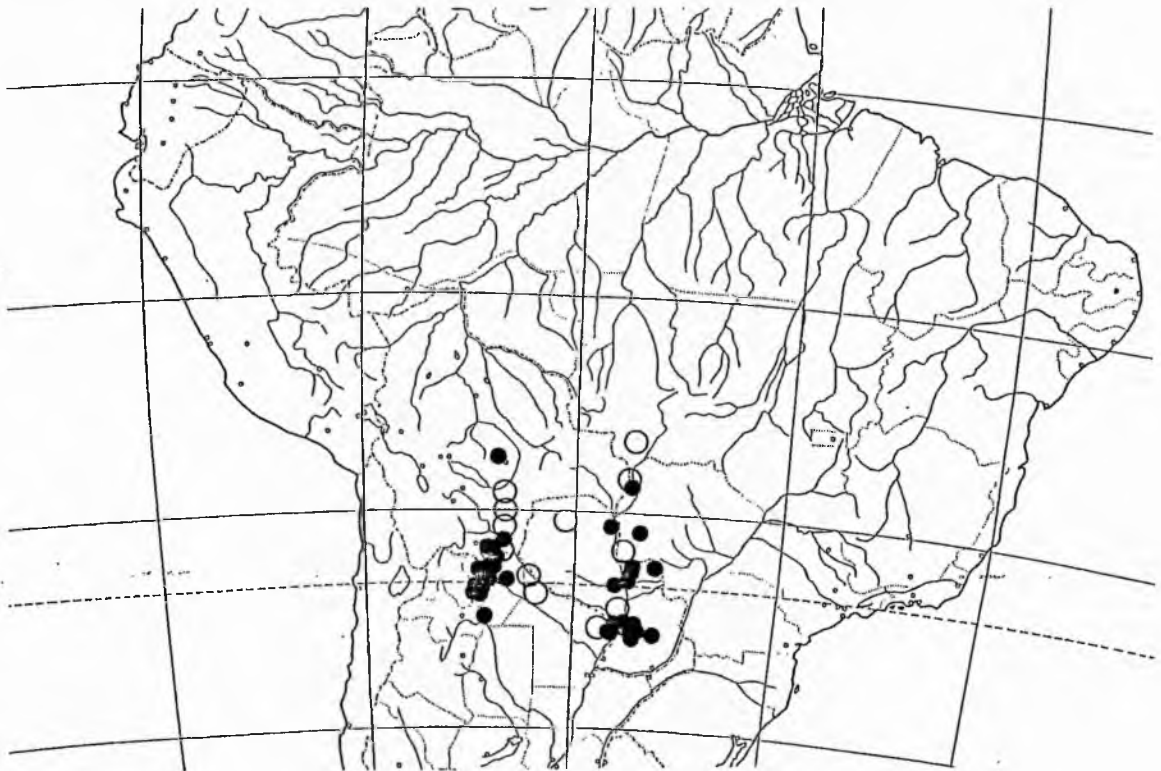
Fig. 5.86: Distribution map of *Diplokeleba floribunda* (dots) and *D. herzogii* (star).

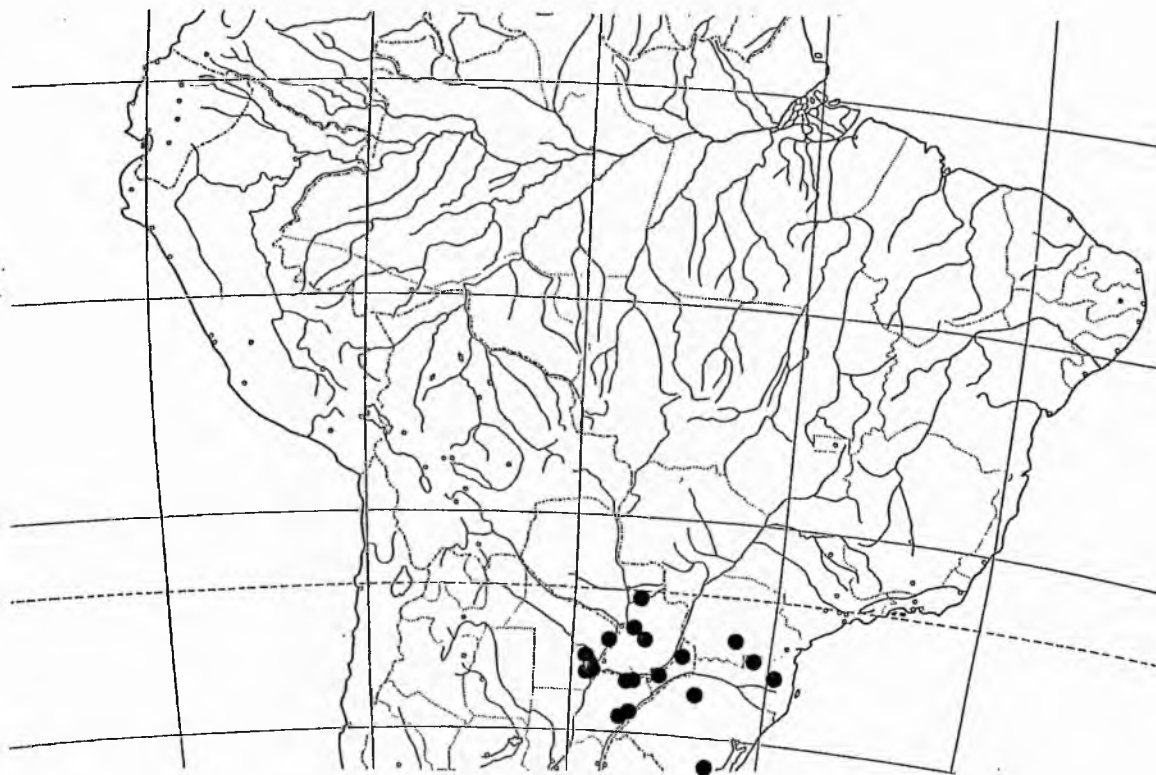




**Fig. 5.87:** Distribution map of *Ziziphus oblongifolius* . Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.

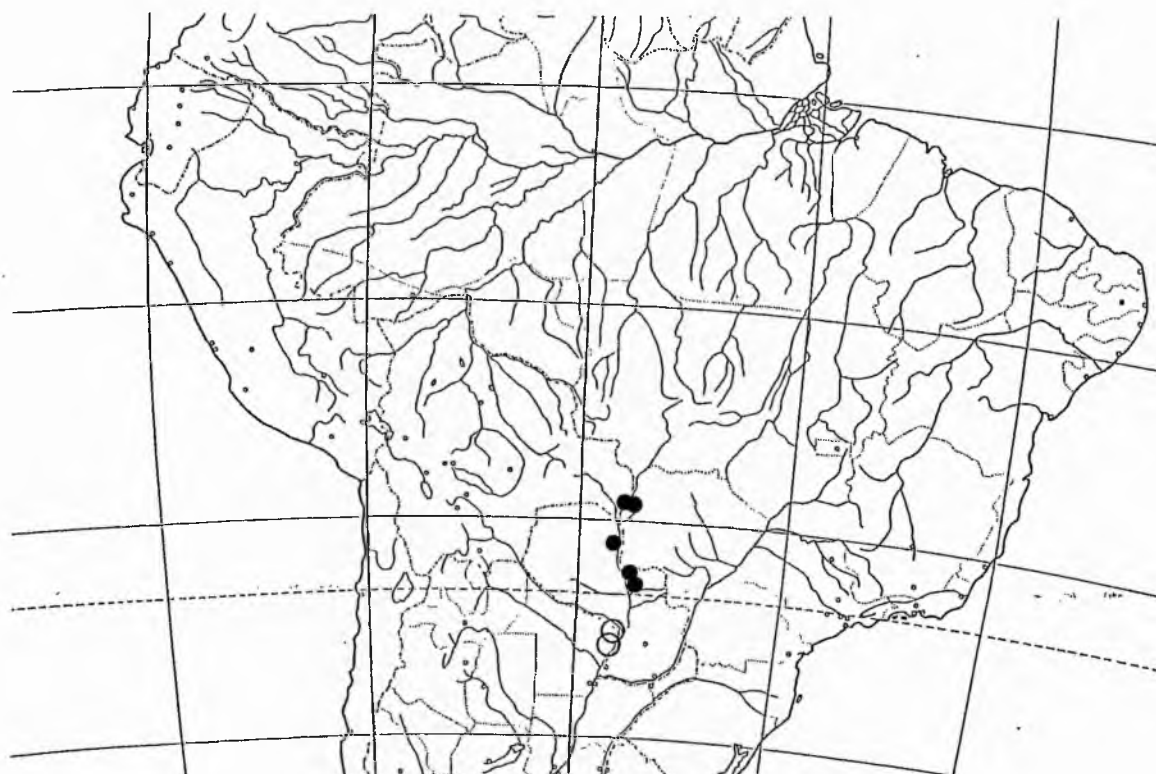
**Fig. 5.88:** Distribution map of *Calycophyllum multiflorum*. Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.





**Fig. 5.89:** Distribution map of *Maytenus ilicifolia*.

**Fig. 5.90:** Distribution map of *Ziziphus guaranitica*. Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.



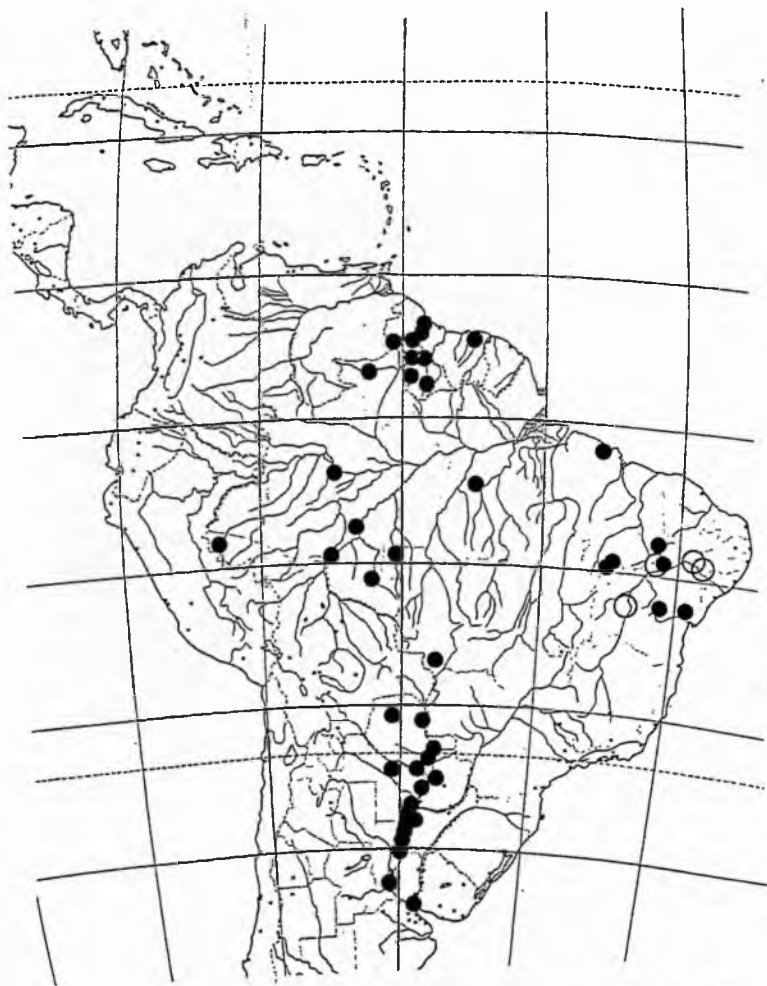
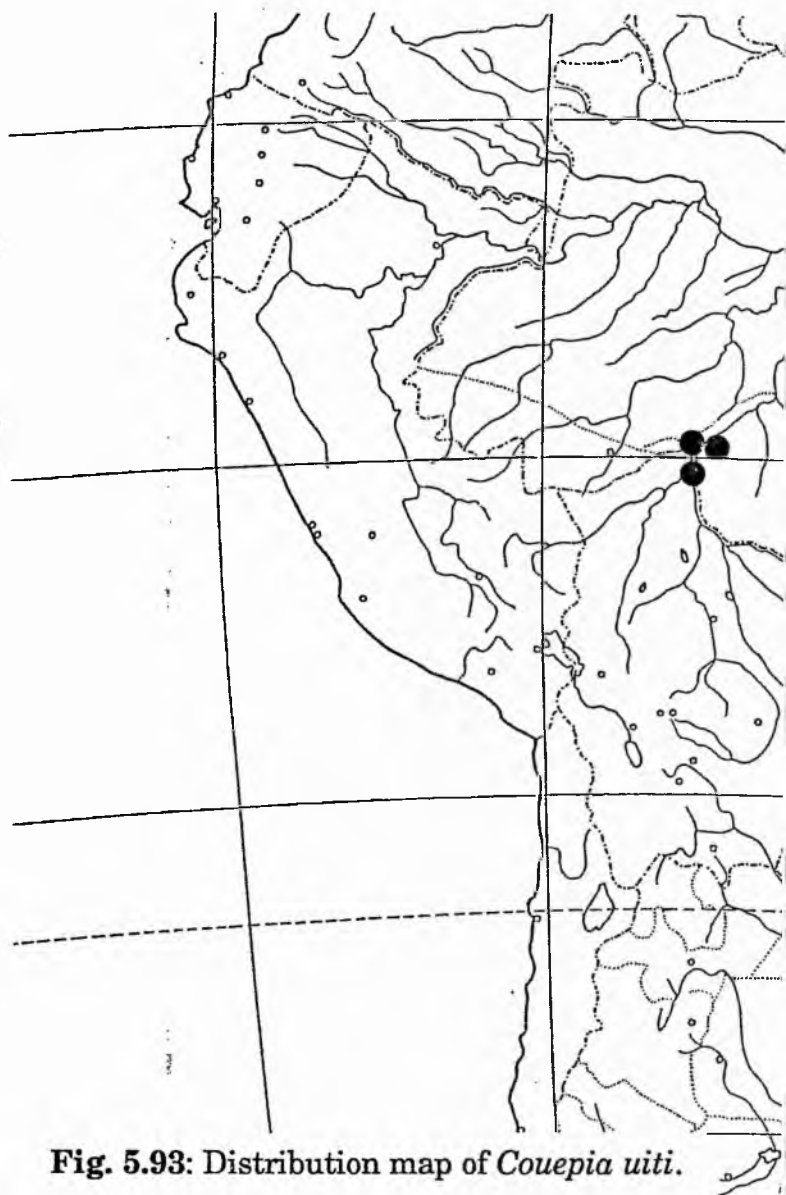


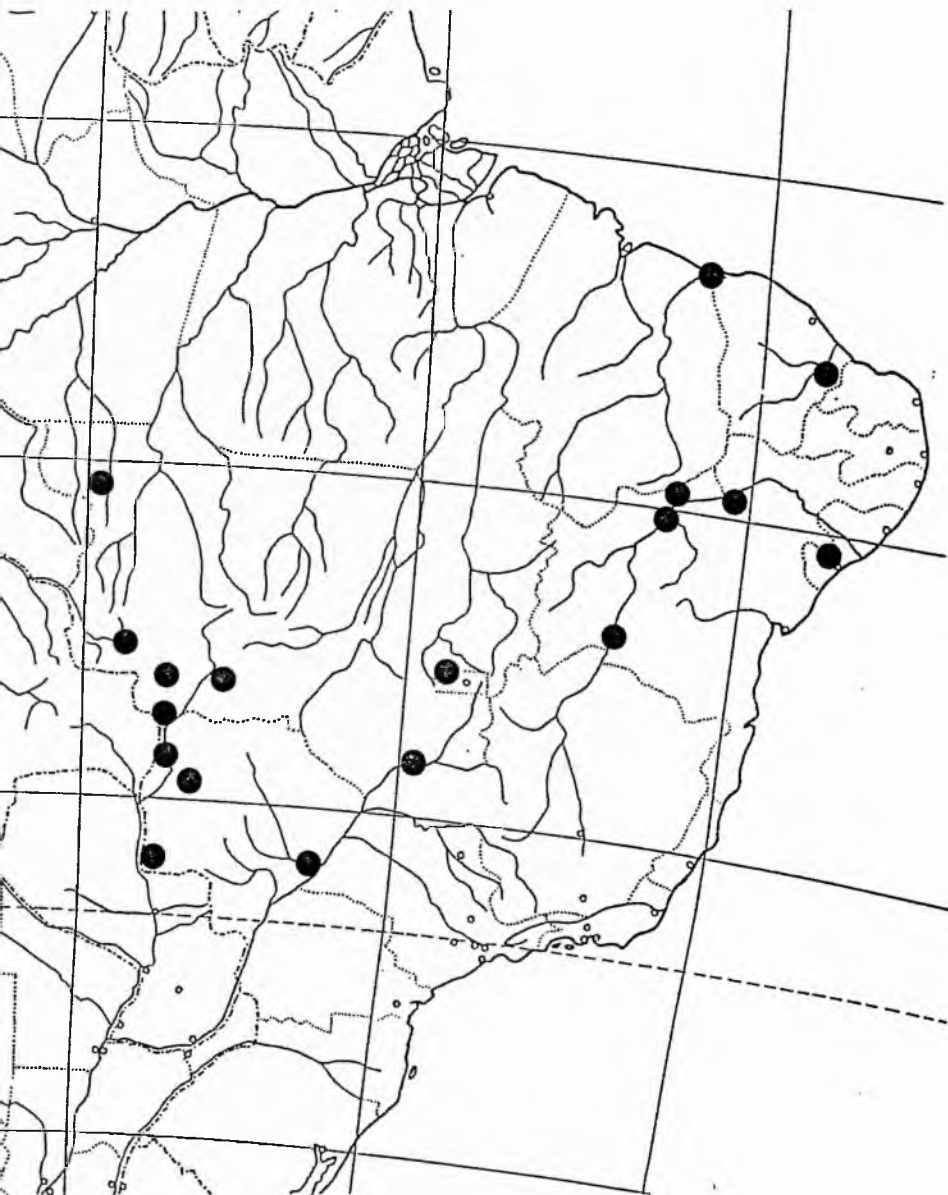
Fig. 5.91: Distribution map of *Albizia polyantha*. Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.



Fig. 5.92: Distribution map of *Aspidosperma discolor*.



**Fig. 5.93:** Distribution map of *Couepia uiti*.





## 6. PHYTOSOCIOLOGICAL ANALYSIS OF NEOTROPICAL SEASONAL FORESTS

In order to assess to what an extent the Neotropical seasonal forests are interrelated and/or to other South American formations, reliable floristic lists were selected from the available literature and worked out in phytosociological tables on a basis of presence-absence of species. These data were then analyzed following three different techniques:

a) Classic phytosociological analysis of the Zürich-Montpellier school, in the more modern version modified by Mueller-Dombois & Ellenberg (1974). This consists essentially in listing all the species (rows) occurring in certain areas or localities (columns), and then mechanically search for species with common patterns of distribution in the columns. Subsequent reshuffling of columns and rows generally results in the grouping of some species which seem to be exclusive to a determined group of localities, exclusive to a single area, or common to most or all of them. These species groups are taken to indicate the presence of common environmental factors by which they are restricted in their phytogeographical distribution. Therefore, such groups have an ecological indicator value, and they are referred to as 'floristic groups (FG)' (Mueller-Dombois & Ellenberg, 1974). Because of the subjective nature of this analysis it is necessary to compare the results with those of more objective statistical studies, as the following.

b) Multivariate numerical methods:

b.1- CLINK (Complete Linkage) algorithm from Wishart's (1987) package, employing Sørensen's (1948) similarity index (also known as Czekanowski-Dice coefficient). This agglomerative technique of classification fuses the individuals (localities/areas) into increasingly larger discrete groups, based on their similarity matrix, and a dendrogram is provided to show their relationships. The fusion is interrupted according to a subjective criterion, generally when recognizable clusters of ecologically-floristically related individuals are formed, or when no individual is left isolated (Mateucci & Colma, 1982).

b.2- PCA (Principal Components Analysis) from the JMP IN™ statistical software. This ordination technique, contrary to the classificatory ones, does not establish discrete classes but displays the individuals under study in a hyper-dimensional space along axes of continuous variation.

The axes ('principal components') are numbered according to the decreasing percentage of accumulated variation they concentrate. Thus, Axis I always comprises the highest value of variation absorbed by any possible axis, which can then be interpreted as representing one particular environmental or ecological factor. The individuals are then displayed in successive two-dimensional plots ('scattergrams'), of which only the Axis I-Axis II coordinates are shown and discussed here.

### 6.1- The woody Chaco communities and neighbouring formations:

All the vegetation types described in Chapter 2 and usually regarded as part of the Gran Chaco region have been analyzed in Table 6.1. A number of FG, namely **II**, **U**, **UI** and **III** amongst others, indicate very close links between those woody communities of wetter and less frost-affected areas, such as **A** (Gallery Forest), **B** ('Selva de Ribera'), **C** ('Tipa-Pacar Forest), **D** ('Palo blanco' Forest) and the Austro-Brazilian Transitional Forest (**E**), alongside the communities described by Prado et al. (in press, b) for Mato Grosso do Sul (**F**, **G**, **H**, **I** and **J**). Apart from FG **III**, which comprises species with a wide ecological plasticity, there are scarce connections between communities **A** to **J** and what is here regarded as Chaco s.s. (communities **K** to **W**). The FG **III** comprises the species that relate the Austro-Brazilian Transitional Forest to the Chaco proper, which are on the one hand of scarce importance here and sometimes accidental, and on the other are overweighed by the much more relevant links to communities **A** to **D**. The Chaco forest of Porto Murtinho (**J**) is the only one between the communities of Mato Grosso do Sul that can be regarded as truly chaquenian, as shown by Table 6.1 and coinciding with Prado et al. (in press, b). The FG **III**, **IV**, **V**, **VI**, **VII**, **VIII**, **IX** and **X** illustrate the strong internal homogeneity of the Chaco s.s. woody communities.

Figure 6.1 shows the dendrogram resulting from the CLINK classification analysis applied to the same set of communities shown in Table 6.1. It is noteworthy that the order of the communities rendered by CLINK is basically very similar to that proposed in the phytosociological table, save for the position of the Chaco at Porto Murtinho. Group  $\alpha$  comprises communities **A** to **E**, while  $\beta$  those of Mato Grosso do Sul (**F** to **I**). Meanwhile, groups  $\gamma$  and  $\delta$  consist of all the communities of the

**TABLE 6.1: Phytosociological analysis of the main woody communities of the Chaco and neighbouring formations.**

Column A: Gallery Forest, Paraná River (Franceschi & Lewis, 1979)

- B: 'Selva de Ribera' (Prado et al., in press a; Morello & Adámoli, 1974)
- C: 'Tipa-Pacarà' Forest (Meyer, 1963; Digilio & Legname, 1966; Brown et al., 1985)
- D: 'Palo blanco' Forest (Meyer, 1944; Coro, 1956; Adámoli et al., 1972; Cabrera, 1976)
- E: Austro-Brazilian Transitional Forest (Lewis & Pire, 1981, and author's field experience; also Morello et al., 1971, Morello & Adámoli, 1974, and Cabrera, 1976)
- F: Calcareous woodlands, M. Grosso do Sul (Prado et al., in press b)
- G: *Schinopsis balansae* parkland, M.G. Sul (Prado et al., in press b)
- H: *Aspidosperma-Mimosa* scrubland, M. Gr. do Sul (Prado et al., in press b)
- I: *Diplokeleba-Tabebuia-Capparis* scrubland, M. Gr. do Sul (Prado et al., in press b)
- J: Chaco forest, Pto Murtinho, M. Grosso do Sul (Prado et al., in press b)
- K: 'Quebrachal' of *Schinopsis balansae* (Lewis & Pire, 1981, and author's field experience)
- L: 'Quebrachal' of 3 'quebrachos' (Ragonese, 1941; Lewis & Pire, 1981, and author's field experience)
- M: 'Quebrachal' of 2 'quebrachos' (Morello & Adámoli, 1968; Adámoli et al., 1972, and author's field experience)
- N: 'Quebrachal' of white 'quebracho' (Morello et al., 1971; Lewis & Pire, 1981)
- O: 'Palosantal' of *Bulnesia sarmientoi* (Morello et al., 1971, and Adámoli et al., 1972)
- P: 'Algarrobal' of *Prosopis* spp. (Morello et al., 1971)
- Q: 'Vinalar' of *Prosopis ruscifolia* (Morello et al., 1971)
- R: 'Palmar' of *Copernicia australis*, Western Chaco (Cabrera, 1976)
- S: 'Palmar' of *Copernicia australis*, Eastern Chaco (Cabrera, 1976; Lewis & Pire, 1981, and author's field experience)
- T: Arid Chaco Woodland (Sayago, 1969)
- U: 'Cardonal' of *Stetsonia coryne* (Sayago, 1969)
- V: North Sierra Chaco (Marlange, 1972)
- W: South Sierra Chaco (Sayago, 1969)

			A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W																										
			Gall	Se	NT	Ip	Pab	Au	B	Calc	Is	Btl	IAs	H	IO	Tn	Ch	Pr	O	Ch	O	x	3	O	x	2	R	W	O	P	asa	Al	gr	V	ini	P	m	w	P	m	E	AC	w	Card	W	S	C	R	S	S	C
Family	Genus	Species																																																	
1 LAUR	Nectandra	falcifolia																																																	
2 LEGM	Albizia	polyantha																																																	
3 MYRT	Hexachlamis	edulis																																																	
4 CAPP	Crateva	tapia																																																	
5 APOC	Peschiera	australis																																																	
6 LEGM	Inga	uruguensis																																																	
7 LEGM	Acacia	monacantha																																																	
6 ULMA	Celtis	Iguanea																																																	
9 EUPH	Croton	urucurana																																																	
10 FLAC	Banara	arguta																																																	
11 AREC	Arecastrum	romanzoffianum																																																	
12 LEGP	Geoffroea	striata																																																	
13 ANNO	Rollinia	emarginata																																																	
14 POLY	Ruprechtia	laxiflora																																																	
15 LEGM	Enterolobium	contortisiliquum																																																	
16 MYRT	Eugenia	uniflora																																																	
17 RUTA	Fagara	naranjillo																																																	
16 COMB	Terminalia	triflora																																																	
19 MYRS	Rapanea	laetevirens																																																	
20 SAPO	Pouteria	gardneriana																																																	
21 LEGC	Holocalyx	balansae																																																	
22 MORA	Ficus	luschnathiana																																																	
23 SAPI	Sapindus	saponaria																																																	
24 MORA	Sorocea	sorucei																																																	
25 MELI	Trichilia	elegans																																																	
25 NYCT	Pisonia	aculeata																																																	
27 CEL	Schaefferia	argentensis																																																	
25 PTER	Acrostichum	aureum																																																	
29 CECR	Cecropia	adenopus																																																	
30 RUTA	Pilocarpus	pennatifolius																																																	
31 STER	Guazuma	ulmifolia																																																	
32 TILI	Luehea	divaricata																																																	
33 LEGC	Peltophorum	dubium																																																	
34 ULMA	Phyllostylon	rhamnoides																																																	
35 ULMA	Celtis	sp																																																	
36 BIGN	Tabebuia	impetiginosa																																																	
37 LEGM	Anadenanthera	colubrina v cebii																																																	
35 ANAC	Astronium	urundeuva																																																	
39 RUTA	Fagara	rholfolia																																																	
40 CAPP	Capparis	aff. retusa?																																																	
41 SAPI	Diplokeleba	floribunda																																																	
42 BORA	Patagonula	americana																																																	
43 MYRT	Myrcianthes	pungens																																																	
44 SAPI	Allophylus	edulis																																																	
45 NYCT	Pisonia	zapallo																																																	
46 LEGC	Gleditsia	amorphoides																																																	
47 SAPO	Chrysophyllum	gonocarpum																																																	
45 MORA	Maclura	tinctoria																																																	
49 LEGM	Pithecellobium	scalare																																																	
50 ARAL	Pentapanax	angelicifolius																																																	
51 CARI	Carica	quercifolia																																																	
52 PHYT	Phytolacca	dioica																																																	
53 SOLA	Brunfelsia	australis																																																	
54 ANAC	Astronium	balansae																																																	
55 LEGC	Pterogyne	nitens																																																	
56 SAPI	Cupania	vernalis																																																	
57 SAPO	Chrysophyllum	marginatum																																																	
56 ULMA	Trema	micrantha																																																	
59 BIGN	Jacaranda	milmosifolia																																																	
60 MYRT	Myrcianthes	mato																																																	
61 BIGN	Tecoma	stans																																																	
62 PIPE	Piper	tucumanum																																																	
63 TILI	Heltocarpus	popayanensis																																																	
64 LEGP	Tipuana	tipu																																																	
95 LEGP	Myroxylon	balsamum																																																	
66 LEGM	Parapiptadenia	excelsa																																																	
67 URTI	Urera	baccifera																																																	
66 BOMB	Pseudobombax	argentinum																																																	
69 MELI	Cedrela	odorata																																																	
70 LEGP	Lonchocarpus	lilloi																																																	
71 LEGM	Acacia	albicorticata																																																	
72 SAPI	Athyana	welmannifolia																																																	
73 LEGC	Senna	spectabilis v sp																																																	
74 BORA	Cordia	trichotoma/allio																																																	
75 AREC	Acrocomia	chonta																																																	
76 MELI	Trichilia	clausenii																																																	
77 ELAE	Mutingia	calabura																																																	
75 RUBI	Pogonopus	tubulosus																																																	
79 COMP	Vernonia	fulva																																																	
50 COMP	Cnicothamnus	lorenzii																																																	
61 BUDD	Buddleja	albomaculata																																																	
52 RUTA	Fagara	hyemalis																																																	
53 BOMB	Celba	spectosa																																																	
54 RUBI	Calycophyllum	multiflorum																																																	
85 LEGP	Amburana	cearensis																																																	
56 EUPH	Cnidocotus	vitifolius v cnic																																																	
57 ANAC	Schinopsis	brasilienis																																																	
55 STER	Helicteres	brasilienis																																																	
59 EUPH	Sapum	sp																																																	
90 RUBI	Randia	armata																																																	
91 STER	Sterculia	striata																																																	
92 LEGP	Machaerium	hirtum																																																	
93 EUPH	Croton	sp l																																																	
94 RHAM	Ziziphus	oblongifolius																																																	
95 POLY	Coccoloba	sp																																																	
95 ERYT	Erythroxylum	sp																																																	
97 CACT	Cereus	uruguayanus																																																	

I

II

III

IV

V

VI

VII

VIII

IX

X

XI

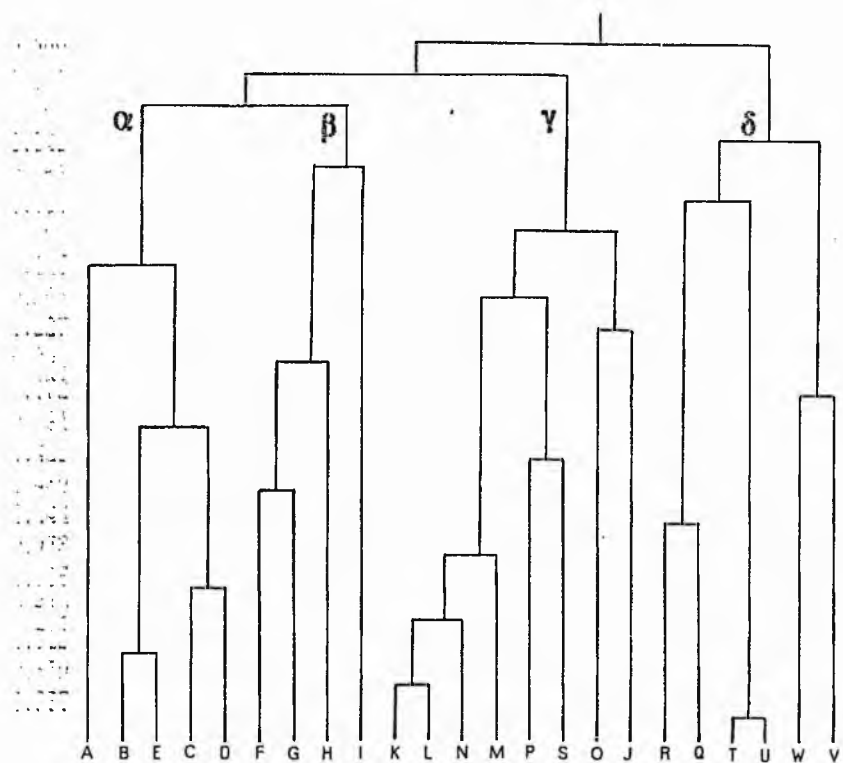
XII

XIII

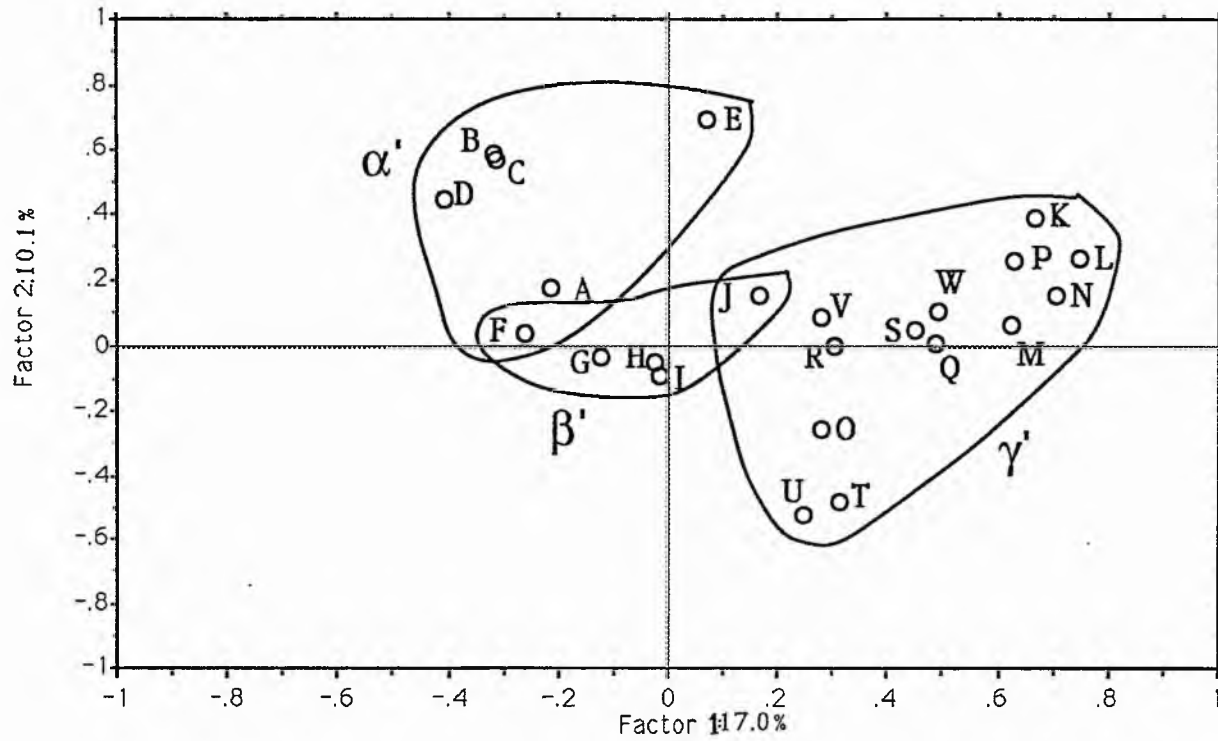
XIV







**Fig. 6.1:** Dendrogram resulting from CLINK classification analysis of the main woody communities of the Chaco and neighbouring formations. Letters in the bottom line indicate the communities studied (see Table 6.1 for key), and the figures in the vertical line the similarity index value at each level of fusion.



**Fig. 6.2:** Scattergram from PCA analysis of the main woody communities of the Chaco and neighbouring formations. See explanation in text.



Chaco s.s., separated into two groups probably because of an east-west floristic gradient within the province.

The results of the PCA analysis shown in Fig. 6.2 present three basic clusterings of communities: the wetter ones (A to F) are together in cluster  $\alpha'$ , the Mato Grosso do Sul communities are grouped in another one ( $\beta'$ ), while the bulk of the Chaco s.s. in cluster  $\gamma'$  shows stronger links within itself than with the rest of the neighbouring formations. Once again the Chaco of Porto Murtinho is in a transitional position and could pertain to either of two clusters, while the Austro-Brazilian Transitional Forest (E) unmistakably joins the group of wetter communities.

## 6.2- South American Seasonal Forests: a global comparison.

The vegetation units involved in this comparative study are:

### Chaquenanian Dominion

- A- The Monte province (*sensu* Morello, 1958).
- B- The Chaco province: the Sierra Chaco is placed here in a separate column to test the consistency of the inclusion of this district within the Chaco s.s..
- C- The Chaco province: the lowland Chaco in its Eastern, Central and Western districts. Floristic list taken from Sect. 4.1, excluded those species exclusive to the Sierra Chaco.

### Neotropical Seasonal Forests of South America

- D- Austro-Brazilian Transitional Forest, as defined and described in Sect. 2.3.3.a; the results of this analysis will further allow to discuss its present position within the Chaco province.
- E- 'Selva de Ribera', on the levee limiting the river Paraná flooding valley, as described in Sect. 2.3.2 and in Prado et al. (in press, a). It is not yet clear if previous phytogeographical accounts have placed this community in the Chaco or other province, basically because it has been ignored as a vegetation unit by most authors, but the present author believes it should be regarded as part of the Paranense province *sensu* Cabrera & Willink (1980).
- F- Gallery Forest in the Paraná river valley, as part of the Paranense province (Cabrera, 1976).
- G- Upper Uruguay River Valley Forests, part of the Paranense province *sensu* Cabrera & Willink (1980).

- H-** Planalto Forest in São Paulo state, part of the Paranense province *sensu* Cabrera & Willink (1980).
- I-** Subandean Piedmont Forests, in both its 'Palo blanco' and 'Tipa-Pacará' variants. Floristic list taken from Sect. 4.3. At present a member of the Yungas province (Cabrera, 1976), but repeatedly regarded as chaquenian by previous authors.
- J-** The Caatingas province, until present regarded as a member of the Chaquenian Dominion by Cabrera & Willink (1980). Floristic list taken from Sect. 4.2.
- K-** Calcareous forests of Mato Grosso do Sul, of uncertain phytogeographical position so far.
- L-** The calcareous forest of Januária area, very close geographically and floristically to the Caatingas (Ratter et al., 1978; Andrade-Lima, 1981).
- M-** The dry Caribbean vegetation of Venezuela. The floristic list is an aggregate, ranging from Aristeguieta's (1968) "selva veranera" (summer-green forest) to semiarid scrublands (Matteucci & Colma, 1982). It corresponds to the Guajira province in the Caribbean Dominion (Cabrera & Willink, 1980).
- N-** Equivalent communities in dry Caribbean Colombia, also part of the Guajira province.
- O-** Dry forests, woodlands and savannas of W Ecuador, as in Acosta-Solís (1966) and Harling (1979). At present in the Pacific province of the Amazonian Dominion (Cabrera & Willink, 1980).

#### Amazonian Dominion

Three floristic lists of localized vegetation areas corresponding to the three more conspicuous provinces of the Amazonian Dominion have been taken as paradigms.

- P-** A central area of the Brazilian Cerrados, in the Federal District (Ratter, 1986; P.E. Oliveira, pers. comm.).
- Q-** One stand of Atlantic rainforest in coastal São Paulo (Silva & Leitão F<sup>o</sup>, 1982).
- R-** An area of Amazon forest close to Manaus (Prance et al., 1976).

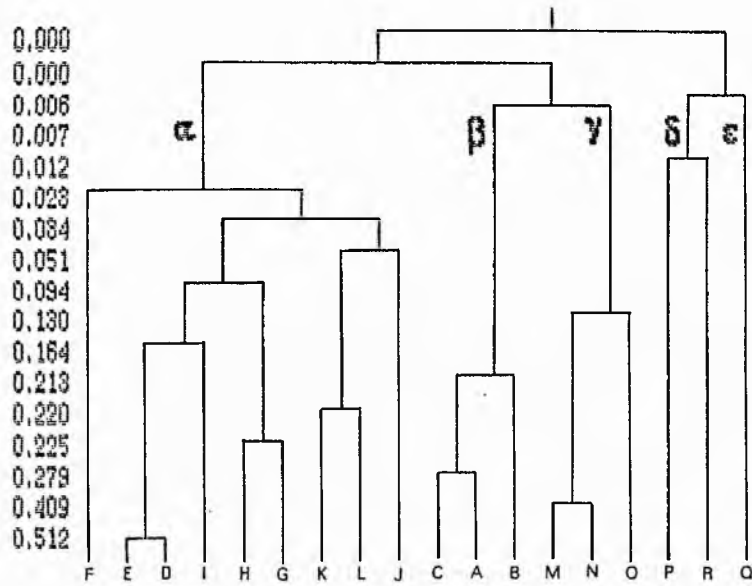
Thus, the analysis performed on these data at both specific and generic level will allow one to establish how close the links Chaco-Caatingas are, vis-à-vis other similar kinds of vegetation in South America, and how well the Caatingas compare with the Chaquenian Dominion *versus* the Amazonian Dominion.

### 6.2.1- Analysis at specific level:

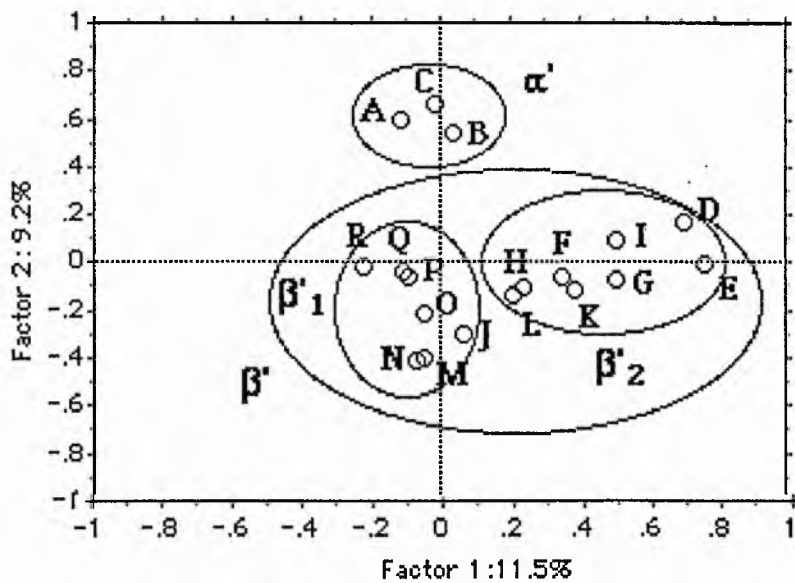
In Table 6.2 the results of the classic phytosociological approach at species level are shown. FG I assembles species of ample distribution in seasonal formations but absent from the more humid provinces (P, Q and R). FG II, III, IV and V indicate different degrees of relationship between the Chaco and also some of its neighbouring communities to the Subandean Piedmont Forests (I). FG VII comprises the rather weak links between the Chaquenan Dominion and the Guajira province and the dry forests in W Ecuador. FG VIII to XI show the consistency of the Chaco Dominion, clearly separating it from the rest of the formations included in this analysis.

The FG XII and XIII comprise those species generally restricted to the Pleistocenic Arc as here defined (see Sect. 5.3.1), although *Tabebuia impetiginosa* extends as far as Mexico. FG XIV and XV show the links between both the southern extensions of the Pleistocenic Arc, not including the Caatingas or related calcareous communities. FG XVI encompasses Caatingas species with a wide distribution in South America from the Pleistocenic Arc to Ecuador and the dry Caribbean area, whereas FG XVII is similar but it excludes the Caatingas. The FG XVIII to XXVI show a number of floristic links of the Upper Uruguay Forests (G), out of which those with the Caatingas must be emphasized (FG XXI). Groups XXVII to XXX indicate varied connections of the Planalto Forest (H) of S Brazil. The FG XXXI, XXXII and XXXIII show the close contacts between the Subandean Piedmont Forests (I) to the Caatingas (J) and related calcareous communities (K and L, in turn connected to J by FG XXXIV to XXXVI). While the links Caatingas/Ecuador+dry Caribbean area are shown in FG XXXVII and XXXVIII, those of the same province with the Amazonian Dominion are evident in FG XXXIX and XL. The dry Caribbean sectors of Colombia and Venezuela are very closely related to each other (FG XLIII), while they show strong connections to the dry formations of W Ecuador (FG XLII and XLIV). FG XLV indicates some loose links of the Cerrados of central Brazil with a number of seasonal forests of South America.

The dendrogram rendered by the CLINK analysis is shown in Fig. 6.3, with four recognizable clusters and one isolated individual.



**Fig. 6.3:** Dendrogram resulting from CLINK classification analysis of the main South American seasonal forests, at specific level. Letters in the bottom line indicate the communities studied (see Table 6.2 for key), and the figures in the vertical line the similarity index value at each level of fusion.



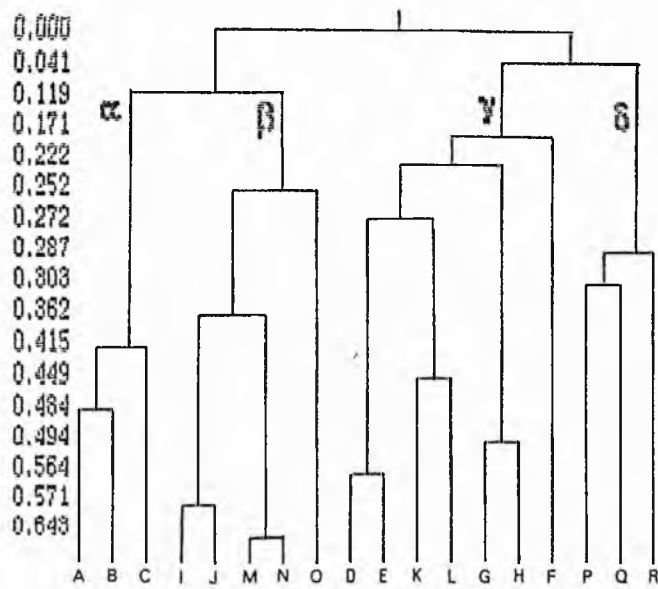
**Fig. 6.4:** Scattergram from PCA analysis of South American seasonal forests. See explanation in text.

Group  $\alpha$  comprises two subclusters, one formed by the Caatingas (**J**) plus Calcareous forests and the other by the southernmost expansions of the Pleistocenic Arc, including both the Subandean Piedmont Forests (**I**) and the Austro-Brazilian Transitional Forest (**D**). Group  $\beta$  comprises the chaquenian vegetation types, whereas cluster  $\gamma$  comprises the vegetation of the dry Caribbean coast and W Ecuador. Finally, the Cerrados are closer to the Amazon forest stand (group  $\delta$ ), while the Atlantic rainforest remains isolated ( $\epsilon$ ).

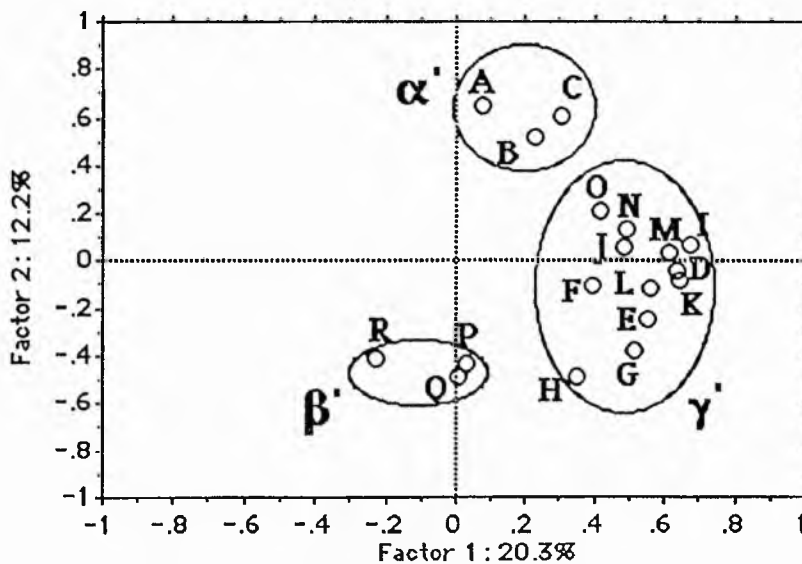
The results of the PCA analysis are shown in Fig. 6.4. Clearly detached from all the rest of the vegetation types are the members of the Chaquenian Dominion (cluster  $\alpha'$ ). The remainder, although showing enough coherence to be regarded as a single cluster ( $\beta'$ ), can be further separated in two subclusters. Subcluster  $\beta'_1$  comprises the Caatingas and, closely related, the dry vegetation of Venezuela, Colombia and Ecuador, along with the three typical representatives of the Amazonian Dominion. Subcluster  $\beta'_2$  consists of the southern half of the Pleistocenic Arc, including the Subandean Piedmont Forests (**I**) and the Austro-Brazilian Transitional Forest (**D**).

### 6.2.2- Analysis at generic level:

In Table 6.3 the results of the classic phytosociological study at generic level are shown. Once again the members of the Chaquenian Dominion (**A**, **B** & **C**) are well defined as a unit by the FG **VI**, **VII**, **VIII** and **IX**, while their links to the seasonal formations are illustrated by FG **X** to **XVI**. The genera restricted to the Pleistocenic Arc are between those in FG **XVIII** and **XXXVI**, whereas the genera which extend from the Pleistocenic Arc to the Guajira province and Ecuador are included in FG **XIX**, **XXIV**, **XXV**, **XXXIX** and **XL**. Some of the relevant genera of the Caatingas (**J**) and Subandean Piedmont Forests (**I**) are widespread in the Pleistocenic Arc but also occur in Colombia, Venezuela, Ecuador and the Amazonian Dominion (FG **XX**, **XXI** and **XXXIX**). The generic links of the Upper Uruguay Forests (**G**) with the Caatingas (**J**) are shown in FG **XXVI**, while those with the Subandean Piedmont Forests (**I**) are indicated in FG **XXVII**. It is noteworthy that FG **XXXVII** emphasizes the floristic contacts at generic level of solely the Caatingas (**J**) and the Subandean Piedmont Forests (**I**), while FG **XLI** and **XLIII** those between the Caatingas and the Guajira province and W Ecuador (**M**, **N** and **O**). The



**Fig. 6.5:** Dendrogram resulting from CLINK classification analysis of the main South American seasonal forests, at generic level. Letters in the bottom line indicate the communities studied (see Table 6.2 for key), and the figures in the vertical line the similarity index value at each level of fusion.



**Fig. 6.6:** Scattergram from PCA analysis of South American seasonal forests at generic level. See explanation in text.

floristic relationship Caatingas/Amazonian Dominion is shown in FG **KLID** and **KLJ**, while FG **L** to **LIII** indicate the internal coherence and close links between the formations of the Amazonian Dominion.

The dendrogram resulting from the CLINK analysis (Fig. 6.5) shows unmistakably that both the Chaquenian Dominion (group  $\alpha$ ) and Amazonian Dominion (group  $\delta$ ) are clearly isolated from the rest of the vegetation types. The group  $\beta$  emphasizes very close links at generic level between the Subandean Piedmont Forests, the Caatingas, the Guajira province and W Ecuador. Group  $\gamma$  comprises the Austro-Brazilian Transitional Forest together with the rest of the southern seasonal forests.

The previous results are remarkably congruent with the scattergram of Fig. 6.6, where again the Chaquenian (cluster  $\alpha'$ ) and Amazonian (cluster  $\beta'$ ) dominia are plainly detached from the seasonal forests, which in this case are together in a single cluster ( $\gamma'$ ). The latter shows anyhow that the Caatingas (**J**) are floristically very close to the Guajira province (**M** and **N**), W Ecuador (**O**) and the Subandean Piedmont Forests (**I**).

**TABLE 6.2: Phytosociological analysis of the main South American Seasonal Forests. Specific level.**

- Column A- The Monte province, Argentina (*sensu* Morello, 1958:145-50).
- B- Chaco s.s.: Sierra Chaco, Argentina (Sayago, 1969, p.224).
  - C- Chaco s.s.: the lowland Chaco in its Eastern, Central and Western districts, Argentina. Floristic list from Sect. 4.1, excluded the species exclusive to the Sierra Chaco.
  - D- Austro-Brazilian Transitional Forest, Argentina (see Sect. 2.3.3.a). Floristic list from Lewis & Pire, 1981, and author's field experience; also Morello et al., 1971, Morello & Adámoli, 1974, and Cabrera, 1976.
  - E- 'Selva de Ribera', Argentina (Prado et al., in press a; Morello & Adámoli, 1974).
  - F- Gallery Forest, Argentina (Franceschi & Lewis, 1979).
  - G- Upper Uruguay River Valley Forests, Santa Catarina and Rio Grande do Sul, Brazil (Klein, 1972; Rambo, 1980).
  - H- Planalto Forest, Vassununga & Bauru, São Paulo, Brazil (Martins, 1979, pp 108-9; Cavassan et al., 1984).
  - I- Subandean Piedmont Forests, in both its 'Palo blanco' and 'Tipa-Pacará' variants. Floristic list taken from Sect. 4.3.
  - J- The Caatingas province, Brazil. Floristic list: Sect. 4.2.
  - K- Calcareous woodlands, Mato Grosso do Sul, Brazil (Ratter et al., 1988b, p.516; Prado et al., in press b).
  - L- Calcareous forest, Januária, MG, Brazil (Ratter et al., 1978).
  - M- Dry Caribbean vegetation of Venezuela. The floristic list is an aggregate of Aristeguieta's (1968) "selva veranera" (summer-green forest) and semiarid scrublands (Matteucci & Colma, 1982, pp 102-4).
  - N- Dry Caribbean vegetation of Colombia (Dugand, 1970, pp 428-31; Rieger, 1976, pp 40-1).
  - O- Dry forests, woodlands and savannas of W Ecuador, as in Acosta-Solís (1966, pp 413-5) and Harling (1979).
  - P- Cerrado and cerrado in Brasília, Federal District (Ratter, 1986; P.E. Oliveira, pers. comm.).
  - Q- Atlantic rainforest, Ubatuba, SP, Brazil (Silva & Leitão F<sup>o</sup>, 1982).
  - R- Amazon forest, km 30 on the road Manaus-Itacoatiara, Amazonas, Brazil (Prance et al., 1976, pp 28-35).





287	LEGB	pyrolyzov	318	LEGB	zlatovam
288	SOLA	bravida	319	LEGB	unifera
289	LEGC	Senna	320	LEGC	spectabilis v. spectabilis
290	AJAC	Sonchopsis	321	LEGC	patiensis v. glabra
291	LEGC	Leptocarpus	322	LEGC	halimifolia
292	LEGC	Leptocarpus	323	LEGC	halimifolia
293	LEGC	Leptocarpus	324	LEGC	halimifolia
294	LEGC	Leptocarpus	325	LEGC	halimifolia
295	LEGC	Leptocarpus	326	LEGC	halimifolia
296	LEGC	Leptocarpus	327	LEGC	halimifolia
297	LEGC	Leptocarpus	328	LEGC	halimifolia
298	LEGC	Leptocarpus	329	LEGC	halimifolia
299	LEGC	Leptocarpus	330	LEGC	halimifolia
300	LEGC	Leptocarpus	331	LEGC	halimifolia
301	LEGC	Leptocarpus	332	LEGC	halimifolia
302	LEGC	Leptocarpus	333	LEGC	halimifolia
303	LEGC	Leptocarpus	334	LEGC	halimifolia
304	LEGC	Leptocarpus	335	LEGC	halimifolia
305	LEGC	Leptocarpus	336	LEGC	halimifolia
306	LEGC	Leptocarpus	337	LEGC	halimifolia
307	LEGC	Leptocarpus	338	LEGC	halimifolia
308	LEGC	Leptocarpus	339	LEGC	halimifolia
309	LEGC	Leptocarpus	340	LEGC	halimifolia
310	LEGC	Leptocarpus	341	LEGC	halimifolia
311	LEGC	Leptocarpus	342	LEGC	halimifolia
312	LEGC	Leptocarpus	343	LEGC	halimifolia
313	LEGC	Leptocarpus	344	LEGC	halimifolia
314	LEGC	Leptocarpus	345	LEGC	halimifolia
315	LEGC	Leptocarpus	346	LEGC	halimifolia
316	LEGC	Leptocarpus	347	LEGC	halimifolia
317	LEGC	Leptocarpus	348	LEGC	halimifolia
318	LEGC	Leptocarpus	349	LEGC	halimifolia
319	LEGC	Leptocarpus	350	LEGC	halimifolia
320	LEGC	Leptocarpus	351	LEGC	halimifolia
321	LEGC	Leptocarpus	352	LEGC	halimifolia
322	LEGC	Leptocarpus	353	LEGC	halimifolia
323	LEGC	Leptocarpus	354	LEGC	halimifolia
324	LEGC	Leptocarpus	355	LEGC	halimifolia

181	AMAC	ACKAPASINIS	241	TILI	Luehea
182	AMAC	ACKAPASINIS	242	LEGP	ACACIA
183	AMAC	ACKAPASINIS	243	PHYT	Gallesia
184	AMAC	ACKAPASINIS	244	PHYT	Chomelia
185	AMAC	ACKAPASINIS	245	RUBI	Chomelia
186	AMAC	ACKAPASINIS	246	VOCH	Qualea
187	AMAC	ACKAPASINIS	247	PHYT	Myrcia
188	AMAC	ACKAPASINIS	248	BIGN	Tabebuia
189	AMAC	ACKAPASINIS	249	LEGC	Leptocarpus
190	AMAC	ACKAPASINIS	250	RUBI	Chomelia
191	AMAC	ACKAPASINIS	251	RUBI	Chomelia
192	AMAC	ACKAPASINIS	252	EUPH	Alchornea
193	AMAC	ACKAPASINIS	253	EUPH	Alchornea
194	AMAC	ACKAPASINIS	254	LAUR	Ocotea
195	AMAC	ACKAPASINIS	255	LAUR	Ocotea
196	AMAC	ACKAPASINIS	256	MYRS	Myrcia
197	AMAC	ACKAPASINIS	257	RUBI	Chomelia
198	AMAC	ACKAPASINIS	258	LEGC	Leptocarpus
199	AMAC	ACKAPASINIS	259	LEGC	Leptocarpus
200	AMAC	ACKAPASINIS	260	LEGC	Leptocarpus
201	AMAC	ACKAPASINIS	261	AMAC	ACKAPASINIS
202	AMAC	ACKAPASINIS	262	AMAC	ACKAPASINIS
203	AMAC	ACKAPASINIS	263	AMAC	ACKAPASINIS
204	AMAC	ACKAPASINIS	264	AMAC	ACKAPASINIS
205	AMAC	ACKAPASINIS	265	AMAC	ACKAPASINIS
206	AMAC	ACKAPASINIS	266	AMAC	ACKAPASINIS
207	AMAC	ACKAPASINIS	267	AMAC	ACKAPASINIS
208	AMAC	ACKAPASINIS	268	AMAC	ACKAPASINIS
209	AMAC	ACKAPASINIS	269	AMAC	ACKAPASINIS
210	AMAC	ACKAPASINIS	270	AMAC	ACKAPASINIS
211	AMAC	ACKAPASINIS	271	AMAC	ACKAPASINIS
212	AMAC	ACKAPASINIS	272	AMAC	ACKAPASINIS
213	AMAC	ACKAPASINIS	273	AMAC	ACKAPASINIS
214	AMAC	ACKAPASINIS	274	AMAC	ACKAPASINIS
215	AMAC	ACKAPASINIS	275	AMAC	ACKAPASINIS
216	AMAC	ACKAPASINIS	276	AMAC	ACKAPASINIS
217	AMAC	ACKAPASINIS	277	AMAC	ACKAPASINIS
218	AMAC	ACKAPASINIS	278	AMAC	ACKAPASINIS
219	AMAC	ACKAPASINIS	279	AMAC	ACKAPASINIS
220	AMAC	ACKAPASINIS	280	AMAC	ACKAPASINIS
221	AMAC	ACKAPASINIS	281	AMAC	ACKAPASINIS
222	AMAC	ACKAPASINIS	282	AMAC	ACKAPASINIS
223	AMAC	ACKAPASINIS	283	AMAC	ACKAPASINIS
224	AMAC	ACKAPASINIS	284	AMAC	ACKAPASINIS
225	AMAC	ACKAPASINIS	285	AMAC	ACKAPASINIS
226	AMAC	ACKAPASINIS	286	AMAC	ACKAPASINIS
227	AMAC	ACKAPASINIS	287	AMAC	ACKAPASINIS
228	AMAC	ACKAPASINIS	288	AMAC	ACKAPASINIS
229	AMAC	ACKAPASINIS	289	AMAC	ACKAPASINIS
230	AMAC	ACKAPASINIS	290	AMAC	ACKAPASINIS
231	AMAC	ACKAPASINIS	291	AMAC	ACKAPASINIS
232	AMAC	ACKAPASINIS	292	AMAC	ACKAPASINIS
233	AMAC	ACKAPASINIS	293	AMAC	ACKAPASINIS
234	AMAC	ACKAPASINIS	294	AMAC	ACKAPASINIS
235	AMAC	ACKAPASINIS	295	AMAC	ACKAPASINIS
236	AMAC	ACKAPASINIS	296	AMAC	ACKAPASINIS
237	AMAC	ACKAPASINIS	297	AMAC	ACKAPASINIS
238	AMAC	ACKAPASINIS	298	AMAC	ACKAPASINIS
239	AMAC	ACKAPASINIS	299	AMAC	ACKAPASINIS
240	AMAC	ACKAPASINIS	300	AMAC	ACKAPASINIS

XXXVIII XXXIX XXXL XXXLI XXXLII XXXLIII XXXLIV XXXLV XXXLVI XXXLVII XXXLVIII XXXLIX XXXLI XXXLXI XXXLXII







A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	X	Y	Z
551	APOC	Alimanda	emycorymbus	dicolor																					
552	APOC	Aspidosperma	ruceini longinatum	ruceini longinatum																					
553	APOC	Ravollia	pacifera	pacifera																					
554	APOC	Ravollia	bertholii	bertholii																					
555	AREC	Cornelia	cericea	cericea																					
557	AREC	Syngnis	coronata	coronata																					
558	AREC	Syngnis	microphylla	microphylla																					
559	AREC	Syngnis	otracea	otracea																					
560	AREC	Syngnis	wabomani	wabomani																					
562	AREC	Syngnis	x malacome	x malacome																					
563	ASTE	Blanchetia	retrofracta	retrofracta																					
564	ASTE	Danophyllum	cardellianum	cardellianum																					
565	ASTE	Pectis	ecumpona	ecumpona																					
567	ASTE	Pectis	erugata	erugata																					
568	ASTE	Pectis	linifolia v. linifolia	linifolia v. linifolia																					
569	ASTE	Temasiphila	schizomastum	schizomastum																					
570	ASTE	Temasiphila	velutium	velutium																					
571	BIGN	Anemopaegna	argentea	argentea																					
572	BIGN	Cusidaria	caranoni	caranoni																					
573	BIGN	Goodenia	peruviana	peruviana																					
574	BIGN	Jacaranda	rostrata	rostrata																					
576	BIGN	Tanbelia	spangosa	spangosa																					
577	BIGN	Tanbelia	glaziovii	glaziovii																					
578	BOB-B	Centia	servillii	servillii																					
579	BOB-B	Erithoea	glazioviana	glazioviana																					
580	BOB-B	Erithoea	glazioviana	glazioviana																					
581	BORA	Auremia	onococlyx	onococlyx																					
582	BORA	Auremia	ardani	ardani																					
583	BORA	Cordia	florosa	florosa																					
584	BORA	Cordia	cordata	cordata																					
585	BORA	Cordia	cordata	cordata																					
586	BORA	Cordia	cordata	cordata																					
587	BORA	Palagoula	bantensis	bantensis																					
588	BRON	Actinnea	erycurymbus	erycurymbus																					
589	BRON	Actinnea	aguliga v. chrysozona	aguliga v. chrysozona																					
590	BRON	Actinnea	aguliga v. chrysozona	aguliga v. chrysozona																					
591	BRON	Bilberia	portana	portana																					
592	BRON	Bromelia	laciniosa	laciniosa																					
593	BRON	Cotemedia	florida	florida																					
594	BRON	Dyckia	distictura	distictura																					
595	BRON	Dyckia	pernamoucana	pernamoucana																					
596	BRON	Dyckia	spectabile	spectabile																					
597	BRON	Enchilium	carangae	carangae																					
598	BRON	Homburgia	variegata	variegata																					
599	BRON	Negastroyia	brasilensis	brasilensis																					
600	CACT	Acanthocereus	tabularis	tabularis																					
1002	CACT	Acynhocereus	brasilensis	brasilensis																					
1003	CACT	Arrojaba	penicillata	penicillata																					
1004	CACT	Arrojaba	montana	montana																					
1005	CACT	Arrojaba	montana	montana																					
1006	CACT	Austrocylindropuntia	parviflora	parviflora																					
1007	CACT	Austrocylindropuntia	parviflora	parviflora																					
1008	CACT	Cereus	brasilianus	brasilianus																					
1009	CACT	Dioscorea	brasilianus	brasilianus																					
1010	CACT	Dioscorea	brasilianus	brasilianus																					
1011	CACT	Dioscorea	brasilianus	brasilianus																					
1012	CACT	Eriocereus	ascendens	ascendens																					
1013	CACT	Esoxaloe	ulei	ulei																					
1014	CACT	Leocereus	bantensis	bantensis																					
1015	CACT	Leocereus	bantensis	bantensis																					
1016	CACT	Pilocactus	horridus	horridus																					
1017	CACT	Pilocactus	oreus	oreus																					
1018	CACT	Pilocactus	zoppi	zoppi																					
1019	CACT	Pycnanthemocereus	penyantius	penyantius																					
1020	CACT	Pycnanthemocereus	brasilianus	brasilianus																					
1021	CACT	Persia	stenantra	stenantra																					
1022	CACT	Persia	stenantra	stenantra																					
1023	CACT	Opuntia	inamena	inamena																					
1024	CACT	Opuntia	palmisoma	palmisoma																					
1025	CACT	Opuntia	brasilianus	brasilianus																					
1026	CACT	Pilosocereus	chrysochloris	chrysochloris																					
1027	CACT	Pilosocereus	chrysochloris	chrysochloris																					
1028	CACT	Pilosocereus	planiflorus	planiflorus																					
1029	CACT	Pilosocereus	planiflorus	planiflorus																					
1030	CACT	Pilosocereus	planiflorus	planiflorus																					
1031	CACT	Pilosocereus	zumbae	zumbae																					
1032	CACT	Stephanocereus	leucostele	leucostele																					
1033	CACT	Tachya	foveolata	foveolata																					
1034	CACT	Zinnierella	zinnierella	zinnierella																					
1035	CAPP	Capriaria	brasilianus	brasilianus																					
1037	CAPP	Haplocarpum	bantense	bantense																					
1039	CARI	Jacaranda	multiflora	multiflora																					
1039	CEL	Francoeria	brasilianus	brasilianus																					
1040	CHR	Chryseia	brasilianus	brasilianus																					
1042	CHR	Ligata	rigida	rigida																					
1043	COB-B	Cambretum	lanceolatum	lanceolatum																					
1044	COB-B	Cambretum	laevis	laevis																					
1045	COB-B	Cambretum	laevis	laevis																					
1047	COB-B	Cambretum	pisonioides	pisonioides																					
1048	COB-B	Cambretum	rubicola	rubicola																					
1049	COB-B	Thlasia	glaucoarpa	glaucoarpa																					
1050	COB-B	Thlasia	glaucoarpa	glaucoarpa																					
1051	COB-B	Thlasia	glaucoarpa	glaucoarpa																					

A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	
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1351	LEGP	Lonchocarpus	ang.
1352	LEGP	hachecium	grindifolium
1353	LEGP	hachecium	sp.
1354	LEGP	hachecium	sp.
1355	LEGP	hachecium	akermanni
1356	LEGP	hachecium	fendleri
1357	LOGA	Strychnos	comifolia
1358	MALP	Banisteria	glaberrima
1359	MALP	Banisteria	undulata
1360	MELI	Trichilia	sp.
1361	MELI	Trichilia	sp.
1362	MELI	Trichilia	sp.
1363	MORA	Ficus	sp.
1364	MYRT	Myrcia	sp.
1365	MYRT	Myrcia	sp.
1366	OCNR	Couratou	grasseardi
1367	AREC	Copernicia	lectatum
1368	AREC	Boritis	sp.
1369	LOCO	Bromelleyera	sp.
1370	POLY	Coccoloba	sp.
1371	POLY	Coccoloba	sp.
1372	RUBI	Aletris	labatiales
1373	RUBI	Genipa	canuco
1374	RUBI	Genipa	sp.
1375	RUBI	Genipa	sp.
1376	RUTA	Zanthoxylum	sincarpum
1377	SAPI	Alibuthyllum	occidentalis
1378	SAPI	Heliconia	sp.
1379	SAPI	Heliconia	sp.
1380	SOLA	Bouffalou	sp.
1381	STER	Sterculia	sp.
1382	TIL	Apelta	sp.
1383	ULNA	Celtis	sp.
1384	VERB	Virola	sp.
1385	VERB	Virola	sp.
1386	VERB	Virola	sp.
1387	ZYGO	Bumelia	sp.
1388	EUPH	Jatropha	sp.
1389	EUPH	Jatropha	sp.
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1448	EUPH	Jatropha	sp.
1449	EUPH	Jatropha	sp.
1450	EUPH	Jatropha	sp.

1451	APOC	Ravallia	ignarina
1452	APOC	Stemmadenia	graciflora
1453	LOCC	Cesalonia	pucata
1454	LOCC	Cesalonia	sp.
1455	ERTT	Erythronium	bazense
1456	ASTE	Lycoseris	croata
1457	OCNH	Oreata	gulfengii
1458	VERB	Virola	sp.
1459	VERB	Virola	sp.
1460	SOLA	Castum	alternifolium
1461	BIGN	Arrabida	molissima
1462	BIGN	Anemopaegna	eribolatum
1463	BIGN	Xylocarpus	curatium
1464	BIGN	Xylocarpus	sp.
1465	BIGN	Xylocarpus	semomaha
1466	MALP	Heterosterys	ferrosa
1467	MALP	Heterosterys	membrifolia
1468	MALP	Heterosterys	sp.
1469	ASCL	Harcenia	trichoma
1470	ASCL	Harcenia	maritima
1471	ANAC	Leopoldtergium	huasango
1472	RHUT	Ziziphus	sp.
1473	RHUT	Ziziphus	sp.
1474	THEO	Jacquinia	sp.
1475	THEO	Chevis	sp.
1476	CACT	Armatocereus	sp.
1477	CACT	Opuntia	sp.
1478	CACT	Opuntia	sp.
1479	LECC	Senna	reticulata
1480	LECC	Senna	sp.
1481	LECC	Senna	sp.
1482	LECC	Senna	sp.
1483	LECC	Senna	sp.
1484	LECC	Senna	sp.
1485	LECC	Senna	sp.
1486	LECC	Senna	sp.
1487	LECC	Senna	sp.
1488	LECC	Senna	sp.
1489	LECC	Senna	sp.
1490	LECC	Senna	sp.
1491	VERB	Lantana	sp.
1492	CAPP	Capparis	sp.
1493	CAPP	Capparis	sp.
1494	CAPP	Capparis	sp.
1495	ANAC	Sonchella	sp.
1496	ANAC	Anacardium	occidentale
1497	APOC	Ravallia	heterophylla
1498	APOC	Ravallia	sp.
1499	ARAL	Notobanana	sp.
1500	CARI	Carica	parviflora
1501	STER	Waltheria	ovata
1502	ASTE	Weinella	sp.
1503	ASTE	Weinella	sp.
1504	BORB	Eriotheca	platanifolia
1505	BORB	Eriotheca	sp.
1506	BORB	Eriotheca	sp.
1507	BORB	Eriotheca	sp.
1508	BORB	Eriotheca	sp.
1509	BIGN	Tronra	sp.
1510	AOHA	Anacardium	sp.
1511	ANNO	Annona	sp.
1512	ANNO	Guatteria	sp.
1513	ANNO	Guatteria	sp.
1514	ANNO	Xilopha	sp.
1515	APOC	Aspidosperma	microcarpum
1516	APOC	Hacoma	pubescens
1517	OCU	Illex	canocarpa
1518	OCU	Illex	sp.
1519	AREC	Stygnus	fraxosa
1520	AREC	Bala	sp.
1521	BORB	Eriotheca	pubescens
1522	BORB	Eriotheca	longitrum
1523	BORB	Eriotheca	sp.
1524	CARY	Caryocarpus	brasilianus
1525	CELA	Austroplancha	poqueia
1526	CELA	Chelidonium	capatum
1527	CELA	Shacca	crassifolia
1528	CHRY	Chrysantherum	sp.
1529	CHRY	Chrysantherum	sp.
1530	CHRY	Chrysantherum	sp.
1531	CLUS	Kilmeyera	hamilis
1532	CLUS	Kilmeyera	sp.
1533	CLUS	Kilmeyera	sp.
1534	ASTE	Eremanthus	sp.
1535	ASTE	Eremanthus	glaucozoides
1536	ASTE	Guennalia	sp.
1537	ASTE	Pilocarpus	reunifolia
1538	CONK	Conarus	sp.
1539	CONK	Conarus	sp.
1540	CONK	Conarus	sp.
1541	DILL	Davilla	sp.
1542	EBEN	Dioporus	barbelli
1543	EBEN	Dioporus	sp.
1544	ERYT	Erythronium	terreum
1545	FLAC	Caesaria	graciflora
1546	FLAC	Emmulum	sp.
1547	LAUR	Ocotea	sp.
1548	LAUR	Ocotea	sp.
1549	LECC	Dimorphantha	sp.
1550	LECC	Hymantha	sp.





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1751	CHRY	Coubeia	obovata	amazonicus																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																			
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**TABLE 6.3: Phytosociological analysis of the main South American Seasonal Forests. Generic level.**

Column A- The Monte province, Argentina (*sensu* Morello, 1958:145-50).

B- Chaco s.s.: Sierra Chaco, Argentina (Sayago, 1969, p.224).

C- Chaco s.s.: the lowland Chaco in its Eastern, Central and Western districts, Argentina. Floristic list from Sect. 4.1, excluded the species exclusive to the Sierra Chaco.

D- Austro-Brazilian Transitional Forest, Argentina (see Sect. 2.3.3.a). Floristic list from Lewis & Pire, 1981, and author's field experience; also Morello et al., 1971, Morello & Adámoli, 1974, and Cabrera, 1976.

E- 'Selva de Ribera', Argentina (Prado et al., in press a; Morello & Adámoli, 1974).

F- Gallery Forest, Argentina (Franceschi & Lewis, 1979)

G- Upper Uruguay River Valley Forests, Santa Catarina and Rio Grande do Sul, Brazil (Klein, 1972; Rambo, 1980).

H- Planalto Forest, Vassununga & Bauru, São Paulo, Brazil (Martins, 1979, pp 108-9; Cavassan et al., 1984).

I- Subandean Piedmont Forests, in both its 'Palo blanco' and 'Tipa-Pacará' variants. Floristic list taken from Sect. 4.3.

J- The Caatingas province, Brazil. Floristic list: Sect. 4.2.

K- Calcareous woodlands, Mato Grosso do Sul, Brazil (Ratter et al., 1988b, p.516; Prado et al., in press b).

L- Calcareous forest of Januária, MG, Brazil (Ratter et al., 1978).

M- Dry Caribbean vegetation of Venezuela. The floristic list is an aggregate of Aristeguieta's (1968) "selva veranera" (summer-green forest) and semiarid scrublands (Matteucci & Colma, 1982, pp 102-4).

N- Dry Caribbean vegetation of Colombia (Dugand, 1970, pp 428-31; Rieger, 1976, pp 40-1).

O- Dry forests, woodlands and savannas of W Ecuador, as in Acosta-Solís (1966, pp 413-5) and Harling (1979).

P- Cerrado and cerrado in Brasília, Federal District (Ratter, 1986; P.E. Oliveira, pers. comm.).

Q- Atlantic rainforest, Ubatuba, SP, Brazil (Silva & Leitão F<sup>o</sup>, 1982).

R- Amazon forest, km 30 on the road Manaus-Itacoatiara, Amazonas, Brazil (Prance et al., 1976, pp 28-35).













## 7. THE ZOOLOGICAL EVIDENCE

### 7.1- The avian evidence:

The strongest evidence which apparently supports the alleged biogeographical link between the Chaco and the Caatingas has come from the zoological field. In a landmark paper, Short (1975) analyzed the Chaco avifauna, and based on what he regarded as a "markedly low endemism" and "the very close affinities with surrounding avifaunas" concluded that "the 'chaco avifauna' [is] a nonentity, the term being useful only in a strictly distributional context" (Short, *op. cit.*, p.329). All other biogeographical areas of South America – divided in two groups: regions adjacent to and regions distant from the Chaco – were compared to his bird species list. Five out of the six neighbouring regions showed very high numbers of common species with the Chaco (e.g. 311 bird taxa in common with the Cerrados), whereas amongst the distant regions the Caatingas proved to have the strongest link: 248 species. The elevated figures of common species between the Chaco and the distant Caatingas attracted the attention of biogeographers (Cabrera & Willink, 1980; Bucher, 1982a; Haffer, 1985) and has seemed to give solid support to the Chaco-Caatingas link. However, an attempt will be made here to analyze in closer detail the component distribution of the bird species discussed by Short (1975).

At the outset, it is important to note that Short's concept of the Chaco differs from that employed by various authorities, and also that used in the present study (as discussed in Ch. 2 & 8). Short (1975, Fig.1) shows an area latitudinally wider and meridianally shorter than that of the actual Chaco according to most authors. He included within it not only the whole of the Eastern Chaco (whose phytogeographical identity is under discussion here), but also a good deal of Paraguay east of the Chaco region which can hardly be considered as part of it. The western sector of the Pantanal is apparently also shown as Chaco in Short's map, an area with little real contact with true Chaco vegetation (Prado et al., in press, b). To the south of the region, Short omitted a considerable area which is the southwestern tip of the Chaco, comprising NW Córdoba, E La Rioja and N San Luis (compare with Ragonese & Castiglioni's [1970] map of the Argentine Chaco). Thus, a lot of tropical and subtropical wetter areas in the north and east of the region were added to the core

area of the Chaco, together with their avifaunas, while the temperate and very dry sectors in the south and very particularly the southwest were excluded by Short.

As a result of these peculiar geographical limits set by Short (1975) the Chaco avifauna was bound to be a 'nonentity'. A good deal of tropical birds of more humid areas elsewhere in South America were encompassed within the 409 list of species for the Chaco provided by Short, which was in sharp contrast with the 220 species listed by Olrog (1963a) for the Argentine Chaco. This latter figure seems much more realistic, given the low environmental diversity in the region, even allowing for an increase in the number of species when the Bolivian and Paraguayan Chaco are included to make it comparable to Short's study. Thus, a number of elements alien to the Chaco *s.s.* were included in the list, which in fact only occur marginally in definitely non-chaquenian areas such as the Pantanal (Mato Grosso do Sul), E Paraguay or along the major river systems bordering the Chaco such as the Paraguay and Paraná watercourses. The addition of such species diminished the relevance of the authentic chaquenian elements, a fact already noted by Müller (1973, p.143), while conversely this increase of elements coming from more humid areas did not incorporate any new endemics to the Chaco *sensu* Short. In Short's view, there is only one endemic species (*Eudromia formosa*), and three endemic subspecies in the Chaco. However, if the missing SW chaquenian sector is added, the region recovers its biogeographical homogeneity since it is a well-defined natural area with concrete and characteristic environmental features (see Ch. 2), and several Chaco bird species can be once again regarded as endemisms.

In Table 7.1 the endemic birds of the Chaco are listed; the source of this information comes mainly from Short (1975), both his maps and comments on the range of distribution, cross-checked with Cory & Hellmayr (1924), Olrog (1963a & b), Vaurie (1964 & 1980), Meyer de Schauensee (1966), Short (1971 & 1976), Müller (1973), and Haffer (1985). On this basis, the Chaco biogeographical region comprises one endemic monotypic genus (*Chunga*), seven endemic species and at least four endemic subspecies in its avian fauna, so that it can be considered a well-defined faunal dispersal centre (*sensu* Müller, 1973). It should be

**TABLE 7.1: Birds endemic to the Chaco.**

	Taxon endemic
<b>RHEIDAE</b>	
<i>Rhea americana araneipes</i>	subsp
<b>TINAMIDAE</b>	
<i>Nothura maculosa chacoensis</i>	subsp
<i>Nothura maculosa pallida</i>	subsp
<i>Nothura maculosa paludivaga</i>	subsp
<i>Eudromia formosa</i>	sp
<b>CRACIDAE</b>	
<i>Ortallis canicollis</i>	sp
<b>CARIAMIDAE</b>	
<i>Chunga burmeisteri</i>	genus
<b>PICIDAE</b>	
<i>Dryocopus schulzi</i>	sp
<b>FURNARIIDAE</b>	
<i>Furnarius cristatus</i>	sp
<b>TYRANNIDAE</b>	
<i>Pseudocolopteryx dillenianus</i>	sp
<b>EMBERIZIDAE</b>	
<i>Lophospingus pusillus</i>	sp

pointed out that this list (Table 7.1) and the subsequent one (Table 7.2), do not pretend to be exhaustive at the **subspecific** level but simply aim to record the most outstanding forms of otherwise widespread species.

The Caatingas are richer in avian endemisms as Table 7.2 shows, which must be essentially due to their far greater environmental diversity in comparison with the Chaco plains (cf. Ch. 2 & 4). This table is derived from careful study of the information provided principally in Hellmayr (1929) and Meyer de Schauensee (1966), but also Cory & Hellmayr (1924), Naumburg (1939), Müller (1973), Coelho (1978), Vaurie (1980), Haffer (1985), Leite (1987) and Silva (1989). There are three monotypic genera endemic to the Caatingas (*Cyanopsitta*, *Megaxenops* and *Rhopornis*), and ten endemic species and at least ten subspecies. The number of endemic genera could be doubled if those presently submerged in synonymy *Nyctipolus* (= *Caprimulgus*), *Anopetia* (= *Phaethornis*) and *Gyalophylax* (= *Synallaxis*) genera were accepted as distinct.

There are considerable differences, not only quantitative but also qualitative, between the endemic taxa to the Chaco and to the Caatingas. The Chaco is richer in elements of southerly origin, such as the very important family Tinamidae. For instance, the genus *Nothura* reaches its highest diversity in the region, and this is essentially a Patagonian-Andean-Pampean-Chaquenian genus barely extending into the Caatingas (Short, 1975), while the genus *Eudromia* does not even reach the Pantanal. In contrast, the genus *Crypturellus* in the same family is basically tropical-Amazonian, with several species in the Caatingas and only one species widespread throughout the Chaco (*C. tataupa tataupa*) where the genus finds its southernmost expansion. In the Caatingas the families with an outstanding degree of endemism are the Psittacidae, Furnariidae and very specially the Formicariidae, which contrarywise, show scarce or no endemism in the Chaco.

It should also be emphasized that between the endemics of both areas there are no cases of very close relatives, with one endemic in either formation and none elsewhere, and likewise no pairs of congeneric, endemic species which would indicate a very strong link. An apparent exception, the case of the caatinga endemic subspecies of

**TABLE 7.2: Birds endemic to the Caatingas.**

	Taxon endemic
<b>TINAMIDAE</b>	
<i>Crypturellus noctivagus zabele</i>	subsp
<i>Nothura maculosa cearensis</i>	subsp
<b>CRACIDAE</b>	
<i>Penelope jacucaca</i>	sp
<b>COLUMBIDAE</b>	
<i>Columba picazuro marginalis</i>	subsp
<b>PSITTACIDAE</b>	
<i>Anodorhynchus leari</i>	sp
<i>Aratinga cactorum cactorum</i>	subsp
<i>Cyanopsitta spixii</i>	genus
<b>CAPRIMULGIDAE</b>	
<i>Caprimulgus (=Nyctipolus) hirundinaceus</i>	sp (genus)
<b>TROCHILIDAE</b>	
<i>Phaethornis (=Anopetia) gounellei</i>	sp (genus)
<b>PICIDAE</b>	
<i>Picummus limae</i>	sp
<b>DENDROCOLAPTIDAE</b>	
<i>Lepidocolaptes squamatus wagleri</i>	subsp
<i>Xiphocolaptes falcirostris</i>	sp
<b>FURNARIIDAE</b>	
<i>Megaxenops parnaguae</i>	genus
<i>Synallaxis (=Gyalophylax) hellmayri</i>	sp (genus)
<b>FORMICARIIDAE</b>	
<i>Formicivora iheringi</i>	sp
<i>Rhopornis ardesiaca</i>	genus
<i>Sakesphorus cristatus</i>	sp
<i>Thamnophilus caerulescens cearensis</i>	subsp
<b>CONOPOPHAGIDAE</b>	
<i>Conopophaga lineata cearae</i>	subsp
<b>TYRANNIDAE</b>	
<i>Idioptilon mirandae mirandae</i>	subsp
<i>Phyllomyias fasciatus cearae</i>	subsp
<i>Phylloscartes roquettei</i>	sp
<b>TROGLODYTIDAE</b>	
<i>Thryothorus longirostris bahiae</i>	subsp

*Nothura maculosa*, is in fact negligible since this species is widespread in southern South America (see Short, 1975, Fig. 16). Short (1975, Fig. 15) indicates the contrary when he mapped the ranges of distribution of both *Nothura boraquira* and *Myrmorchilus strigilatus* with two disjunct nuclei in the Caatingas and northern Chaco. However, the ranges of these species need to be analyzed in detail, as below.

## 7.2- Avian patterns of distribution:

In his study Short (1975, p. 337) listed 16 species as disjuncts between the Chaco and the Caatingas (Table 7.3). None of them occur exclusively in the Chaco and the Caatingas and nowhere else; on the contrary, all of them can be found in at least one other biogeographical natural zone (generally neighbouring areas to either of them), and some do not occur in the Chaco s.s. at all. The first listed species is *Nothura boraquira* (Tinamidae). In Fig. 7.1 all known localities for this species are shown (Conover, 1950; Short, 1975 & 1976). It is evidently a true caatinga bird, extending even to a locality in Maranhão very close (a few kilometers away) to those indicated by Bigarella et al. (1975) as disjunctions of the Caatingas vegetation in that state. This Tinamidae then reappears in Santa Cruz de la Sierra and Chiquitos areas in Bolivia, close to but out of bounds of the Chaco, and finally there is a group of collections in the more humid Eastern Chaco in Paraguay. Closely following the distribution of *Nothura boraquira* is the Furnariidae *Pseudoseisura cristata* (Fig. 7.2), with the nominate<sup>1</sup> subspecies in the Caatingas, and *P. cristata unirufa* spreading along the upper Paraguay river in SW Brazil and Paraguay, and across E Bolivia to Santa Cruz and El Beni.

A very similar pattern of distribution is followed by *Myrmorchilus strigilatus* (Fig. 7.3), again a true caatinga species with disjunctions in the area usually regarded as Eastern Chaco on the western bank of the river Paraguay, from Urucum (a calcareous hill close to Corumbá in Mato Grosso do Sul) to the river Bermejo in the Formosa province, Argentina. To the west of the Chaco this Formicariidae is restricted to the Subandean Piedmont Forests from Santa Cruz in Bolivia to eastern Jujuy in Argentina (Cory & Hellmayr,

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<sup>1</sup> The term "nominate" in Zoology equates to "typical" as employed in plant systematics.

**TABLE 7.3: Alleged Chaco–Caatingas disjuncts (Short, 1975).**

## TINAMIDAE

*Nothura boraquira*

## RALLIDAE

*Aramides ypecaha**Porzana albicollis*

## COLUMBIDAE

*Columba picazuro*

## PSITTACIDAE

*Aratinga acuticauda*

## CUCULIDAE

*Coccyzus cinereus*

## STRIGIDAE

*Glaucidium minutissimum*

## FURNARIIDAE

*Synallaxis (=Schoeniophylax) phryganophila**Pseudoseisura cristata*

## FORMICARIIDAE

*Myrmorchilus strigilatus*

## COTINGIDAE

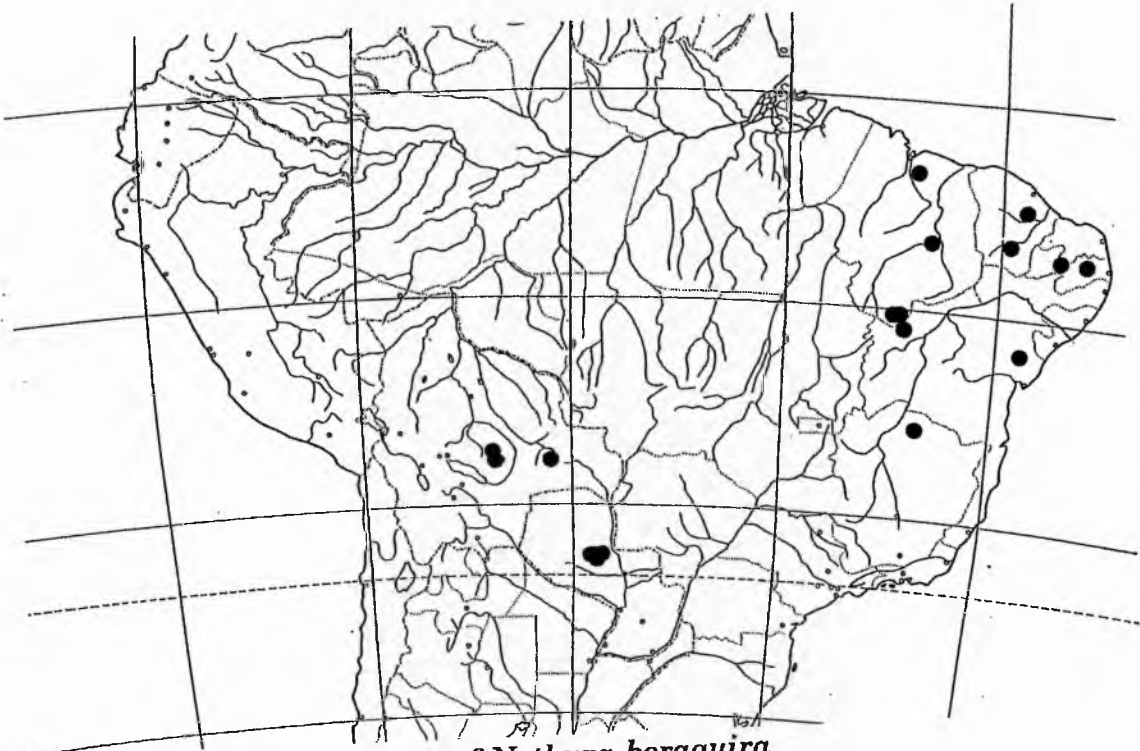
*Xenopsaris albinucha*

## TYRANNIDAE

*Xolmis irupero**Stigmatura budytoides*

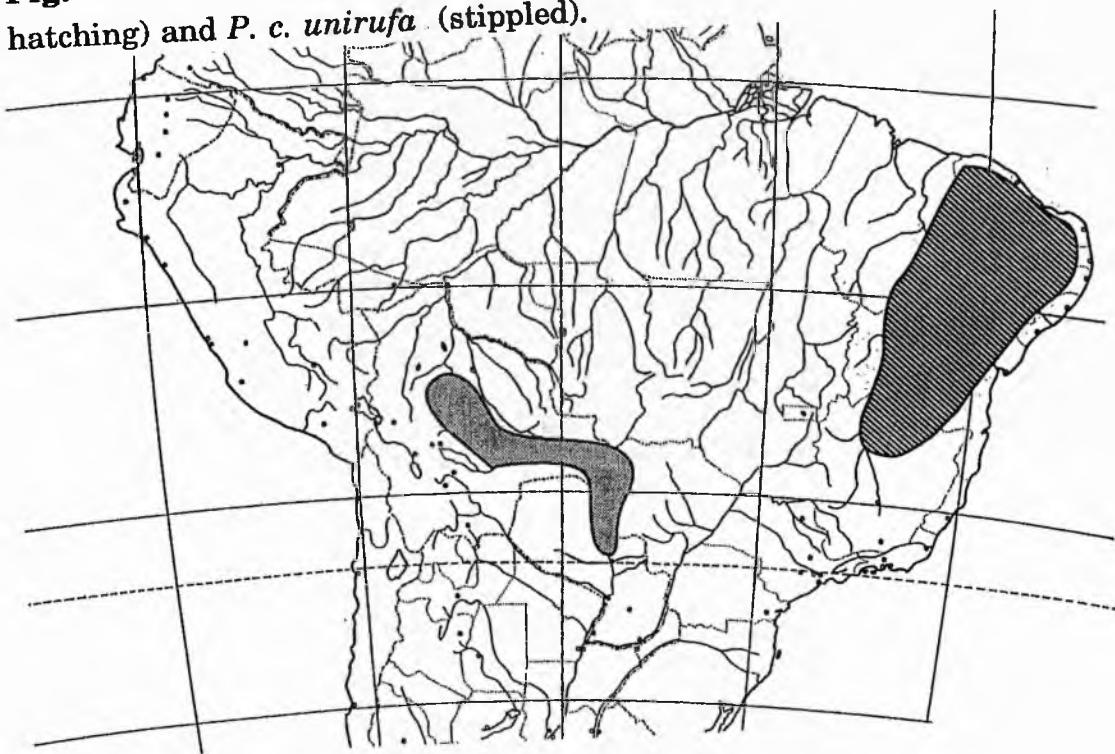
## ICTERIDAE

*Molothrus badius**Icterus icterus*



**Fig. 7.1:** Distribution map of *Nothura boraquira*.

**Fig. 7.2:** Distribution map of *Pseudoseisura cristata cristata* (oblique hatching) and *P. c. unirufa* (stippled).





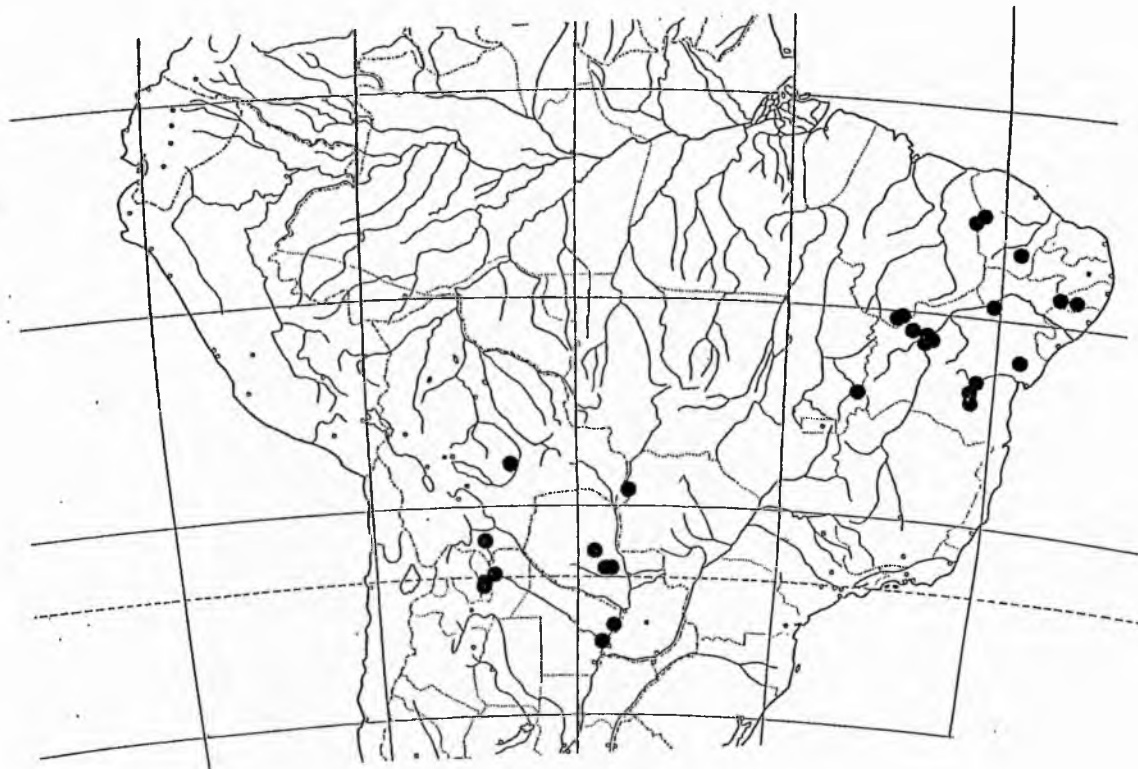


Fig. 7.3: Distribution map of *Myrmorchilus strigilatus* .

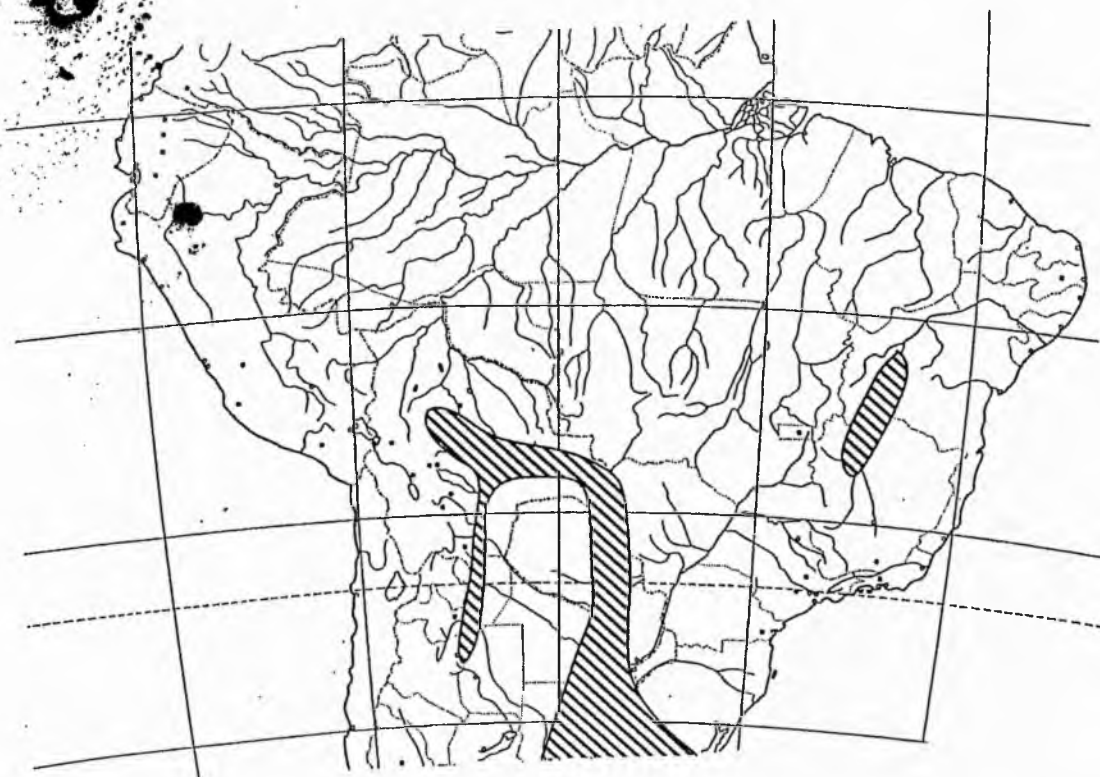
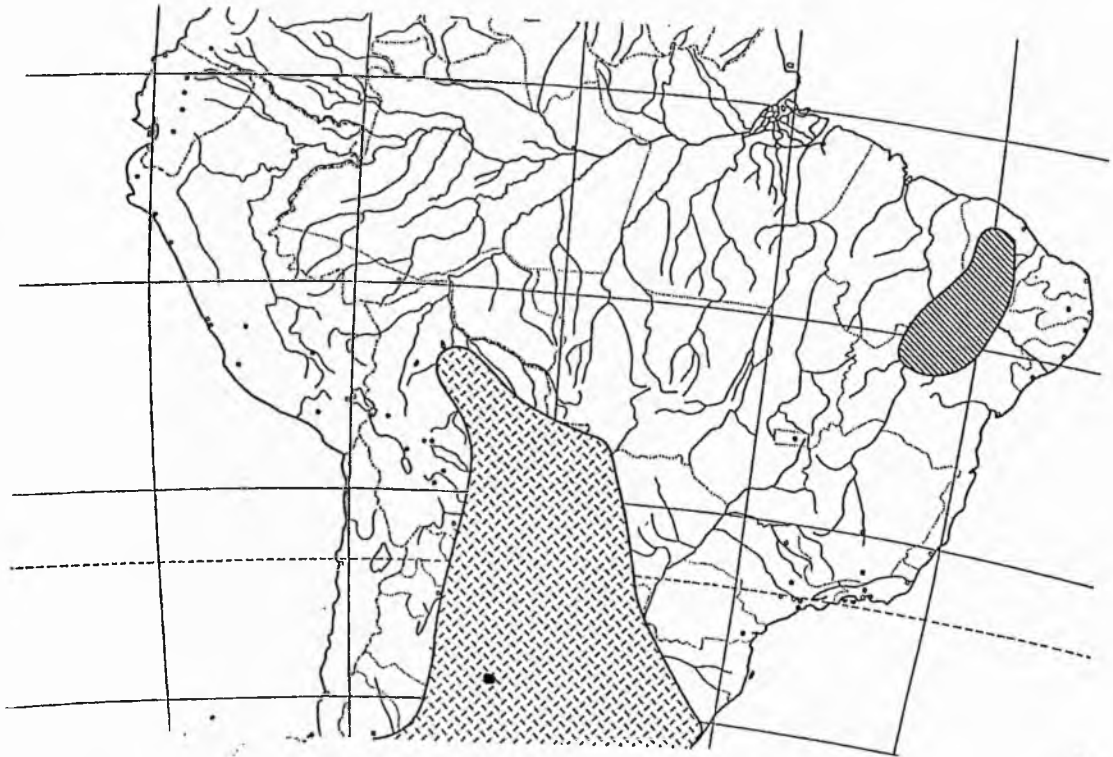


Fig. 7.4: Distribution map of *Synallaxis [Schoeniophylax] phryganophila*.

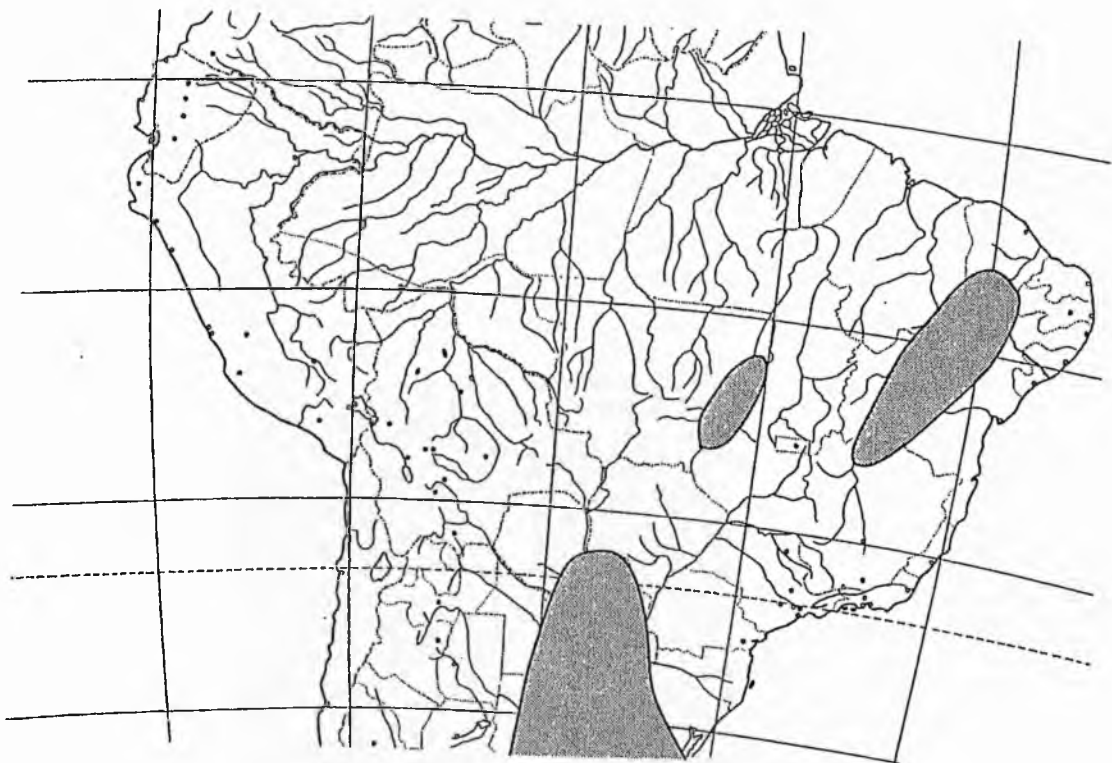
1924; Naumburg, 1939). Thus both *Nothura boraquira* and *Myrmorchilus strigilatus* leave in fact a huge blank in their range of distribution in between two N-S orientated arms. This blank corresponds to the main bulk of the Chaco s.s. , contrary to Short's map in his Fig. 15.

Another such a case is the Furnariidae *Synallaxis phryganophila* (Fig. 7.4), previously considered a monotypic genus, *Schoeniophylax* , but later submerged into *Synallaxis* by Vaurie (1980), though still as the only monotypic subgenus. The present author has been unable to trace itemized lists of localities for this species, but its distribution can be reconstructed from Olrog (1963a), Meyer de Schauensee (1966), Short (1975) and Vaurie (1980). This bird shows again a blank for the area occupied by the Chaco, surrounding it from west, north and east, and with an additional expansion of range to the Argentine Mesopotamia, Rio Grande do Sul in Brazil, and Uruguay. On the other hand, it occupies a reduced sector in the middle São Francisco river within the Caatingas. It is reported in the literature (Vaurie, 1980) that it can reach the Santiago del Estero province in Argentina, but owing to the nature of its general pattern of distribution (highly coincidental with the Pleistocenic Arc, see Sect. 5.3.1) it is likely to appear there only in upland areas such as those in the west of the province or some isolated low-altitude hills in the extreme northwest, e.g. Cerro del Remate.

There is another group of species, amongst those listed by Short (1975) as Chaco-Caatingas disjuncts, which are certainly Chaco avian elements, and which do also occur in the Caatingas. However, they are not restricted to the Chaco area itself but spread widely on to neighbouring and distant formations. This is the case of the Tyranniidae *Xolmis irupero* (Fig. 7.5), with a geographical race *nivea* in the central dry area of the Caatingas (Short, 1975; Fitzpatrick, 1980), whilst the nominate form occurs in the Beni department in Bolivia (Cabot et al., 1986) south to SE Bolivia, SW Mato Grosso do Sul in Brazil, practically all of Paraguay, the dry subtropical forests in the Subandean piedmont, the Chaco-Pampean plains and Mesopotamia in Argentina, the Uruguay Republic and adjoining Rio Grande do Sul in SE Brazil, extending west into San Juan and Mendoza at the foothills of the Andes.



**Fig. 7.5:** Distribution map of *Xolmis irupero irupero* (race *nivea* in oblique hatching).



**Fig. 7.6:** Distribution map of *Aramides ypecaha*.

The disjunction in this species is obviously much wider than simply a Chaco-Caatingas one, but it includes the Moxos savannas in NE Bolivia, subtropical rainforests in E Paraguay, Misiones and Rio Grande do Sul, the treeless Pampas and the semidesert of the Monte in W Argentina.

Other cases reported by Short as Chaco-Caatingas disjuncts but which in fact are similarly more widespread are: *Columba picazuro* (Columbidae), isolated in Caatingas and spreading throughout the Subandean piedmont, Chaco and Pampas, the Paraguay-Paraná river system, and occasionally reaching N Patagonia (Olrog, 1963a); *Aratinga acuticauda* (Psittacidae), occurring in N Colombia and Venezuela, disjunct in the Caatingas, and then reappearing in the Subandean piedmont, Chaco, Argentine Mesopotamia, Pampas and Espinal; the Tyranniidae *Stigmatura budytoides* occurs in the Caatingas in isolation (Short, 1975; Fitzpatrick, 1980), but then is distributed mainly in W Argentina from the Rio Negro province in Patagonia, throughout the Monte and the Subandean piedmont in Argentina and Bolivia (Tarija, Santa Cruz de la Sierra), and apparently also extends into dry Andean valleys in Cochabamba and Chuquisaca, and barely reaches the Chaco in its SW sector; *Molothrus badius* (Icteridae) is the most widespread species of this set of cases, with isolated populations in the Caatingas but with a continuous distribution from central Bolivia and Mato Grosso in the Pantanal, throughout Paraguay, the Paraguay-Paraná river system, the dry forests in the Subandean piedmont (Vuilleumier, 1986), Chaco, Pampas and Monte to Rio Grande do Sul and Uruguay, being sometimes accidental in Chile across the Andes.

A different case is posed by the cuckoo *Coccyzus cinereus* (Cuculidae) which should be considered as a Chaco-dry Caribbean area disjunct as shown in Short's map of Fig. 29, while its presence in the Caatingas remains unproven. This cuckoo has been reported as an accidental migrant in the São Francisco river in Bahia and also in Goiás (Meyer de Schauensee, 1966), but it is not listed for the Caatingas or Goiás by Hellmayr (1929), Coelho (1978), Leite (1987) or Silva (1989). It is a widespread species not only in the Chaco but also in NW Bolivia (Cabot et al., 1986), E Paraguay, Argentine Mesopotamia, the Pampas and to the west into the Monte and the Subandean piedmont (Short, 1975). Also different is the range of distribution of the Aramididae *Aramides ypecaha*

(Fig. 7.6), disjunct in NE Brazil (Bahia, Piauí, etc.), E Mato Grosso, and then from E Paraguay and Misiones south to Buenos Aires following the major water-systems (Paraguay, Paraná and Uruguay rivers), and east to Rio Grande do Sul and Uruguay. Within the Chaco this wood-rail is confined to the Eastern Chaco, whose phytogeographical position will be discussed later.

The remaining five species of the 16 alleged disjuncts listed by Short (1975) share a common factor: they are completely or nearly completely absent from the Chaco *s.s.* . The Rallidae *Porzana albicollis* shows a very exciting range (Fig. 7.7), following the Tropical and Subtropical Seasonal Forests Pattern described in Sect. 5.3.2.. It occurs in the dry Caribbean coast of Colombia and Venezuela, dry interandean valleys in SW Colombia, some parts of the Orinoco river valley and in the Guianas. The collections from around Obidos and Santarem in the Amazon valley are noteworthy, since this is an area where some caatinga tree species have been collected as well. There seems to be a continuous distribution from central Caatingas to Minas Gerais and São Paulo, to then reappear in the Paraguay-Paraná river system involving much of E Paraguay, Misiones and NW Corrientes. Finally, whilst being absent from the Chaco, it is reported for the deciduous forests in NW Argentina and central Bolivia from Santa Cruz de la Sierra to La Paz.

To some extent the Strigidae *Glaucidium minutissimum* overlaps the previous pattern of distribution, spreading from Mexico and Panamá to NW Colombia, with an Amazonian nucleus in Guyana and adjoining Roraima, Amapá and Pará in Brazil, occurring in the Caatingas of Bahia and with disjunct populations in Mato Grosso and NE Paraguay, but not recorded for the Chaco. The Cotingidae *Xenopsaris albinucha minor* (Fig. 7.8) occurs in two apparently isolated areas in Venezuela, whereas the nominate form is known from the Caatingas, and also disjunct populations along the Paraguay-Paraná river valleys, in the Córdoba hills and the Subandean Piedmont Forests in NW Argentina, and in El Beni in Bolivia. This distribution clearly contradicts Short's map (1975, Fig. 45) in which he showed *X. albinucha albinucha* covering the whole of the Chaco. The map of Fig. 7.8 follows Olrog (1963a, p. 23) who cites this cotingidae for both subtropical areas on

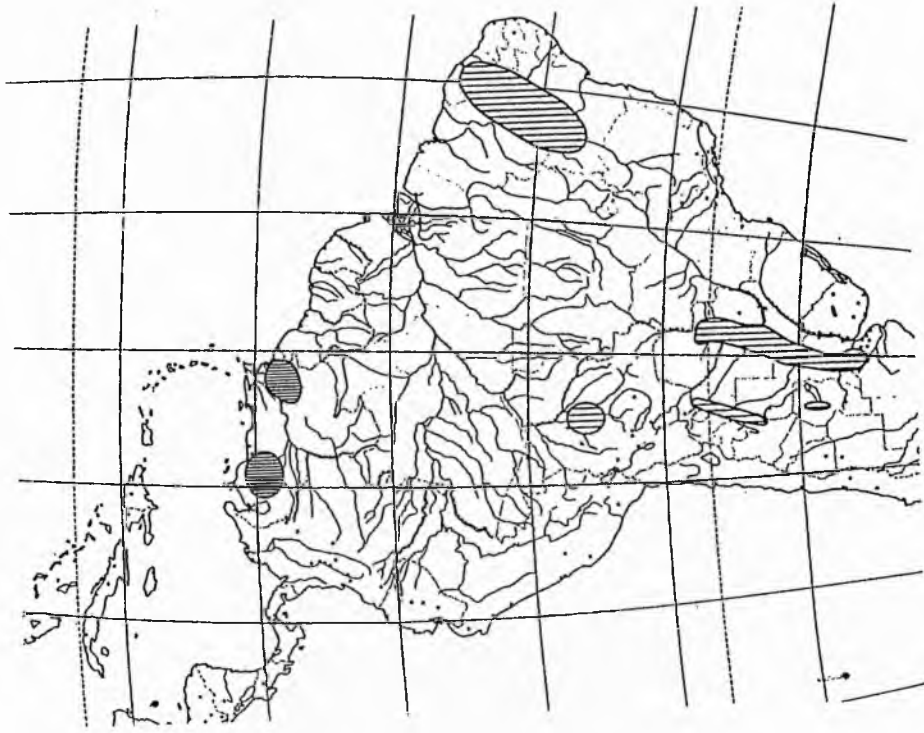


Fig. 7.8: Distribution map of *Xenopsaris albinucha* race *albinucha* (race *minor* : more heavily lined area).

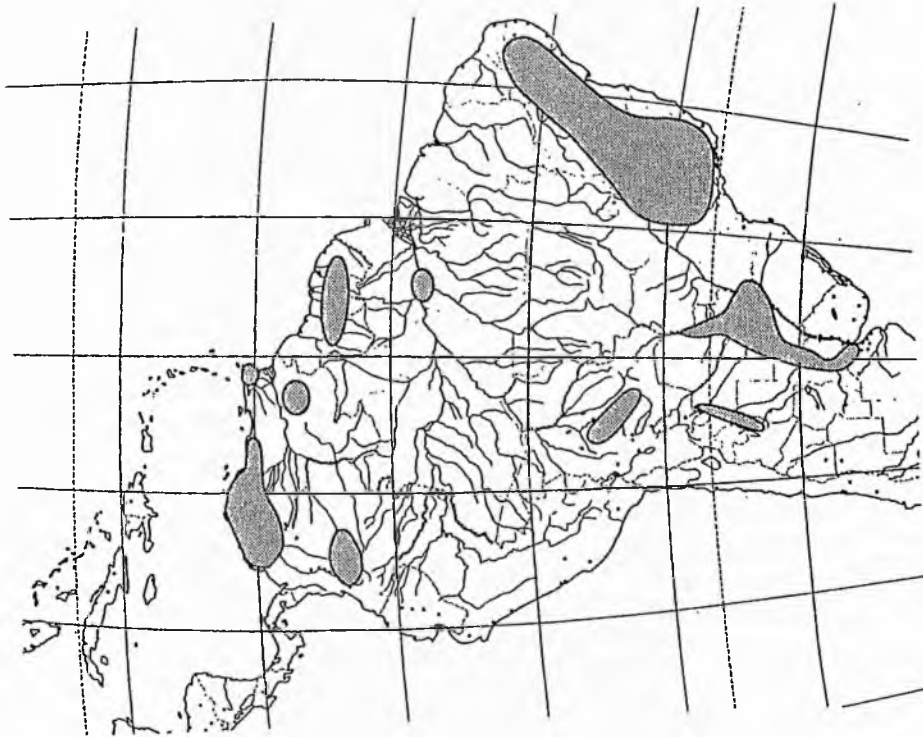
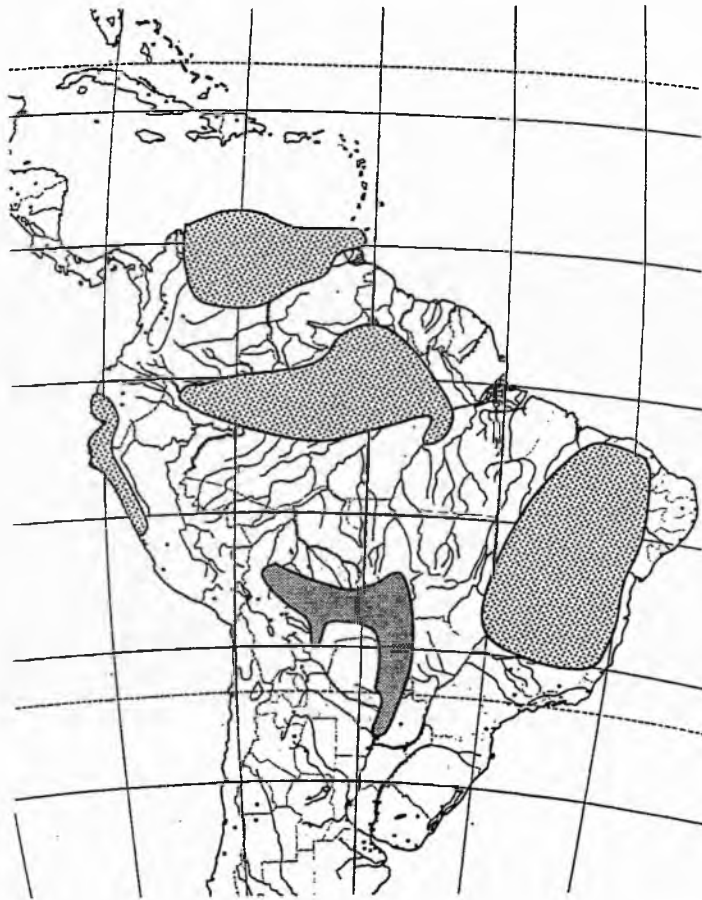


Fig. 7.7: Distribution map of *Porzana albicollis*.

the east and west of the Chaco, but not for the Chaco itself (Olrog, 1963a, p. 28-29). Finally, the Icteridae *Icterus icterus* (Fig. 7.9) has a distribution similar to that of *Porzana albicollis* (see Fig. 7.7), but it is much more widespread in the central Amazon, the Caatingas and part of the Cerrados, and it occurs in SW Ecuador and NW Peru, from where *P. albicollis* is absent. *Icterus icterus* is not entirely absent from the Chaco since Short (1976) found collections from the Eastern Chaco in Lichtenau, Paraguay.

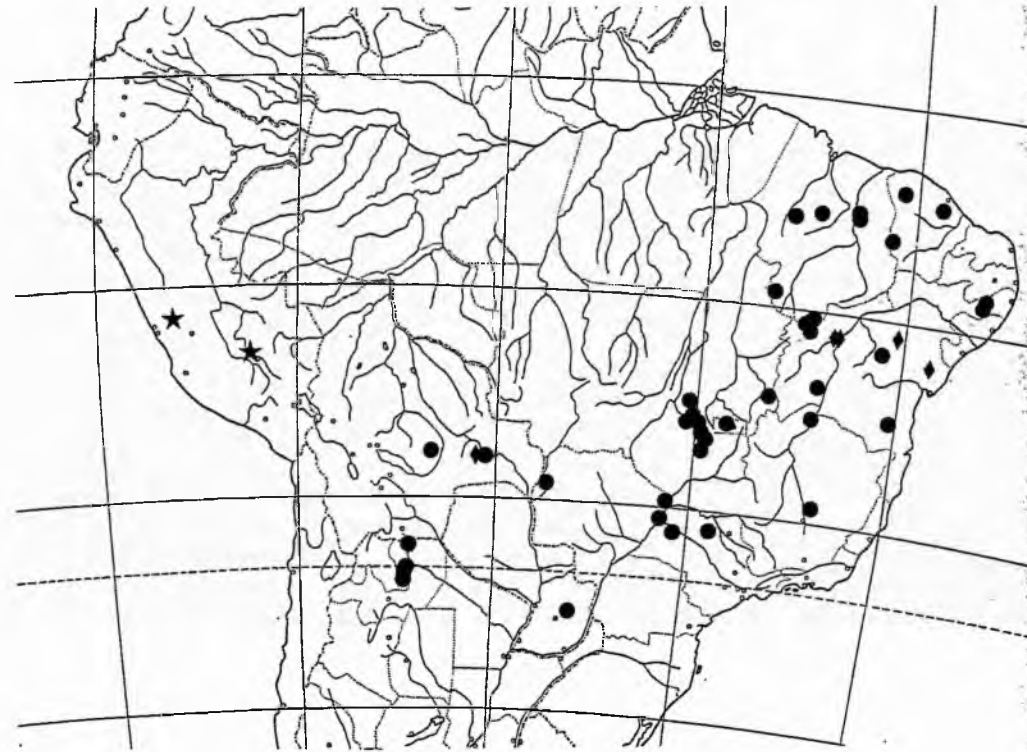
A number of other bird species which are listed in the 409 'Chaco' species by Short (1975) do not occur within the Chaco *s.s.* or only marginally in certain parts of Eastern Chaco. Some of these birds in fact follow a distribution range which resembles that of some of the typical caatinga tree species. One such example is the range of *Herpsilochmus pileatus* (Fig. 7.10), of which the typical form is essentially a Caatinga element (Hellmayr, 1929) with a disjunct collection in the area of Chiquitos, Bolivia (Olrog, 1963b). The subspecies *H. pileatus atricapillus*, also basically a Caatingas bird where it is sympatric to the nominate form, spreads further west into Maranhão in perhaps deciduous formations related to the 'sertão', south to the Planalto in Minas Gerais and São Paulo, and southwest in calcareous mesophilous forests in Goiás and Federal District (Silva, 1989). Further west it reaches the Corumbá area and E Paraguay, and also extends to the Serranías of Chiquitos, Santa Cruz de la Sierra, and the deciduous forests in the Subandean piedmont in NW Argentina. The Urubamba and Marañón valleys in Peru comprise the few known collections of the subspecies *H. pileatus motacilloides* (Cory & Hellmayr, 1924). There is thus a conspicuous similarity between the pattern of distribution of the polytypic Formicariidae *Herpsilochmus pileatus* and some woody species such as *Anadenanthera colubrina* var. *cebil*, *Astronium urundeuva* or *Pterogyne nitens*, outstanding members of what is called here Residual Pleistocenic Seasonal Formations Arc (see Sect. 5.3.1).

The whole of the genus *Melanopareia* in the Rhinocryptidae seems to have this distribution (Fig. 7.11), in which case it would be endemic to the Pleistocenic Arc. The nominate form of *Melanopareia torquata* covers a rather reduced sector of the caatingas, while the subspecies *rufescens* and *bitorquata* link NE Brazil to the Planalto in



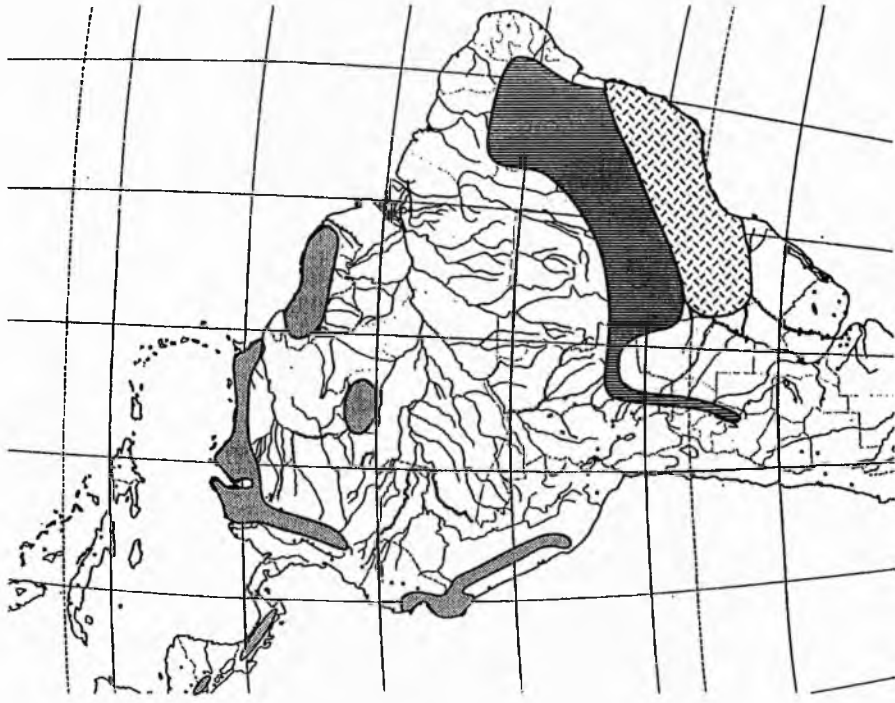
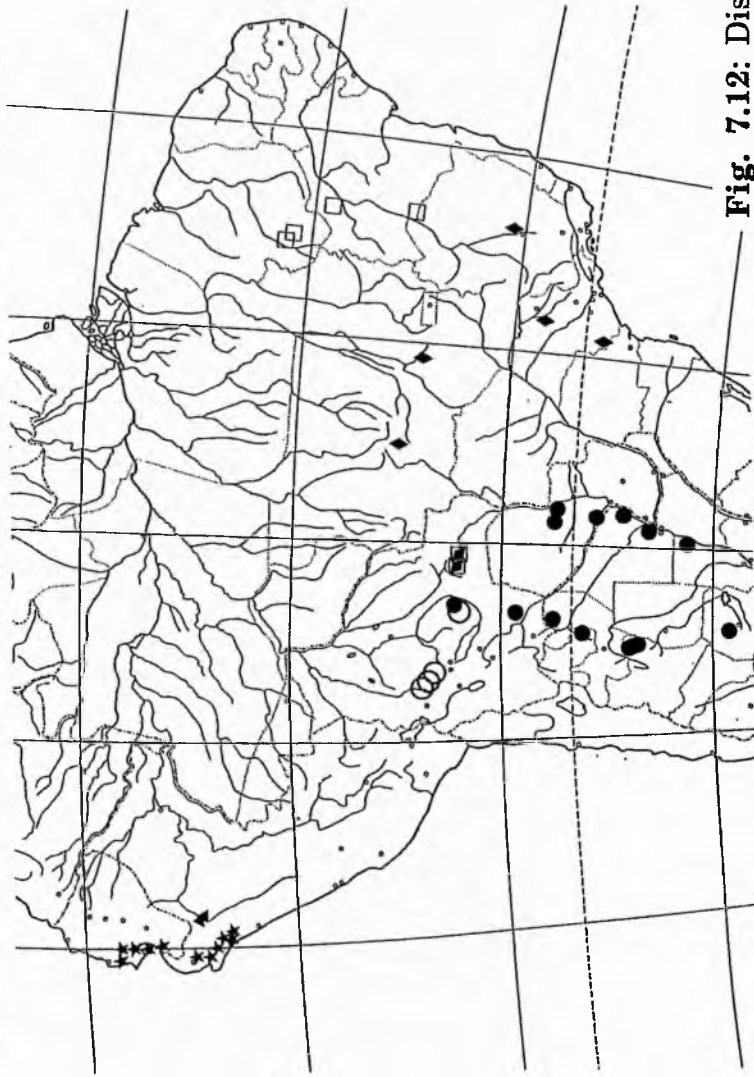
**Fig. 7.9:** Distribution map of *Icterus icterus* (*I. i. strictifrons* : more densely stippled).

**Fig. 7.10:** Distribution map of *Herpsilochmus pileatus pileatus* (diamonds), *H. p. atricapillus* (dots) and *H. p. motacilloides* (stars).





**Fig. 7.11:** Distribution map of the genus *Melanopareia* : *M. torquata torquata* (open squares), *M. t. rufescens* (diamonds), *M. t. bitorquata* (diamond in squares); *M. maximiliani maximiliani* (open circles), *M. m. argentina* (dots); *M. elegans* (stars); *M. maranonica* (triangles).



**Fig. 7.12:** Distribution map of *Contopus cinereus cinereus* (diagonal pattern), *C. c. pallescens* (vertical hatching) and *C. c. brachytarsus* (stippled).

São Paulo and isolated areas in Goiás and Mato Grosso, and to the Chiquitos sector in Bolivia respectively. *Melanopareia maximiliani argentina* shows a typical amphichaquenian distribution, sticking to the Paraguay-Paraná system on the east, and to piedmont areas from Santa Cruz de la Sierra to Córdoba, in the west; the nominate *maximiliani* spreads only in central Bolivia. Finally, *M. elegans* is restricted to SW Ecuador and NW Peru, while *M. maranonica* seems to be an endemic of the neighbouring dry valley of the lower Marañón river.

Another species listed by Short but not considered chaquenian here is the Tyranniidae *Contopus cinereus*, with the nominate form in SE Brazil, Misiones and E Paraguay, whilst *C. cinereus pallescens* spreads from the Caatingas through central Brazil to the Subandean piedmont in Bolivia and Argentina (Fig. 7.12). Another subspecies, *brachytarsus*, on the other hand, shows disjunct populations in the Guianas, Amazonian Venezuela, SW Ecuador and NW Peru area connected to the Marañón valley, the dry Caribbean coast of Venezuela and Colombia spreading south via the Magdalena river valley, and then into Central America. The euphonic Icteridae *Gnorimopsar chopi* is also what is here regarded as an amphichaquenian species (see also Olog, 1963a, p. 24), though frequent in the Eastern Chaco of Paraguay and Argentina. Its subspecies *sulcirostris* shows an exciting disjunction between the Brazilian Caatingas and the Subandean Piedmont Forests in S Bolivia and NW Argentina (Fig. 7.13), thus closely paralleling the distribution of the tree *Piptadenia viridiflora* (see Fig. 5.48). Amphichaquenian as well is the Tyranniidae *Inezia inornata* (Fig. 7.14), whose closest ally (*I. tenuirostris*) occurs in the driest areas of Colombia and Venezuela Caribbean coast. The parakeet *Aratinga nenday* (also referred to the monotypic genus *Nandayus*) is clearly restricted to the major river valleys and to the axis Santa Cruz-Corumbá (Fig. 7.15), thus bordering the Chaco but not getting into it and coinciding with the Pleistocenic Arc in its 2<sup>nd</sup> nucleus (see Sect. 5.3.1); the latter pattern of distribution seems to be closely followed by another monotypic genus and species in the Tyranniidae, *Culicivora caudacuta* (Olog, 1963a; Meyer de Schauensee, 1966; Fitzpatrick, 1980). There must also be a number of species which were not cited by Short for the Chaco but which follow the Pleistocenic Arc. Such is the case of *Formicivora melanogaster* (Fig. 7.16), mapped from data in Cory & Hellmayr (1924).

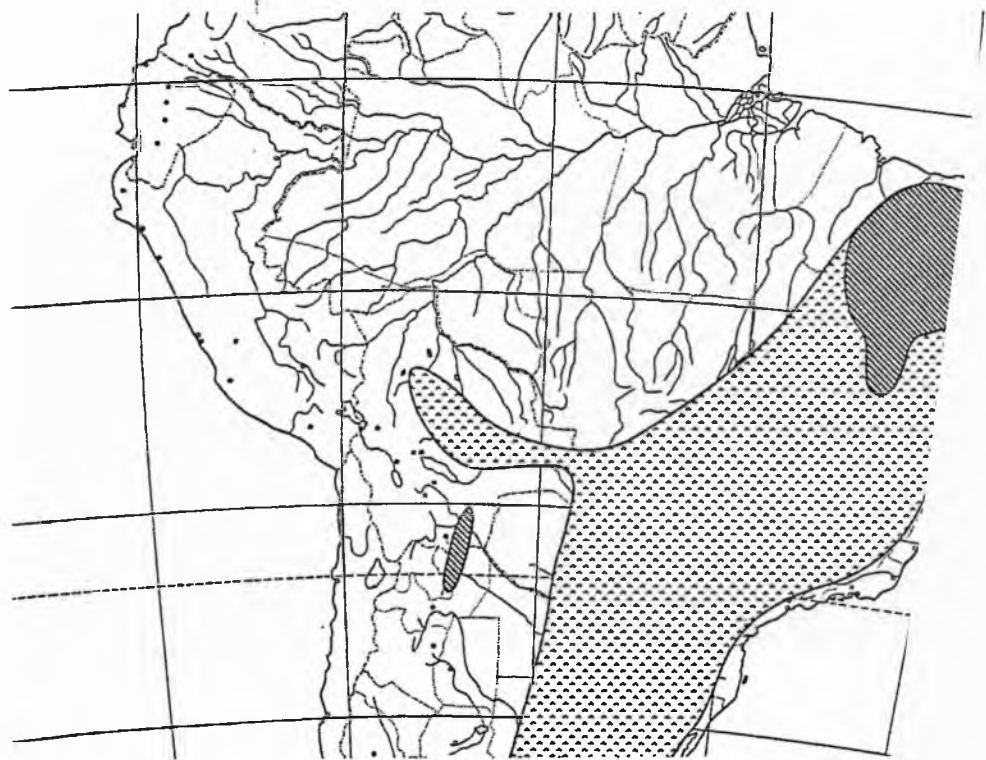


Fig. 7.13: Distribution map of *Gnorimopsar chopi chopi* (stippled) and *G. c. sulcirostris* (oblique hatching).

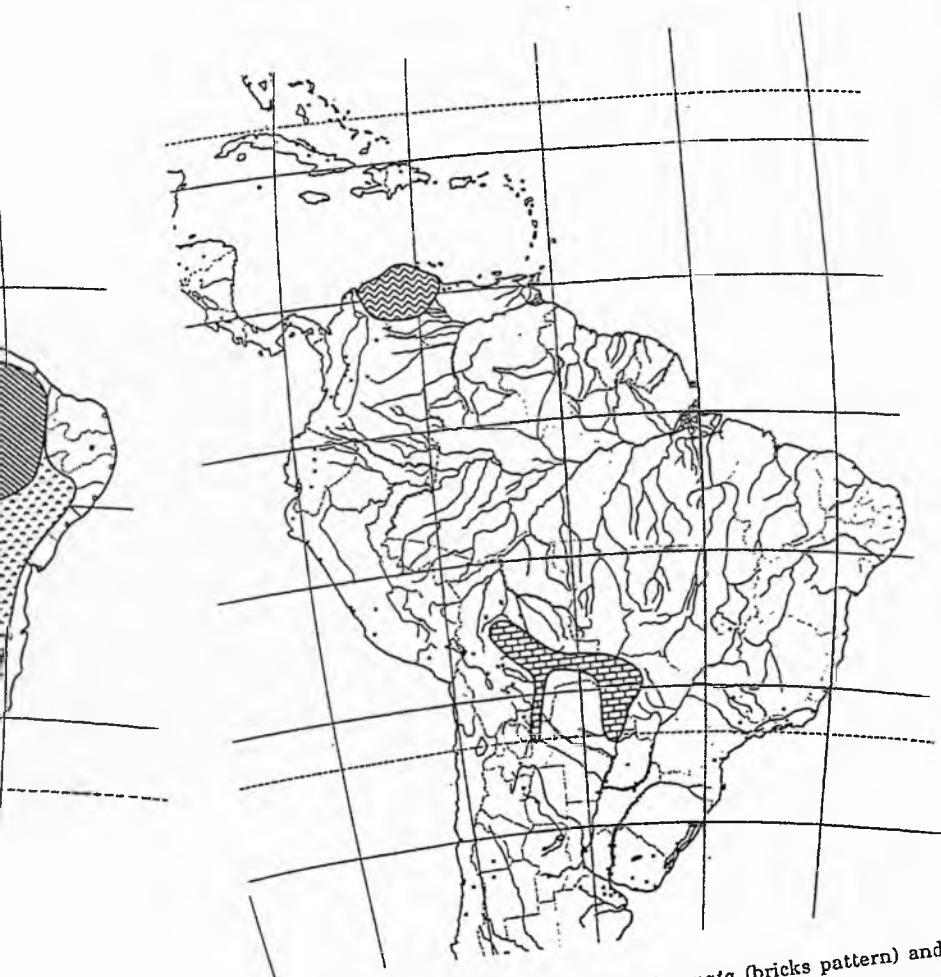


Fig. 7.14: Distribution map of *Inezia inornata* (bricks pattern) and *I. tenuirostris* (wavy pattern).

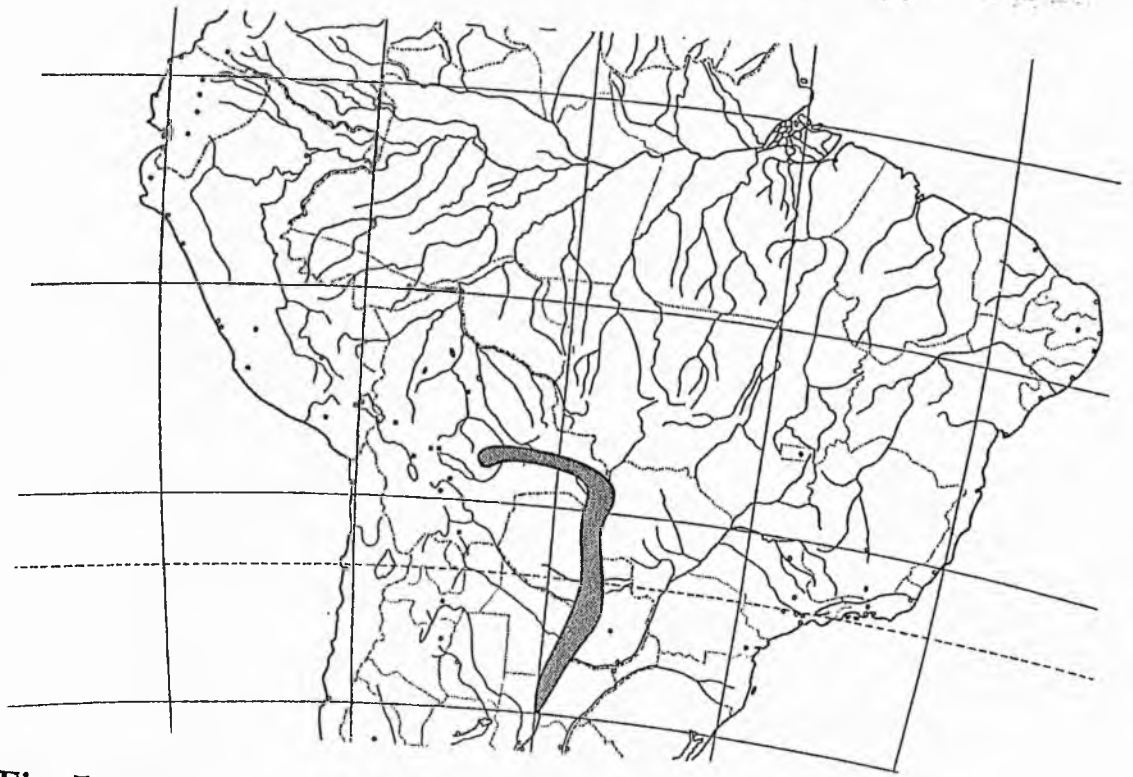
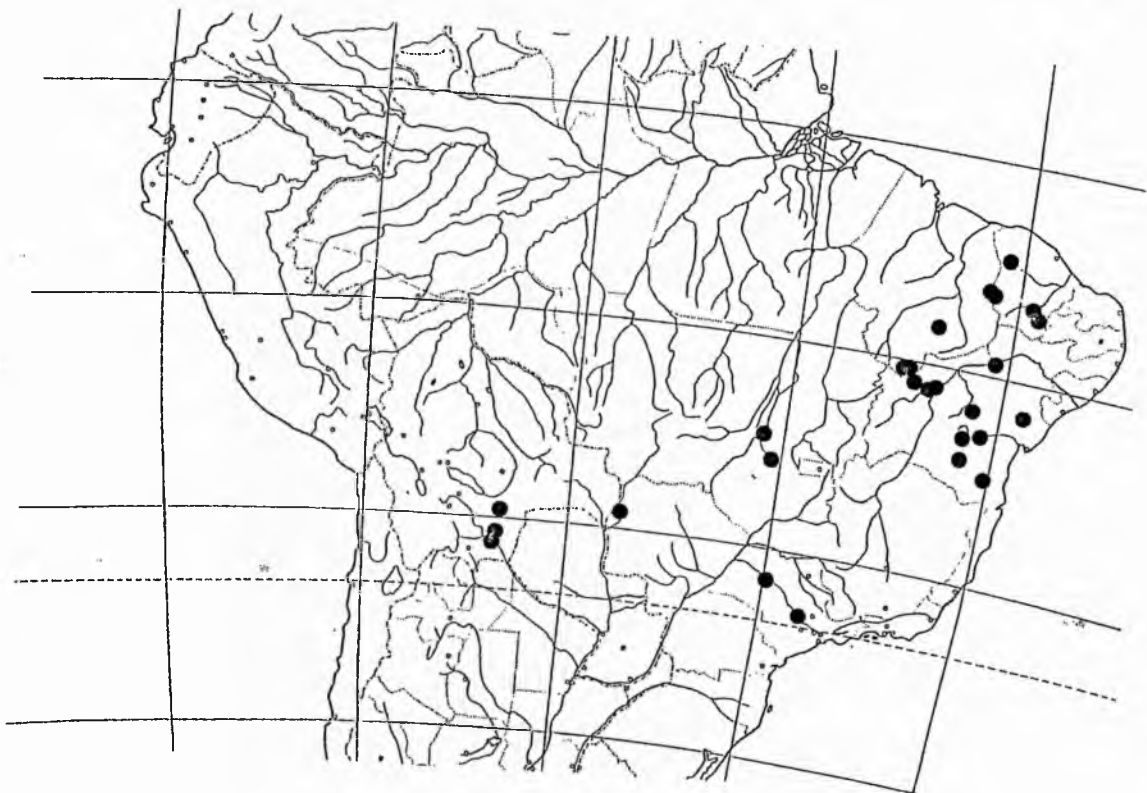


Fig. 7.15: Distribution map of *Nandayus* [*Aratinga*] *nenday*.

Fig. 7.16: Distribution map of *Formicivora melanogaster* (both *melanogaster* and *bahiae* forms).



The close relationship between the Caatingas and the dry SW Ecuador-NW Peru vegetation, already pointed out in Ch. 5, can be emphasized by the range of the Furnariidae *Fluvicola nengeta* (Fig. 7.17), whose nominate form covers the Brazilian NE (Vaurie, 1980) while subspecies *atripennis* occurs exclusively on the other side of the continent in the aforementioned area. The even closer links, from the phytogeographical point of view, between the Caatingas and the dry Caribbean sector in northern South America is illustrated by *Spinus yarrellii* (Fringillidae) in Fig. 7.18, erroneously regarded as a Caatinga endemic by Müller (1973, p.115). This case is paralleled by the Caatingas' endemic *Phylloscartes roquettei*, known only from arboreal caatinga in the Januária area (Silva, 1989), whose closest relative *P. flaviventris* occurs sympatrically with *Spinus yarrellii* in northern Venezuela, plus an isolated collection in Peru in, presumably, dry Andean valleys.

Numerous other examples of bird species following the patterns of plant distributions presented in this thesis can be found in the literature. Vaurie's (1980) monograph on the Furnariidae shows several cases, such as that of *Furnarius figulus* (see his map 5) which clearly links the Caatingas to the central Amazonian area around Santarem in Pará, and *Furnarius leucopus* (same map) with three disjunct populations in NW Venezuela and N Colombia (surrounding the lake Maracaibo), in SW Ecuador-NW Peru, and then a wider distribution from the Guianas and Rio Branco in Brazil to central Amazon valley and west of Obidos, south to Bolivia and central Mato Grosso, to finally reach the Caatingas. The whole of Vaurie's *Synallaxis* group 4 seems to be confined to the Amphitropical Seasonal Forests pattern of distribution (see his map 15 vis-à-vis Sect. 5.3.3), with *S. erythrothorax* in Yucatán, Tehuantepec and Guatemala, *S. candei* and *S. cinnamomea* in dry coastal Colombia and Venezuela, *S. gularis* in Andean valleys of Colombia, Ecuador and Peru, and therefore linking with *S. stictothorax* of SW Ecuador-NW Peru, *S. kollari* isolated in Rio Branco (where one of the most typical caatinga tree species, *Commiphora leptophloeos*, Fig. 5.35, has been collected), and finally *S. scutata* which spreads from the Caatingas to the Subandean piedmont through the Cerrados and mesophilous forests within the latter savannas (Silva, 1989). *Certhiaxis*

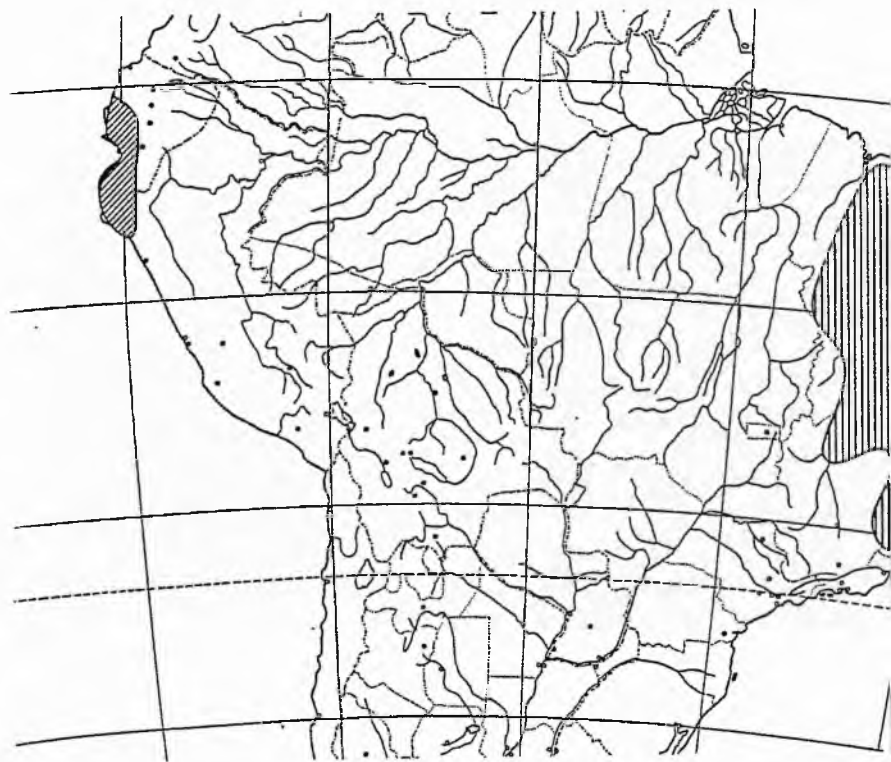


Fig. 7.17: Distribution map of *Fluvicola nengeta nengeta* (vertical hatching) and *F. n. atripennis* (oblique hatching).

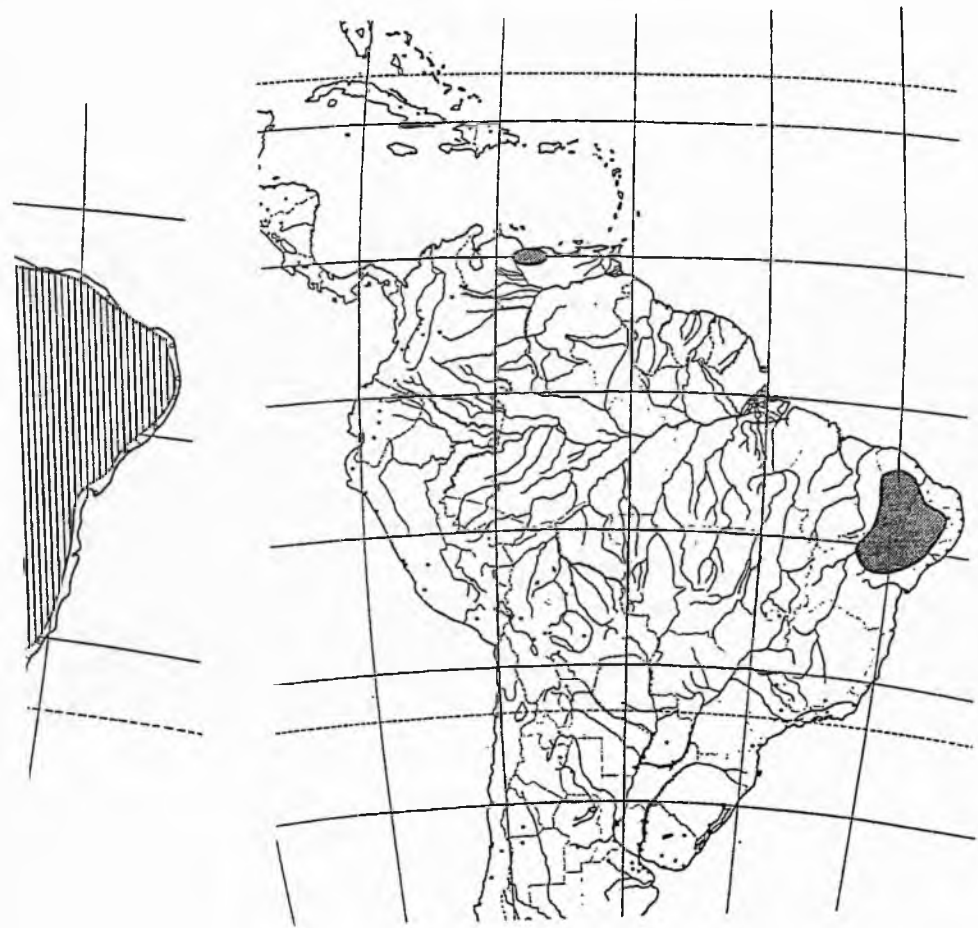


Fig. 7.18: Distribution map of *Spinus yarrellii*.



(=*Cranioleuca*) *semicinerea* would be a caatinga endemic but for some isolates in south central Goiás (Vaurie, 1980; Teixeira & Luigi, 1989). From Short's work (1975) some few other examples can be extracted, such as the Corvidae superspecies *Cyanocorax chrysops* or the Trochilidae *Phaethornis pretrei*, which link the Subandean piedmont in NW Argentina to the Caatingas. However, an exhaustive analysis of avian distribution is beyond the scope of this thesis.

### 7.3- The mammalian evidence:

The mammalian fauna of South America can shed further light onto the nature of the relationship of the two regions under study. The Caatingas mammals have been studied and listed by Mares et al. (1981b), Mares et al. (1985) and updated by Willig & Mares (1989), who found *Kerodon rupestris* as the only endemic of the region. They consider the Caatingas mammals essentially a subset of the cerrado fauna (Mares et al., 1985), with the paradoxical situation of a largely mesic-adapted tropical fauna in an area distinctive for its aridity and drought-adapted flora. The Chaco mammals have been more extensively studied (Massoia, 1970; Wetzel & Lovett, 1974; Myers & Wetzel, 1979 & 1983; Bucher, 1980; Mares et al., 1981a; Myers, 1982; Mayer & Brandt, 1982), and seem to show a higher degree of endemism. The Chaco has the peccary with the most restricted distribution, the monotypic *Catagonus wagneri* (Wetzel et al., 1975; Sowers, 1980-83; Mayer & Brandt, 1982), and several endemic rodent species (Müller, 1973; Myers, 1982). No endemic bats to the Chaco are known to occur to date, and its bat fauna appears to result more from the deletion of species from neighbouring areas, rather than from the differentiation or incorporation of new elements (Myers & Wetzel, 1983).

Thus, although some comparative studies of South American mammalian faunas suggest a strong affinity between the Chaco and Caatingas dispersal centres, e.g. Müller (1973), once again an analysis of individual cases provides a different picture. The excellent studies by Michael Mares and collaborators (Mares et al., 1981a & b), both in a central area of the Caatingas in Pernambuco (Brazil) and in the Chaco of E Salta (Argentina), provide extensive mammal lists with detailed habitat comments. It is particularly important that these authors studied not only the animal communities of reference, but also those of

neighbouring (Puna, Prepuna, Yungas and Subandean Piedmont Forests) and enclosed formations (such as the cerrado of the Chapada do Araripe). A comparison of the lists indicates that the dry deciduous forests of the Subandean piedmont (so-called Transitional Forests) holds six species and two genera in common with the Caatingas, but these are absent from the Chaco. In contrast, only one of the species in common between Chaco and Caatingas is also absent from the Piedmont Forests (*Euphractes sexcinctus*). These results confirm the pattern that has emerged for birds and tree species, i.e. that there is a strong floristic and faunistic link between the Caatingas and the narrow fringe of deciduous subtropical forests in NW Argentina and SW Bolivia, but not with the main Chaco area.

The Chiropteran fauna of the Paraguayan Chaco was analyzed by Myers & Wetzel (1983), with comparative listings between the Chaco Boreal and several South American biomes: Venezuela, Surinam and Guianas as one single block, Amazonian Peru, Bolivia, Caatingas, SE Brazil (basically the coastal states from Rio de Janeiro to Rio Grande do Sul), E Paraguay, and Uruguay. They reckoned the number of species in common of each of these biomes with the Chaco Boreal, and the Simpson's index of faunal resemblance was calculated. In all likelihood they were expecting to find a high similarity between Chaco and Caatingas, but these two regions rendered the second lowest number of species in common (Uruguay was the lowest), and the lowest similarity index. The highest similarities for the Chaco were found with neighbouring eastern Paraguay and the Venezuela-Guianas block. Myers & Wetzel (op. cit.) blamed sampling techniques for this result: "The stronger relationship between Chacoan and Venezuelan faunas than between Chacoan and NE Brazilian faunas, for example, is probably an artifact of incomplete sampling". This statement merits two comments: firstly, whatever sampling errors may exist, they are likely to be of little impact compared with the attempt by these authors to compare faunas of well-defined natural biomes, such as the Chaco, Caatingas, Amazonian Peru or what they called SE Brazil, with those of political areas such as Bolivia and Uruguay, or a concoction of different environments such as those included under the heading 'Venezuela' (which involves some West Indies as well, and ranging ecologically from tropical rainforests to the Caribbean semidesert). Secondly, the quoted

sentence reveals the deep-rooted prejudice evident in many South American biogeographical studies that a strong relationship between Chaco and Caatingas must exist, even when their own data indicates otherwise. Furthermore, a number of the bat species regarded by Myers & Wetzel (1983) as chaquenian have never, in fact, been seen or collected in Chaco proper but only in marginal areas here not regarded as Chaco s.s. (as it happens with a number of avian species listed by Short, 1975): *Peropteryx macrotis*, *Phyllostomus hastatus*, *Glossophaga soricina*, *Carollia perspicillata*, *Sturnina lilium*, *Vampyrops dorsalis*, *V. lineatus*, *Artibeus lituratus*, *Tadarida macrotis*. Since several of these species are members of the Caatingas volant mammals fauna, their exclusion from the Chaco weakens even more the links between the regions.

The bat species *Lonchophylla mordax*, a caatinga element (Willig & Mares, 1989), follows to a certain extent some of the distributional patterns described in previous sections, such as that of the bird *Fluvicola nengeta* (Fig. 7.17) or those of some of the trees included in Ch 5.3.2, e.g. the *Geoffroea striata/spinosa* complex (Fig. 5.58). It occurs in S Central America, W Colombia (probably in dry interandean valleys), dry coastal E Ecuador and NW Peru, to then reappear in the east of Brazil including the Caatingas (Koopman, 1981, Fig. 10, & 1982). Except for an specimen from Belém, Pará, it has not been recorded for the Amazon.

#### **7.4- Herpetological distribution and other sources of evidence:**

It is very difficult to draw conclusions from alleged herpetological relationship between Chaco and Caatingas. Vanzolini has repeatedly stated that much more collecting is needed and taxonomical studies are required to fully understand the herpetofauna distribution in South America (Vanzolini, 1970 & 1974). The degree of endemism of the Chaco, although a very contentious matter – compare Müller (1973, pp. 143-145), to Blair (1976), Gallardo (1979), and Bucher (1980) – seems to be much higher than that of the Caatingas. Tropical forms penetrate along the western and eastern boundaries of the Chaco via gallery forests, such as *Iguana iguana* and *Anolis chrysolepis*, overlapping sometimes with true chaquenian elements and motivating some authors to include very different entities as faunal elements of the region, as already emphasized by Müller (op .cit .). Basically, however,

endemic elements of the Chaco are at least one monotypic genus, *Chacophrys* (Müller, op . cit .), and some species such as *Tropidurus melanopleurus*, *Liolaemus chacoensis* (Müller, op . cit .), and *Leptodactylus laticeps* (Bucher, 1980). The Caatingas have apparently only one endemic lizard, *Tropidurus semitaeniatus*, so that there is no lizard fauna characteristic of the region but it is simply part of the so-called diagonal of open formations extending from Maranhão to NW Argentina (Vanzolini, 1970, 1974 & 1976). This would imply that there should be strong affinities between Chaco and Caatingas by way of the central Brazilian Cerrados, as shown by *Phyllopezus pollicaris* and *Gymnophthalmus multisculatus* vs. *G. rubricauda* (Vanzolini, 1974). However, Duellman's (1979) analysis at familial level of the South American herpetofauna renders little evidence for such a link; his Brazilian Shield ecophysiological region (lumping together Cerrados and Caatingas) has 31 families in common with the Atlantic Forest and with the Guianas Shield, 27 with the Caribbean-Orinoco area, and only 20 with the Chaco. Analyzing only the data for the Caribbean-Orinoco area, the Brazilian Shield and Chaco, there are eight families in common between the two first regions which are absent from the Chaco, while only three are absent from the Brazilian Shield but common to Chaco and the Caribbean sector (Duellman, 1979). These data seem to indicate a somewhat stronger relationship between the Caribbean-Orinoco area and the Brazilian Shield, than between the latter with the Chaco.

Finally, the Caatingas as a biogeographical province seem to be very well defined also by their scorpion fauna: there are at least five endemic species (Lourenço, 1990). The nine species of the scorpion genus *Rhopalurus* provide additional information of the actual Caatingas links (Lourenço & Sastre, 1988). Apart from three endemisms in the West Indies, there are four species in the Caatingas (*R. agamemmon*, *R. acromelas*, *R. debilis*, *R. rochae*), two of which also occur in the Cerrados, another one is endemic to campos around Santarém, Pará (*R. amazonicus*; Lourenço, 1986), and the last one, *R. laticauda*, is distributed in the dry Caribbean sector of Colombia and Venezuela plus the Llanos in both countries, with one subspecies in the Guianas. Once again the evidence suggest a great affinity Caatingas-Caribbean dry area via Amazonia – and Guianas – isolated disjunctions, rather than the Chaco-Caatingas links postulated by Lourenço (1990).

Cladistic analysis performed by Lourenço & Sastre (1988) indicates that *R. amazonicus* is in an intermediate taxonomic position between the Caribbean species and two of those from the Caatingas that spread to the Cerrados (*R. agamemmon*, *R. acromelas*), whereas the other two caatinga species are closer to the West Indies endemics. Lourenço & Sastre (1988) regard *R. amazonicus* as a vestige of an ancient continuous distribution of the genus across the lower Amazon river valley.

## 8. DISCUSSION

In any study of floristic links such as that between Chaco and Caatingas vegetation in South America there is an underlying dilemma: vicariance or dispersal?. That is, are present-day distribution patterns the result of a previously continuous expanse, later interrupted, or are they simply the consequence of propagule dispersal which have found propitious terrain in areas with seasonal climate?. Harley (unpubl. mscrp.), in a study of 'campo rupestre' floristics in SE Brazil which emphasized the links to the Mesa and Tepui formations in Venezuela, suggested that the number of species in common is too high to suppose that mechanisms of long-distance dispersal could have acted in this case, and argued that there must have been an earlier physical connection. This reasoning, which could be certainly applied here, lies at the core of the 'vicariance' argument. Whilst occasional 'unusual' distributions may be the consequence of chance long-distance dispersal effects, repeated distributions of taxa in a similar pattern give support to a vicariance explanation. The recurrent occurrence of a disjunct distribution outline, or endemisms whose closest relatives are vicariant in other segments of the same disjunct distribution pattern, provide a firm conviction that a common event (or events), a common migration pathway, a common expansion-regression phenomenon has taken place. This view finds further support in the fact that plant taxa following these patterns come from widely different families, phylogenetically very distant in most cases; that the patterns can also be found repeated in animal distribution cases (Ch. 7) and when the latter are bird species, those that follow the particular distribution patterns studied here are non-migratory and some of them virtually non-flying taxa.

### 8.1- Redefinition of the Chaco province:

Attention has been drawn for some time to the physiognomic, floristic and faunistic connections between the Caatingas of NE Brazil and the Gran Chaco region of Bolivia, Paraguay and Argentina, an established view that has prevailed unchallenged so far. In studying this problem the need of a thorough analysis of the present-day notion of the Chaco arose. In the literature available to date the concept of the Chaco as a phytogeographical province has simply been equated with the Chaco as a geographical region. However, the comparative study and

phytosociological analyses undertaken here show that the geographical region known as the 'Gran Chaco' in fact includes rather different kinds of vegetation. Such analyses then provide the basis for an attempt to redefine the 'Chaco proper'.

In Sect. 6.1 the results of three different types of analysis applied to the Gran Chaco vegetation have been presented : the classical phytosociological approach and, as a more objective yardstick to evaluate this, two numerical analyses were performed, one to classify (CLINK) and one to ordinate (PCA) the samples. The congruence between the different results is striking. Out of the 23 vegetation units that had been regarded as chaquenian by different authors (see Ch. 2 & Table 6.1), five are definitely non-chaquenian (Gallery Forest, 'Selva de Ribera', 'Tipa-Pacará' Forest, 'Palo blanco' Forest, and Calcareous Forest), four are here considered transitional with neighbouring formations (the Austro-Brazilian Transitional Forest and three of the communities of Mato Grosso do Sul), and 14 correspond to what is here defined as Chaco *sensu stricto* : the four 'Quebrachales', 'Palosantal', 'Algarrobal', 'Vinalar', 'Cardonal', the two 'Palmares', both Sierra Chaco, the Arid Chaco Woodland and the Chaco Forest at Pto Murtinho. A brief discussion on the excluded communities follows.

(a) Excluded communities:

Between the communities listed in Table 6.1, none of the Gallery Forest (A), 'Selva de Ribera' (B), 'Tipa-Pacará' Forest (C), 'Palo blanco' Forest (D) and the Calcareous Forest of Mato Grosso do Sul (F) can be regarded as chaquenian in character. Climate, soils and water regime are entirely different from that which prevails in the Chaco *s.s.*, and as a result their flora is essentially of Amazonian lineage (*sensu* Cabrera & Willink, 1980). All of these vegetation types are well defined, each characterized by a floristic group comprising the species which are exclusive to them within the scope of this study. Moreover, the numerical analyses (Figs 6.1 & 6.2) have shown that they are more closely inter-related, and linked to what has been called in the present study 'Austro-Brazilian Transitional Forest', than to the Chaco *s.s.* communities. Therefore, none of these five vegetation types should be included in the Chaco phytogeographical province.

(b) Transitional communities:

The four transitional units consist of three from the Mato Grosso do Sul area studied by Prado et al. (in press b): the *Schinopsis balansae* parkland (G), the *Aspidosperma-Mimosa* scrubland (H), and the *Diplokeleba-Tabebuia-Capparis* scrubland (I), and finally the here-named 'Austro-Brazilian Transitional Forest' (E). The first three communities contain a very low percentage of true Chaco species (Prado et al., in press b), along with a number of cerrado and semi-deciduous forest elements, and none of the three can be fully ascribed to any of the major phytogeographical units which converge in the Pantanal, i.e. Cerrados, Amazonian, Paranense and Chaco provinces (Adámoli, 1982). Furthermore, the numerical analyses (Fig. 6.2) show these communities in a clear transitional position between the Chaco s.s., and the wetter vegetation units.

The Austro-Brazilian Transitional Forest (E) is undoubtedly the climax community in the east of the Gran Chaco area (Lewis & Pire, 1981, *sub* 'bosque chaqueño'), i.e. the sector referred to as 'Eastern Chaco' in all phytogeographical classifications (Morello & Adámoli, 1968; Ragonese & Castiglioni, 1970; Cabrera, 1971 & 1976). Four true Chaco communities also manage to extend into this eastern area. These are the *Schinopsis balansae* 'quebrachal' (K), *Prosopis* spp. 'algarrobales' (P), *Copernicia australis* 'palmares' (S), and *Stetsonia coryne* 'cardonales' (see Sect. 2.3.7.b). They are evidently edaphic-dependent, and their presence in an area of over 900 mm yearly rainfall is allowed only by the physiological drought caused by the high salt content of the soil and consequent higher osmotic potential. Consequently, and contrary to the position sustained by Ragonese & Castiglioni (1970) and Cabrera (1976), the 'quebrachal' of *Schinopsis balansae* should not be regarded as a climax community, since rather it thrives on non-climatogenic saline soils, with high clay level, periodical waterlogging, elevated Na<sup>++</sup> concentration and very strongly alkaline subsoils (Espino et al., 1983). Thus, true Chaco vegetation is found in a strip of some 100 km wide, parallel to the Paraguay and Paraná rivers, in an area where climatic, edaphic



and geomorphological conditions are different from those in the center and west of the Gran Chaco. Presumably, the salinity factor is responsible for this outlying representation, since Chaco elements can survive in edaphic conditions which are hostile for the subtropical humid forests species of the Austro-Brazilian Transitional Forest. This hypothesis is exactly the opposite to Hueck's (1972), who postulated that chaquenian species would occur on higher, drier ground within the floodable, water-modelled Eastern Chaco. On the contrary, such drier areas are covered by a different kind of forest dominated by species such as *Patagonula americana*, *Phytolacca dioica*, *Ruprechtia laxiflora*, *Gleditsia amorphoides*, *Tabebuia impetiginosa*, *Pisonia zapallo*, and *Enterolobium contortisiliquum*. All of these species occur elsewhere in subtropical humid forests in S Brazil, E Paraguay and N Argentina. Indeed, the species listed above are all widespread in South American forests, and extend to NE Brazil or humid Atlantic forests (Klein, 1967), or even to Central America and Mexico in similar ecosystems (*Tabebuia impetiginosa*, in Gentry, 1979).

Most species of the Austro-Brazilian Transitional Forest are elements which are common to the five vegetation types here excluded altogether from the Chaco s.s., e.g. the species listed above together with *Diplokeleba floribunda*, *Astronium balansae*, *Chrysophyllum gonocarpum*, *Pithecellobium scalare* or *Brunfelsia australis* (see Table 6.1). Seven of the most typical Chaco species<sup>1</sup> can also appear in this transitional unit, but they are never dominant trees and seem to be at the extreme of their ecological range in this area. Hardly any of these chaquenian intruders can be found further east in wetter areas either in Argentina, Paraguay or Brazil, and it is likely that their existence in this unit could be due to anthropogenic alteration of the environment (overgrazing, selective felling), or even brought in by cattle. Therefore it is proposed that this vegetation type, which has

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<sup>1</sup> These are: *Geoffroea decorticans*, *Aspidosperma quebracho-blanco*, *Ziziphus mistol*, *Prosopis nigra*, *Schinus fasciculatus*, *Acacia praecox* and *Caesalpinia paraguariensis* (see Table 6.1, FG XXII). Sometimes even *Schinopsis balansae* may appear in this forest, but its occurrence is very occasional and marginal to the unit (Lewis, J.P., *in litt.*).

received several different names by different authors, and has generally been included in the Chaco province (Cabrera, 1971 & 1976), is better called **Austro-Brazilian Transitional Forest** and should be excluded altogether from the Chaco s.s. .

This forest is basically a very impoverished version of the Brazilian Subtropical Forests (*sensu* Andrade-Lima, 1966a, and Klein, 1972), which is here at the extreme western limit of its distribution. Furthermore, and despite the presence of some chaquenian elements in it, the Austro-Brazilian Transitional Forest should be regarded as a component of the Paranense province of the Amazonian Dominion (*sensu* Cabrera & Willink, 1980), since the dominant trees are species which are mainly distributed in other districts of this province where, however, they may be of lesser importance. Thus, of the Paranense province floristic stock, these species are probably those that can tolerate a few frosts each year, and can still compete successfully in areas with less alkaline and less waterlogged soils against the chaquenian species pushing east.

This interpretation is reinforced by the fact that most of the dominant species of the Austro-Brazilian Transitional Forest reappear further west, jumping over 700 km of dry Chaco plains, in the Yungas province (Smith, 1962; Ragonese & Castiglioni, 1970; Cabrera, 1976) in the 'Tipa-Pacar\'a' (C) and 'Palo blanco' (D) Forests. There is a very close relationship between those three vegetation units, as shown by several floristic groups of Table 6.1 and strongly supported by the numerical analysis. However, although units C & D also include some widespread chaquenian species, it is of interest that few authors tried to include these two forest types in the Chaco (e.g. Hueck, 1972), whilst virtually all phytogeographers have merged without hesitation the Austro-Brazilian Transitional Forest with the Chaco, with perhaps the sole exception of Castellanos & P\'erez-Moreau (1944) in their map of vegetation of Argentina.

The fact that the so-called 'Eastern Chaco' is in effect a meeting point of quite diverse floristic elements, i.e. true xerophytic

chaquenian communities and humid subtropical and tropical species, has been perceived by some previous authors. Thus, Cabrera (1970) was aware that the boundary between the Chaquenian and Amazonian Domina, which meet in the Eastern Chaco, is confused, and he remarked that the whole of the river Paraguay basin is an immense transition area with a very complicated intermingled pattern. A striking example of such intermingling is that the current concept of 'Eastern Chaco' even includes 'paratodales' of *Tabebuia caraiba* in floodable localities associated with the river Pilcomayo valley in SE Paraguayan Chaco region and NE Formosa in Argentina (Chodat & Vischer, 1977; Fiebrig, 1933; Ragonese & Castiglioni, 1970; Morello & Adámoli, 1974, p.42). *T. caraiba* can hardly be accepted as Chaco species (see map 5.52) since it also occurs in NE Brazil in the 'sertão' and 'agreste' (Andrade-Lima, 1960 & 1989), is also an abundant species in the Cerrados (Heringer et al., 1977; Furley & Ratter, 1988; Ratter et al., 1988a), and the 'paratodales' are one of the main features of the Pantanal landscape (Ratter, 1984; Allem & Valls, 1987)!

Although edaphic factors can explain the eastward expansion of some Chaco taxa, the reason why southern or central Brazilian hygrophilous elements can expand westwards to interdigitate with chaquenian communities must be climatic. In Chaco vegetation maps the line drawn to separate the so-called 'Eastern Chaco' from the rest of the province (see Fig. 2.1; also Hueck & Seibert, 1981) seems to coincide roughly with a rainfall isoline somewhere between 950 to 1000 mm per year (see Fig. 2.4), and also with the alleged limit between humid and dry climates, the MI(Moisture Index)=1 line (Box, 1986). In Ragonese & Castiglioni's map (1970), where their concept of 'Eastern Chaco' covers the eastern half of the Gran Chaco region, this line coincides roughly with the western boundary of the 'Pilaguense' and 'Bosque Chaqueño' districts.

The climate classification systems of Koeppen and the two systems proposed by Thornthwaite have been compared for Argentina by Burgos & Vidal (1951), who concluded that Thornthwaite's 2<sup>nd</sup> System is the most fitted to the distribution of the natural vegetation. For the Argentine Chaco, this correlation is very good : the transitional belt proposed here (Fig. 8.2) matches very well with an equivalent narrow

band along the river Paraná with C<sub>2</sub>B<sub>4</sub>'ra' climate (Fig. 8.1), and so does the zero isoline for the MI according to Thornthwaite's 2<sup>nd</sup> System (Burgos & Vidal, 1951, Fig.7 D). The similarities extend even to most of the chaquenian districts proposed by Ragonese & Castiglioni (1970), such as the Pilaguense, Maticense, and Santiagueño districts, to which the corresponding climate types are C<sub>1</sub>A'da', DA'da' and DB<sub>4</sub>'da' respectively, and the districts Campestre, Mixed Forests & Savannas and Chaquenian Forest as a group with the corresponding climate type C<sub>1</sub>B<sub>3</sub>'da'. It is noteworthy that a very similar kind of climate to that of the eastern Transitional Belt appears to the west of the Chaco in areas occupied by both the 'Tipa-Pacará' and 'Palo blanco' Forests!

Given the weight of floristic and correlated climatic and edaphic evidence, the question could be posed now why the 'Eastern Chaco' has traditionally been considered as truly chaquenian, as in Morello & Adámoli (1968), Ragonese & Castiglioni (1970), Cabrera (1976), Hueck & Seibert (1981), and Ramella & Spichiger (1989). The reasons are more historical than botanical. The rainforests or thorny dry woodlands formed a barrier to an eastward expansion for centuries with the result that most of the exsiccata collected on the eastern side of the Paraná and Paraguay rivers have simply the locality 'Chaco', whether they are xerophytic or humid forest species, just because the collector ferried the river or sailed along the tributaries. The NE Argentine Chaco region and the Paraguayan Chaco region were cautiously explored by naturalists in a narrow fringe parallel to the big rivers or their tributaries, mainly the Pilcomayo (see the picturesque account by Kerr, 1968), at the beginning of this century. Hochreutiner (1923) remarked that the Paraguayan Chaco was known only along the banks of the Paraguay and Pilcomayo rivers, and Fiebrig (1933) was honest enough to admit that up to that time scientific exploration extended only for 100 to 150 km west of the river Paraguay (though the present author still believes that is an over-estimate)<sup>2</sup>. Geographically speaking the term Chaco will continue as the denomination of the whole of the region, but

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<sup>2</sup> The first botanical collector to cross the Paraguayan Chaco by land was Teodoro Rojas, who followed the Paraguayan lines during the 'Chaco War' and reached the Parapetí river in Bolivia in 1935. More evidence comes from the zoological field; the endemic peccary genus *Catagonus*, considered for long as extinct and known only from fossils, was rediscovered as late as in 1972 in the heart of the Paraguayan Chaco (Wetzel et al., 1975).

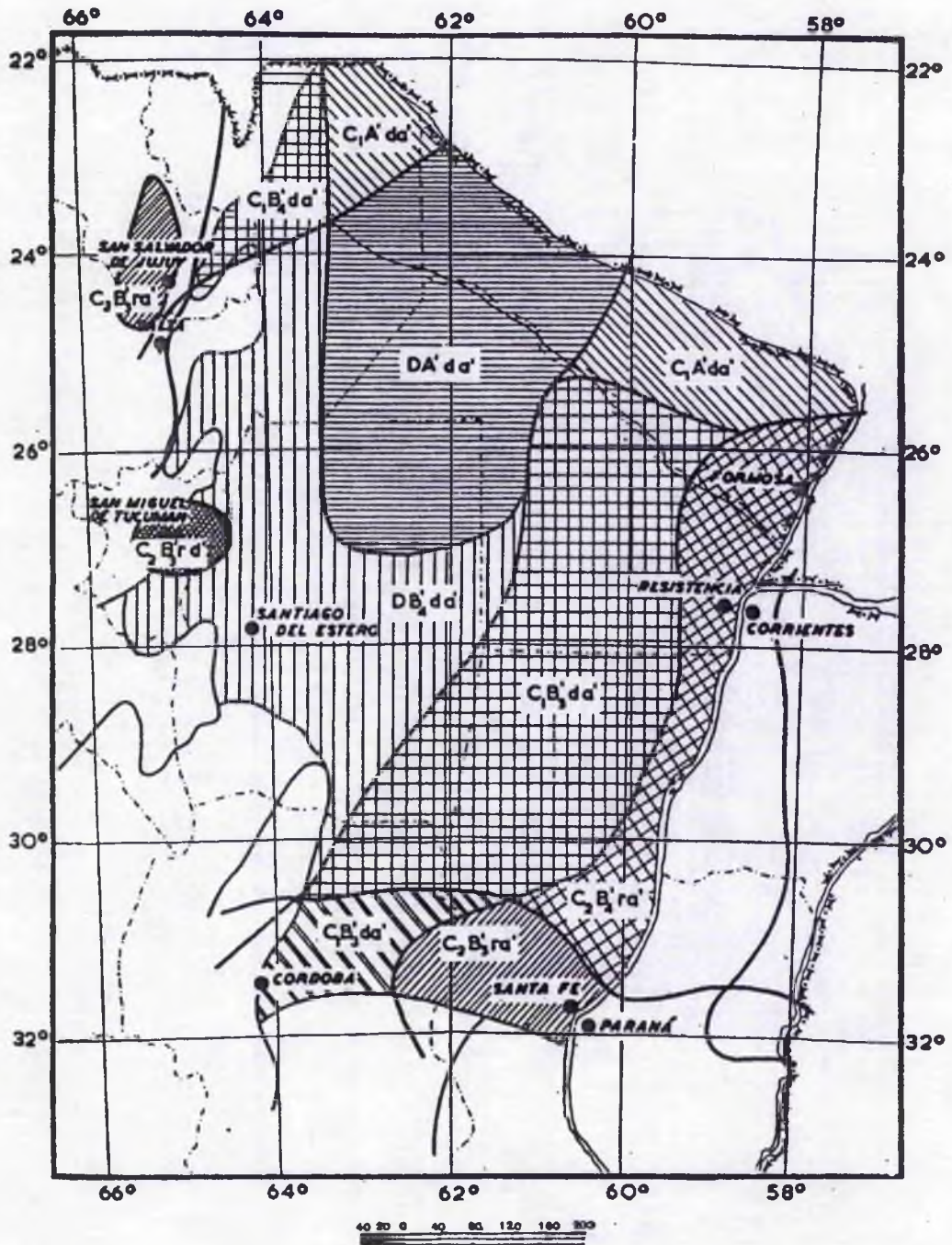


Fig. 8.1: Climate types for the Argentine Chaco, according to the 2nd system of Thornthwaite. Modified from Galmarini & Raffo del Campo, 1964.

from a phytogeographical point of view the name must have a more restricted usage.

There are no comprehensive surveys or descriptions of the Bolivian Chaco. Only Herzog's travel notes (1910, 1912), and brief comments in Cárdenas (1945), Braun (1956), Coro (1956), Unzueta (1975), Werding (1976), and Velásquez et al. (1988) are available. Herzog (op. cit.) found west of Puerto Suárez up to the Santiago Sierras communities resembling those of Prado et al. (in press b) surveyed in Mato Grosso do Sul, and he correctly regarded them as related to the Pantanal vegetation and the Caatingas rather than to the Chaco. No true Chaco vegetation is described in his notes until, when travelling from the Sierras of Chiquitos to the Río Grande, he found a low xerophilous formation, rich in spiny shrubs and cacti, known as 'Monte' and comprising *Aspidosperma quebracho-blanco*, *Caesalpinia paraguariensis*, *Capparis* spp., *Maytenus vitis-idaea*, *Bulnesia sarmientoi*, etc.. The description of Chaco vegetation in Unzueta (1975, pp 209-218, sub 'Bosque Seco Templado') is very shallow, and the mixed floristic list indicates that no distinction was made between the true Chaco and the non-chaquenian neighbouring formations (such as the 'Palo blanco' forest), differences that have been pointed out by previous authors (Herzog, 1910 & 1912; Coro, 1956) in their skilful, albeit brief, surveys.

However, to what extent the Chaco vegetation expands to the north of the line Chiquitos-Santa Cruz de la Sierra remains to be seen. Herzog (1912) hypothesized that the 'monte' would not go beyond 16° LS, whereas Ellenberg's (1981) map of the Bolivian ecoregions presents the Chaco (sub 'monte semiárido bajo') extending north through the Rio Grande plains only up to 17° LS. What is certain is that the Chaco does not reach the Llanos de Mojos in NE Bolivia (approx. 12° LS to 15° LS), as implied by Cabrera & Willink's (1980) map. The Llanos de Mojos have been studied in part by Beck (1984), Haase & Beck (1989), and Haase (1989 & 1990), and some communities show strong links with the savannas of N. South America, while the 'chaparral' resembles the Humaitá savannas and the Cerrados of central Brazil (Haase & Beck, 1989). Although the vegetation of this area comprises some very few and isolated Chaco elements (Beck, 1984), it is far from being chaquenian in character.

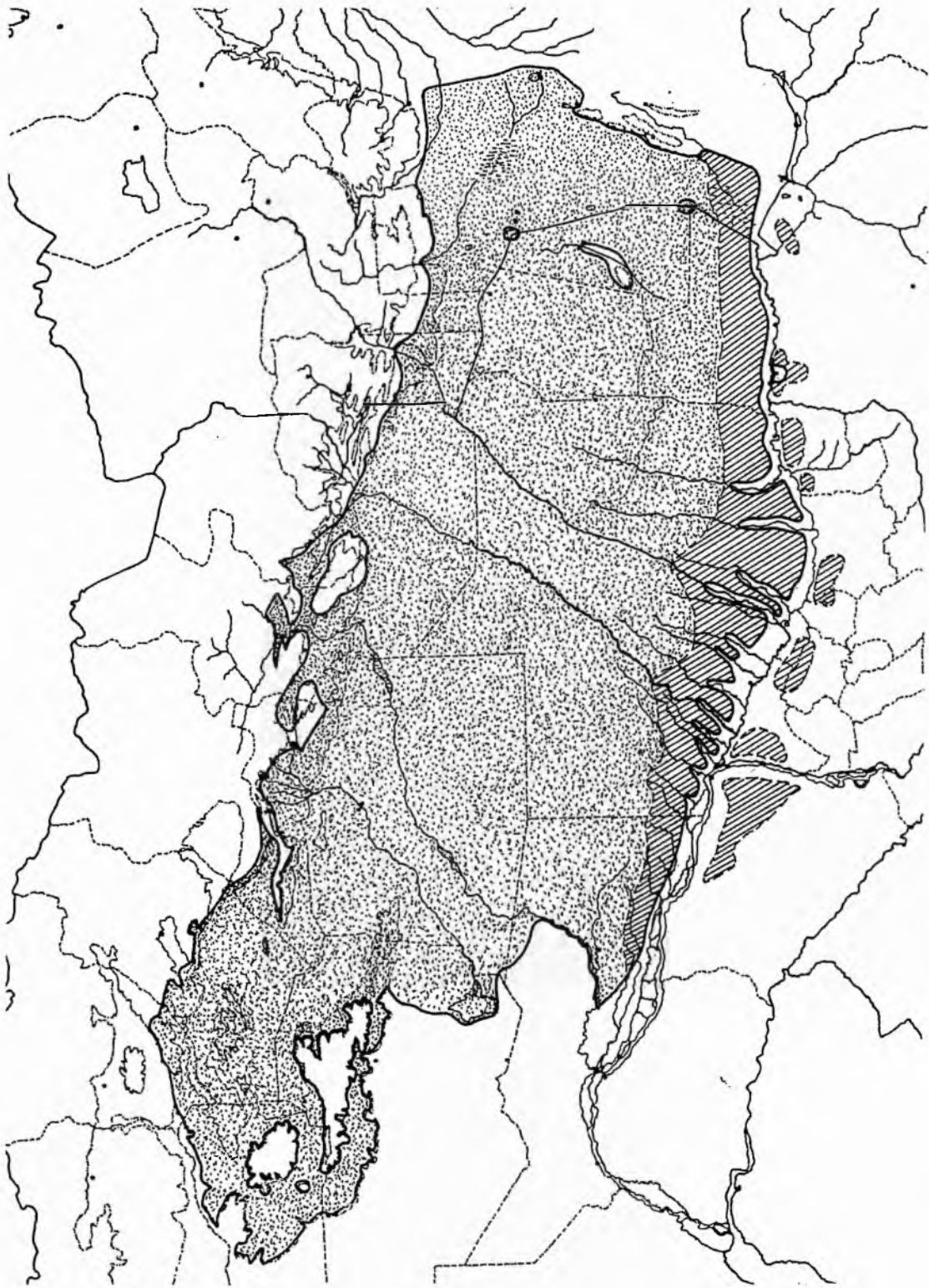
Most of the works on the Paraguayan Chaco (Hochreutiner, 1923; Fiebrig, 1933; Rojas & Carabia, 1945; Tortorelli, 1967) have been very shallow. More recent works have improved the state of the knowledge of the area. Esser's contributions (1982 & 1984) although focused mainly in cacti vegetation have provided a very interesting classification of the Paraguayan Chaco formation and the most detailed vegetation map available (Esser, 1982). It is noteworthy that this last author has characterized the vegetation of the eastern Paraguayan Chaco as transitional ('Übergangsgebiet') since in this area the hygrophilous elements find their westernmost limit (Esser, 1982 & 1984), which is in agreement with the views of the present author.

More recently, during the course of this study, a general survey of the Paraguayan Chaco was published by Ramella & Spichiger (1989; see also Spichiger & Ramella, 1989). Their data on the gallery forests along the river Paraguay tributaries in SE Paraguayan Chaco and those along the Timane-Lagerenza river in the northwest of the region show a floristic composition which unmistakably excludes them from the Chaco s.s.. They are dominated by relatively hygrophilous species such as *Calycophyllum multiflorum*, *Pisonia zapallo*, *Maclura tinctoria*, *Albizia polyantha*, *Geoffroea striata* (Spichiger & Ramella, 1989; Ramella & Spichiger, 1989), which clearly link these forests to communities A, B, D and E in Table 6.1 and separated here from the Chaco s.s.. The descriptions, diagrams and remarks of Ramella & Spichiger (1989) on the vegetation of the scattered hills of NW Paraguayan Chaco are of extreme interest. While surrounded by true Chaco vegetation on the plains, the slopes of the Cerro León and Cerro Cabrera are covered by a deciduous forest of *Anadenanthera colubrina* (very probably var. *cebil*), accompanied by *Pterogyne nitens*, *Astronium urundeuva*, *Amburana cearensis* and *Aspidosperma pyriformis*, which not only show a very strong link with the 'Palo blanco' forest in NW Argentina and the calcareous forests around Corumbá, but also an amazing resemblance of the arboreal caatinga vegetation of NE Brazil (cf. Ch. 3). On top of these hills cerrado-like vegetation has been found, that is savannas of *Tabebuia caraiba*, *Jacaranda cuspidifolia* and *Pseudobombax campestre* (Ramella & Spichiger, 1989). This sequence of

vegetation seems to be repeated in the Santiago and Chiquitos Sierras of Bolivia (Herzog, 1910 & 1912).

By excluding these extraneous communities it is now possible to re-establish the geographical limits of the Chaco as a phytogeographical province. On the basis of a strict floristic list of woody and succulent species (Sect. 4.1), phytosociological study of the more relevant plant communities in the region both in classical and numerical analyses (Ch. 6), and putting the vegetation of this area against the background of similar formations in South America, a map of what is here regarded as Chaco s.s. is presented (Fig. 8.2). It must be noted that the Sierra Chaco, although taken as a separate entity throughout the analysis in Ch. 6, is accepted as part of the Chaco s.s.; however, the *Polylepis australis* woodlands occurring in the Córdoba Sierras should not be regarded as chaquenian, as in Cabrera (1976). These communities comprise basically an Andean flora with little contact with the Chaco itself (Vuilleumier, 1986; Cabido, *in litt.*), and their restriction to N Argentina appear to be attributable to range retraction of the progenitor of *P. australis* during Pleistocene events (Simpson, 1986). In the construction of this new map some previous vegetation maps have been employed; i.e. Coro (1956) and Ellenberg (1981) for the Bolivian Chaco, Verveer (in Hawkes & Hjerting, 1969) for NW Argentina up to La Rioja province, Ragonese & Castiglioni (1970) for SW Chaco in the provinces of La Rioja, San Juan, San Luis and Córdoba in part, Sayago (1969) and Luti et al. (1979) for the Córdoba province, and Lewis (1981) for the southern and eastern limit in the Santa Fe province. Also taken into consideration were the maps of the neighbouring phytogeographic provinces Monte (Morello, 1958) and Espinal (Lewis & Collantes, 1973). The extremely patterned vegetation in the east of the Chaco s.s. cannot be mapped with any precision at this stage with the knowledge available to date. A wide belt of transitional vegetation has been left open to further studies which could determine the exact localities where true Chaco vegetation can be found. However, to delimit this belt, information was taken from maps in Castellanos & Pérez-Moreau (1944), Morello & Adámoli (1967), Ragonese & Castiglioni (1970), Lewis (1981), Esser (1982), and Prado et al. (in press b), together with the present author's field experience and the plant distribution maps here presented (Ch. 5).





**Fig. 8.2:** A new proposal for the geographical limits of the Chaco s.s.. The transitional belt is indicated by oblique hatching.

## 8.2- Chaco *versus* Caatingas:

The idea that there exist strong links between the flora of the Caatingas and Chaco provinces owes much to Dárdano de Andrade-Lima, and the views he expressed in his analysis of the origins of the caatinga flora. Andrade-Lima firmly believed that the flora of the Caatingas was "largely of alien origin, especially at the generic level, and to a lesser degree at the species level", and that these elements "appear have reached the area by a SW-NE migratory route", such that "the source of the majority of caatinga taxa appears to have been the northern part of the Argentinian-Paraguayan-Bolivian Chaco" (Andrade-Lima, 1982, p. 247).

In this latter work Andrade-Lima listed some tree species which, according to him, are subxerophytic or xerophytic plants which are common in arid areas elsewhere but possess disjunctions in NE Brazil. Such examples for the Chaco-Caatingas disjunction were: *Schinopsis brasiliensis*, both the typical and the *glabra* varieties, *Anadenanthera colubrina* var. *cebil* (sub *A. macrocarpa*), *Amburana cearensis*, *Pterogyne nitens*, *Phytolacca dioica*, and *Prosopis ruscifolia*. In fact, however, except *P. ruscifolia* none of these last species are found in any typical Chaco s.s. forest community, but only in river valley vegetation in the eastern border of the Chaco (rivers Paraná, Paraguay, and tributaries), and in the 'Palo blanco' and 'Tipa-Pacará' forests to the west of the Chaco (see Sect. 8.1). This is particularly the case of *Anadenanthera colubrina* var. *cebil* (Altschul, 1964, and Fig. 5.38), *Amburana cearensis* and *Pterogyne nitens* (Fig. 5.40 & 5.43), which are sometimes members of gallery forests in Western Chaco in Argentina but are regarded as non-chaquenian species (Morello & Saravia Toledo, 1959a & b; Adámoli et al., 1972). *Schinopsis brasiliensis* is not a Chaco species in any sense, but rather it is a common tree in NE Brazil in arboreal caatinga (Andrade-Lima, 1981), and its distribution extends towards south, interrupted by cerrado formations, to reappear in Mato Grosso do Sul and northern Paraguay in the vicinity of the river Paraguay, and in Bolivia along the Santiago and Chiquitos ranges and the Yungas area (see Fig. 5.46). Likewise, the Argentine 'ombú', *Phytolacca dioica*, is not a true Chaco species but rather a common tree in the tall forests bordering the river Paraná valley with very few

intrusions of chaquenian character (see Fig. 5.81; also Klein, 1972, and Prado et al., in press a).

The case of *Prosopis ruscifolia* merits a separate analysis; it is in fact a Chaco endemic, since its dispersion area is fully located inside the Chaco s.s. (Fig. 5.7), whereas its presence in the Monte province as stated by Andrade-Lima (1982) has never been established. What is extremely doubtful, however, is whether this species occurs in the Caatingas. All known exsiccata come from a single very old tree in the vicinity of Cachoeira do Roberto, Pernambuco (Neiva & Pena, 1916; Luetzelburg, 1922-23; Ducke, 1953; Andrade-Lima, 1954; Bigarella et al., 1975), which was "once a prosperous village on the cattle trail from Bahia to Piauí" (Andrade-Lima, 1954, p.57). Burkart monographed the genus and confirmed the identity of this specimen but he wondered if this single tree could be a casual introduction to the area (Burkart, 1976, p.248). However, Andrade-Lima (1954 & 1982) took this isolated individual as proof of Chaco species migration to NE Brazil in a drier climatic phase, assuming that other individuals have probably disappeared through the progressive erosion of the area. But *Prosopis ruscifolia* trees live only a moderate life-span, reaching occasionally 80 years (Morello et al., 1971), and it is a very aggressive woody weed in its natural area in Argentina, with a highly palatable indehiscent pod for large herbivores and very particularly for cattle, and so with seeds suited to endozoochorous dispersion (Morello et al., 1971; Burkart, 1976). These characteristics make this species a successful colonizer of disturbed environments in the Chaco. Moreover, the location of this individual in the Caatingas is separated by more than 2,300 km from the bulk of the species in the Chaco, and there is not a single collection or reference to its presence in the intervening area, contrary to what has been shown in Ch. 5 for numerous other species which do link the Caatingas to other seasonal formations of South America. Thus, the evidence points to its occurrence as a casual introduction to NE Brazil, probably through imported cattle.

The levels of generic and specific endemism given for Chaco and Caatingas in Ch. 5 are in agreement with the Takhtajan (1986) criteria employed to characterize floristic provinces of the world, and the higher figures for the Brazilian area seem to follow an expected

latitudinal increment of endemisms (see Major, 1988): tropical Caatingas, as opposed to temperate/subtropical Chaco. Moreover, the Caatingas are far richer than the monotonous Chaco plains in providing varied and numerous habitats (cf. Ch. 3 & 2). Both provinces are then very well defined from this point of view, and even allowing for an overestimation of the degree of endemism, when compared to Major's table (1988) for several regions of the world they are equivalent to those e.g. of the Sonoran desert and the Sahara as regards the Chaco, and to the California floristic province and the Canary islands for the Caatingas. There is no reason, therefore, to regard the Caatingas flora as too low in endemics, as repeatedly stated by Rizzini (1963 & 1979), and more emphatically by Andrade-Lima (1982), who even suggested that the area could not have its own unique flora. On the contrary, the percentages of autochthonous and alien genera and species in the Caatingas are in all probability as high as those of any other well defined floristic province of the world, and even comparable to those of certain islands which usually concentrate the highest figures of endemism (Major, 1988).

In the Introduction of this thesis it has been mentioned that most of the alleged botanical links between Chaco and Caatingas are usually described as pairs of vicariant species (Rizzini, 1963; Veloso, 1964). The currently generally accepted concept of vicariance states that "if populations occupying separate areas are clearly descended from an immediate common ancestor, but are distinct enough in external morphology so that the systematist can always tell them apart, they are known as vicarious species" (Stebbins, 1950). Thus, a detailed knowledge of systematic relationships within the genus is a prerequisite to establish vicariant status with a reasonable degree of certainty. Some of the genera involved in the Chaco-Caatingas links have never been studied monographically since Martius' Flora Brasiliensis, e.g. *Ziziphus*, *Caesalpinia*, *Capparis*. Other genera have had formal taxonomic revisions, e.g. *Schinopsis* (Meyer & Barkley, 1973), *Astronium* (Barkley, 1968), and *Copernicia* (Dahlgren & Glassman, 1961), but with no emphasis on species relationships presented by these authors. However, some preliminary comments and conclusions can be made in these cases.

The genus *Schinopsis* consists of eight species, seven of which were accepted by Meyer & Barkley (1973), and the eighth is the recently reinstated *S. heterophylla* (Muñoz, 1990), apparently a hybrid between *S. quebracho-colorado* and *S. balansae*. However, the present author believes that *S. heterophylla* is conspecific with *S. cornuta*, another species recognized by Meyer & Barkley (1973) and which is the earlier binomial of the two available. With regard to the other species, the characters employed to separate the poorly collected *S. peruviana* from *S. brasiliensis*, that is to say smaller, more numerous leaflets for the former, can be found on the juvenile shoots of the latter. It is presumed likely, therefore, that *S. peruviana* is in fact conspecific with *S. brasiliensis*. Moreover, it is considered that another species, *S. glabra*, likewise does not merit specific status and should be kept as a variety of *S. brasiliensis*, as originally described by Engler. Thus, the genus would be reduced to only five species: *S. brasiliensis*, endemic to the Pleistocenic Arc; *S. quebracho-colorado* and *S. cornuta*, two Chaco endemics; the unifoliolate *S. balansae*; and the orophilous *S. haenkeana*, characteristic of the Sierra Chaco but sometimes present in the 'palo blanco' Forest. If vicariant taxa occur in this genus, it is considered that the most likely case is the pair *S. brasiliensis* - *S. haenkeana*, which are morphologically very close. Vicariance between *S. brasiliensis* and *S. quebracho-colorado* cannot be ruled out, but they show rather more strongly delimited morphological differences (see Prado et al., in press b) than the previous pair of species.

In the genus *Astronium*, the most obviously closest species to the Caatingas tree *Astronium urundeuva* is *A. balansae*<sup>3</sup>, clearly distributed along the Paraguay-Paraná river system (Fig. 5.83) and not in the Chaco s.s. (although a number of researchers would argue it is a true Chaco species). The case of the genus *Copernicia* also allows for some preliminary conclusions, based on the infrageneric arrangement by Dahlgren & Glassman (1961). There are only three species in South America, which are regarded as relatively recent immigrants (Uhl & Dransfield, 1987, pp 204-5): *C. tectorum* (= *C. sancta-martae*) in the Venezuelan Llanos and dry Caribbean vegetation; *C. cerifera* (= *C.*

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<sup>3</sup> Recently Santin (1991) has separated these two species in the reinstated genus *Myracrodruon*.

*prunifera*) exclusive to the Caatingas; and *C. alba* (= *C. australis*) in the Brazilian Pantanal, E Bolivia, central Paraguay along the river Paraguay, and NE Argentina extending well inside the Chaco s.s.. The rest of the genus is mainly confined to the center of distribution in the Greater Antilles, with more than 20 species in Cuba, and two in neighbouring Hispaniola. Both *C. tectorum* and *C. cerifera* have been placed in the Subgenus *Copernicia*, but *C. alba* is on its own in the Subgenus *Coperniciopsis*. The most plausible vicariant pair, therefore, is likely to be a Caribbean-NE Brazil species link, and not *C. cerifera* - *C. alba* as claimed by Rizzini (1963).

The genus *Aspidosperma*, recently studied by Marcondes-Ferreira (1988) and widespread in every subtropical and tropical woody community from Mexico to Argentina (except Chile), consists of 33 species grouped in two subgenera, one with 9 sections and comprising 31 species. The Caatingas species are mainly placed in two sections; sect. *Polyneura*, considered to be relatively unspecialized within the genus, contains *A. polyneuron* and *A. cuspa*, the latter regarded as ancestral species by Marcondes-Ferreira (1988); and sect. *Aspidosperma*, where *A. pyriformium* (by far the most important *Aspidosperma* in the Caatingas) is located together with the widespread cerrado species *A. tomentosa* and *A. macrocarpum*. On the other hand, the two very close chaquenian species *A. quebracho-blanco* and *A. triternatum* are isolated in the most evolved and southernmost sect. *Pungentia*, which is very easily distinguished from the rest of the genus. If this infra-generic scheme is correct, it is unlikely that any vicariad-type links exist between the caatinga and chaquenian species of *Aspidosperma*, as alleged by Rizzini (1963) and Veloso (1964).

A different case is posed by the genus *Geoffroea*; if the present author's criterion is accepted, i.e. regarding *G. striata* and *G. spinosa* as a polymorphic unit and very probably a single species, *Geoffroea* would be reduced to only two species which are certainly vicariads: *G. decorticans* in the Chaco and some related provinces (see Fig. 5.16), and *G. striata/spinosa* in Caatingas, W Ecuador, N Venezuela, central Bolivia and the Paraguay-Paraná system (Fig. 5.58). This would constitute the only unmistakable example of vicariance involving Chaco

and Caatingas at species level, but it should be noted that neither of the two are exclusive to their provinces.

It can be concluded that vicariance links between Chaco and Caatingas are very weak if they exist at all, and that Andrade-Lima's (1982) proposed migratory route SW-NE, in so far it refers to the Chaco flora has to be rejected altogether. There is no chaquenian floristic element following that route up to the Caatingas, and as noted above all of Andrade-Lima's examples are flawed. On the contrary, in some cases the route seems to be exactly the opposite, as the genera *Copernicia* and *Aspidosperma* suggest. We can thus safely reject the proposal that a strong component of the Caatingas flora derives from the Chaco province (Andrade-Lima, 1982), and likewise Rizzini's (1963 & 1979) statement that the Caatingas elements have their origin in equal proportions from the Chaco and the Atlantic rainforest.

There are in fact only three woody species in common between Chaco and Caatingas (Table 8.1): *Parkinsonia aculeata*, *Ximenia americana*, and *Sideroxylon obtusifolium*. Their presence in both areas, however, is meaningless in this context since all three species have very widespread distributions from Mexico to Argentina, occurring in numerous vegetation types, whilst *Ximenia americana* is even pantropical. Besides, the floristic links of the Chaco should be looked for in another direction. Sarmiento (1972 & 1975) showed that the relationship Monte-Chaco is stronger than any other link Monte-arid and semiarid areas in South America, and furthermore, the floristic contacts of the Chaco with dry Andean valleys and the Sonora desert must not be overlooked.

Rather, the floristic dissimilarities between the Chaco and Caatingas are striking, and these most likely lie in the lack of common physical environmental features between these two areas. Thus, there is a fundamental difference in their geological origin and geomorphology: the Chaco comprises huge sedimentary, monotonous plains of both æolian and more recent alluvial genesis, modelled by a basically endorheic river system. In contrast, the Caatingas are undulating peneplains of erosive origin which left the ancient Pre-Cambrian Brazilian shield exposed and furrowed by numerous short-lived exorheic

**TABLE 8.1:** Genera and species in common between Chaco s.s. and Caatingas.

GENERA	SPECIES	References for Chaco
1- <i>Acacia</i>		Cialdella, 1984
2- <i>Aspidosperma</i>		Marcondes-Ferreira, 1988
3- <i>Ayenia</i>		Cristóbal, 1960
4- <i>Bauhinia</i>		Fortunato, 1986
5- <i>Bougainvillea</i>		Toursarkissian, 1975
6- <i>Bromelia</i>		Smith & Downs, 1974-79
7- <i>Caesalpinia</i>		Burkart, 1952
8- <i>Capparis</i>		Gómez, 1953
9- <i>Ceiba</i>		Gibbs (pers. comm.)
10- <i>Celtis</i>		Morello & Adámoli, 1974
11- <i>Cereus</i>		Kiesling, 1975
12- <i>Copernicia</i>		Morello & Adámoli, 1974
13- <i>Coursetia</i>		Lavin, 1988
14- <i>Croton</i>		Sayago, 1969
15- <i>Desmanthus</i>		Burkart, 1952
16- <i>Dyckia</i>		Smith & Downs, 1974-79
17- <i>Eriocereus</i>		Kiesling, 1975
18- <i>Erythroxylum</i>		Morello et al., 1971
19- <i>Euphorbia</i>		Subils, 1977
20- <i>Geoffroea</i>		Burkart, 1952
21- <i>Ipomoea</i>		Sayago, 1969
22- <i>Jacaratia</i>		Badillo, 1971
23- <i>Jatropha</i>		Castellanos, 1958
24- <i>Lippia</i>		Luti et al., 1979
25- <i>Maytenus</i>		Morello & Adámoli, 1974
26- <i>Mimosa</i>		Burkart, 1952
27- <i>Opuntia</i>		Kiesling, 1975



28- <i>Parkinsonia</i>	<i>aculeata</i> L.	Burkart, 1952
29- <i>Pavonia</i>		Sayago, 1969
30- <i>Pereskia</i>		Leuenberger, 1986
31- <i>Quiabentia</i>		Castellanos, 1952
32- <i>Ruprechtia</i>		Cocucci, 1958
33- <i>Sapium</i>		Jablonski, 1967
34- <i>Schinopsis</i>		Meyer & Barkley, 1973
35- <i>Senna</i>		Irwin & Barneby, 1982
36- <i>Sida</i>		Sayago, 1969
37- <i>Sideroxylon</i>	<i>obtusifolium</i> (Roem. & Schult.) Pennington <b>subsp. <i>obtusifolium</i></b>	Pennington, 1990
38- <i>Solanum</i>		Morton, 1976
39- <i>Tabebuia</i>		Morello & Adámoli, 1974
40- <i>Wissadula</i>		Morello & Adámoli, 1974
41- <i>Ximenia</i>	<i>americana</i> L.	Sleumer, 1984
42- <i>Ziziphus</i>		Morello & Adámoli, 1974

streams. There are also important differences in climate between the two areas: no area within the Chaco s.s. is free from frosts, and although the mean annual temperature is relatively low (17 to 24°C, from south to north), most of the area is enclosed within the highest absolute maxima isotherm of South America (47°C), and there is a moderate variation coefficient of yearly rainfall (from 0.2 to 0.3, in Galmarini & Raffo del Campo, 1964). In contrast, the occurrence of frosts in the tropical Caatingas has never been registered, and whilst the mean annual temperature is higher (26 to 28°C), the absolute maxima is rarely over 40°C. There is an extreme rainfall irregularity with the variation coefficient up to 0.55 and periodical catastrophic droughts lasting over a year long. With regard to soils, the main features of the Chaco s.s. are particles smaller than 2 mm, generalized poor drainage because of clay textured horizons, abundance of salts and high pH. The Caatingas soils, on the other hand, are characteristic for the abundance of pebbles, stones and massive rock outcroppings, scarcity of saline areas because of the good drainage and the exorheic river system, and pH probably tending to neutral.

There is an additional and interesting ecological-floristic difference between Chaco and Caatingas. The river valleys vegetation and gallery forests in NE Brazil comprise some widespread species (*Erythrina velutina*, *G. striata/spinosa*, *Sideroxylon obtusifolium*), endemic elements of the Caatingas (*Ziziphus joazeiro*, *Maytenus rigida*, *Capparis yco*, *Pilosocereus gounellei*, *Cereus jamacaru*), and even two species which are not only endemic but can be found solely in these environments: *Copernicia cerifera* and *Licania rigida*. On the contrary, the homologous vegetation in the Chaco plains is generally dominated by alien elements of widespread tropical distribution (including extensions to the Caatingas!), or species which grow in nearly pure populations in riverine conditions all over the continent (*Salix humboldtiana*, *Tessaria integrifolia*). There is certainly no endemic chaquenian species restricted to riparian environments, as found in the Caatingas. This may reflect a relative lack of isolation, or indicate that present climatic conditions in the Caatingas, and consequently the hydrographic regime, have prevailed for a longer period than those of the Chaco, where there was not enough evolutionary time for speciation of

Chaco taxa but rather a more recent invasion of alien elements better adapted to such habitats.

At the beginning of this study two basic methodological approaches were adopted: (a) to build up reliable data base of floristic lists of the major phytogeographical units involved, and (b) to map accurately the distributions of the more important woody species involved in the Chaco and Caatingas regions. It soon became apparent that the Caatingas species, far from appearing in the Chaco, were conspicuous by their absence from this area, although many taxa occurred in formations peripheral to the Chaco *s.s.*. From the comparison of the Chaco and Caatingas floristic lists (Sect. 4.1 & 4.2) arouse Table 8.1 shown above, recording all genera and the only three woody species they have in common. The same comparison was made for the Caatingas and the Subandean Piedmont Forests floristic lists; the results are shown in Table 8.2. There are 51 woody and succulent species and 109 genera in common between the Caatingas and the 'Palo blanco' and 'Tipa-Pacar' deciduous forests.

A similar comparison was performed with what was called here '2<sup>nd</sup> nucleus' of the Pleistocenic Arc (see Sect. 5.3.1), that is to say the area encompassed by the Paraguay-Paraná river system in central Paraguay and NE Argentina. This area groups a number of different but related formations of which a floristic list is not here provided, and consists of a rather arbitrary clustering of plant communities that can be provisionally equated to Cabrera & Willink's (1980) 'Selva Subtropical Paranense' in the Paranense phytogeographic province. However, the presence or absence of Caatingas elements was anyhow confirmed through the relevant literature, as cited in Table 8.3, and they share 66 species and 109 genera.

In Table 8.4 the results of the floristic comparison is summarized; the percentages of the total flora of the Caatingas represented by the number of species and genera in common is provided. Thus, it can be seen that only 0.69% of the woody and succulent species of the Caatingas are recorded for the Chaco *s.s.*, and 21.11% of all Caatingas genera. More striking figures are obtained derived from the comparison of the Caatingas flora with the '2<sup>nd</sup> nucleus' and '3<sup>rd</sup>

TABLE 8.2: Genera and species in common between the Subandean Piedmont Forests and Caatingas.

GENERA	SPECIES	References for Sub-Andean Piedmont Forests
1- <i>Acacia</i>		Cialdella, 1984
2- <i>Aechmea</i>		Ragonese & Castigl., 1970
3- <i>Aeschynomene</i>		Burkart, 1952
4- <i>Albizia</i>	<i>polyantha</i> (Spr. f.) Lewis	Adámoli et al., 1972
5- <i>Amburana</i>	<i>cearensis</i> (Fr. All.) Smith	Cabrera, 1976
6- <i>Anadenanthera</i>	<i>colubrina</i> (Vell.) Bren. var. <i>cebil</i> (Grisebach) Altschul	Cabrera, 1976
7- <i>Arrabidaea</i>	<i>corallina</i> (Jacq.) Sandw. [Bolivia]	Fabris, 1965
8- <i>Aspidosperma</i>		Marcondes-Ferreira, 1988
9- <i>Astronium</i>	<i>urundeuva</i> (Fr. All.) En.	Cabrera, 1976
10- <i>Ayenia</i>	<i>tomentosa</i> L. [Bolivia]	Cristóbal, 1960
11- <i>Bauhinia</i>		Fortunato, 1986
12- <i>Bougainvillea</i>		Toursarkissian, 1975
13- <i>Brasiliopuntia</i>		Castellanos, 1944
14- <i>Bromelia</i>		Smith & Downs, 1974-79
15- <i>Brunfelsia</i>	<i>uniflora</i> (Pohl) D. Don	Plowman, 1979
16- <i>Byttneria</i>	<i>scabra</i> L. [Bolivia]	Cristóbal, 1976
17- <i>Caesalpinia</i>		Burkart, 1952
18- <i>Calliandra</i>		Burkart, 1952
19- <i>Canavalia</i>	<i>brasiliensis</i> Mart. ex Benth.	Burkart, 1952
20- <i>Capparis</i>		Meyer, 1944

21- <i>Carica</i>	<i>quercifolia</i> (St.-Hil.) Hier.	Badillo, 1971
22- <i>Ceiba</i>		Gibbs (pers. comm.)
23- <i>Celtis</i>	<i>pubescens</i> (Kth.) Spreng.	Romanczuk & Mart., 1978
24- <i>Cereus</i>		Adámoli et al., 1972
25- <i>Chamaecrista</i>		Irwin & Barneby, 1982
26- <i>Cnidoscolus</i>	<i>vitifolius</i> Mill. ex Pohl	Legname, 1982
27- <i>Cochlospermum</i>	<i>vitifolium</i> (W.) Spr. [Bol.]	Poppendieck, 1981
28- <i>Combretum</i>	<i>leprosum</i> Mart. [Bolivia]	Exell, 1953
29- <i>Copaifera</i>	[Bolivia]	Dwyer, 1951
30- <i>Copernicia</i>		Dahlgren & Glass, 1961
31- <i>Cordia</i>	<i>trichotoma</i> (Vell.) Arrab. ex Steud.	Legname, 1982
32- <i>Courseia</i>		Lavin, 1988
33- <i>Coutarea</i>	<i>hexandra</i> (Jacq.) Schum.	Legname, 1982
34- <i>Croton</i>		Legname, 1982
35- <i>Dasyphyllum</i>		Cabrera, 1953
36- <i>Desmanthus</i>	<i>virgatus</i> (L.) Willd.	Burkart, 1952
37- <i>Ditaxis</i>		O'Donnell & Lourteig, 1942
38- <i>Dyckia</i>		Smith & Downs, 1974-79
39- <i>Enterolobium</i>	<i>contortisiliquum</i> (Vell.) Morong	Cabrera, 1976
40- <i>Eriotheca</i>		Robyns, 1963
41- <i>Erythrina</i>		Cabrera, 1976
42- <i>Erythroxylum</i>		Legname, 1982
43- <i>Espositoa</i>	[Bolivia]	Buxbaum, 1959 & 1969
44- <i>Euphorbia</i>		Subils, 1977
45- <i>Galphimia</i>	<i>brasiliensis</i> (L.) A. Juss. [Bolivia]	Niedenau, 1928

46- <i>Geoffroea</i>	<i>striata</i> (W.)Morong [Bol.]	herbarium specimens
47- <i>Heteropterys</i>	<i>syringifolia</i> Griseb.[Bol.]	Niedenzu, 1928
48- <i>Ipomoea</i>	<i>carnea</i> Jacq. subsp. <i>fistulosa</i> (Mart. ex Ch.) D. Austin	O'Donnell, 1959
49- <i>Jacaranda</i>		Digilio & Legname, 1966
50- <i>Jacaratia</i>		Badillo, 1971
51- <i>Jatropha</i>		Pax, 1959
52- <i>Lagascea</i>	<i>mollis</i> Cav.	Stuessy, 1978
53- <i>Lantana</i>		Devoto & Rothkugel, 1942
54- <i>Lippia</i>		Devoto & Rothkugel, 1942
55- <i>Lonchocarpus</i>		Legname, 1982
56- <i>Loxopterigium</i>		Legname, 1982
57- <i>Luehea</i>		Legname, 1982
58- <i>Machaerium</i>	<i>acutifolium</i> Vog.	Burkart, 1952
59- <i>Maclura</i>	<i>tinctoria</i> (L.)Don ex Steud	Vázquez Ávila, 1985
60- <i>Manihot</i>		Rogers & Appan, 1973
61- <i>Maytenus</i>		Legname, 1982
62- <i>Melochia</i>		Goldberg, 1967
63- <i>Mimosa</i>		Burkart, 1952
64- <i>Myroxylon</i>	<i>balsamum</i> (L.) Harms	Cabrera, 1976
65- <i>Opuntia</i>		Kiesling, 1975
66- <i>Parapiptadenia</i>		Cabrera, 1976
67- <i>Patagonula</i>		Legname, 1982
68- <i>Pavonia</i>		Meyer, 1963
69- <i>Peltophorum</i>	<i>dubium</i> (Spr.)Taub. [Bol.]	herbarium specimens
70- <i>Pentapanax</i>		Meyer, 1944
71- <i>Pereskia</i>		Leuenberger, 1986
72- <i>Petiveria</i>	<i>alliacea</i> L.	Meyer, 1944
73- <i>Phyllostylon</i>		Cabrera, 1976

74- <i>Phytolacca</i>		Meyer, 1963
75- <i>Piptadenia</i>	<i>viridiflora</i> (Kth.) Benth.	Burkart, 1952
76- <i>Pisonia</i>		Meyer, 1963
77- <i>Pithecellobium</i>		Hoc, 1981
78- <i>Platypodium</i>	<i>elegans</i> Vog. [Bolivia]	herbarium specimens
79- <i>Pouteria</i>	<i>gardneriana</i> (DC.)Radlk. [Bolivia]	Pennington, unpubl. ms.
80- <i>Prockia</i>	<i>crucis</i> P.Browne ex L.	Cabrera, 1976
81- <i>Pseudobombax</i>		Robyns, 1963
82- <i>Pterocarpus</i>	<i>violaceus</i> Vog. [Bolivia]	Rojas, 1972
83- <i>Pterogyne</i>	<i>nitens</i> Tul.	Cabrera, 1976
84- <i>Ptilochaeta</i>		Niedenau, 1928
85- <i>Quiabentia</i>	<i>zehntneri</i> (Br. & Rose) Br. & Rose [Bolivia]	Castellanos, 1952
86- <i>Randia</i>	<i>armata</i> (Sw.) DC.	Legname, 1982
87- <i>Rauwolfia</i>		Legname, 1982
88- <i>Ruprechtia</i>	<i>laxiflora</i> Meissn.	Cabrera, 1976
89- <i>Sapindus</i>	<i>saponaria</i> L.	Legname, 1982
90- <i>Sapium</i>		Jablonski, 1967
91- <i>Schinopsis</i>	<i>brasiliensis</i> Engler [Bol.]	Meyer & Barkley, 1973
92- <i>Schoepfia</i>		Sleumer, 1984
93- <i>Sebastiania</i>		Digilio & Legname, 1966
94- <i>Seguiera</i>	<i>aculeata</i> Jacq.	Rohwer, 1982
95- <i>Senna</i>	<i>spectabilis</i> (DC.) Ir. & Bar.	Irwin & Barneby, 1982
96- <i>Serjania</i>	<i>glabrata</i> Kunth	Radlkofer, 1956
97- <i>Sesbania</i>	<i>exasperata</i> Kunth	Burkart, 1952
98- <i>Sida</i>	<i>cordifolia</i> L.	herbarium specimens
99- <i>Sideroxylon</i>	<i>obtusifolium</i> (Roem. & Schult.) Pennington subsp. <i>obtusifolium</i>	Pennington, 1990
100- <i>Solanum</i>	<i>granuloso-leprosum</i> Dunal	Legname, 1982

101- <i>Sterculia</i>	<i>stricta</i> S - H . & Naud.[Bol.]	herbarium specimens
102- <i>Stigma. phyllum</i>	[Bolivia]	Niedenau, 1928
103- <i>Suaresia</i>	[Bolivia]	Cowan, 1968
104- <i>Tabebuia</i>	<i>caraiiba</i> (Mart.) Bur.[Bol.]	herbarium specimens
<i>Tabebuia</i>	<i>impetiginosa</i> (Mart. ex DC.) Standley	Gentry, 1979
105- <i>Terminalia</i>		Exell, 1940
106- <i>Tournefortia</i>	<i>rubicunda</i> Salzm. ex DC.	Devoto & Rothkugel, 1942
107- <i>Trichilia</i>		Pennington, 1981
108- <i>Ximenesia</i>	<i>americana</i> L. var. <i>argentinensis</i> De Filipps	Sleumer, 1984
109- <i>Ziziphus</i>		Escalante, 1946

TABLE 8.3: Genera and species in common between the vegetation of the Paraguay-Paraná river system and the Caatingas.

GENERA	SPECIES	References for the Paraguay-Paraná river syst. vegetation
1- <i>Acacia</i>	<i>farnesiana</i> (L.) Willd.	Cialdella, 1984
<i>Acacia</i>	<i>maritii</i> Benth.	Cialdella, 1984
<i>Acacia</i>	<i>monacantha</i> Willd.	Cialdella, 1984
<i>Acacia</i>	<i>polyphylla</i> DC.	Cialdella, 1984
2- <i>Acosmium</i>		Burkart, 1952
3- <i>Aechmea</i>		Ragonese & Castigl., 1970
4- <i>Aeschynomene</i>		Burkart, 1952
5- <i>Albizia</i>	<i>polyantha</i> (Spr. f.) Lewis	Burkart, 1952
6- <i>Amburana</i>	<i>cearensis</i> (Fr.All.) Smith	Burkart, 1952
7- <i>Anadenanthera</i>	<i>colubrina</i> (Vell.) Bren. var. <i>cebil</i> (Grisebach) Altschul	Cabrera, 1976
8- <i>Arrabidaea</i>	<i>corallina</i> (Jacq.) Sandw.	Fabris, 1965
9- <i>Aspidosperma</i>	<i>cuspa</i> (Kunth) Blake	Marcondes-Ferreira, 1988
<i>Aspidosperma</i>	<i>polynuron</i> Müll. Arg.	Marcondes-Ferreira, 1988
<i>Aspidosperma</i>	<i>pyrifolium</i> Mart.	Marcondes-Ferreira, 1988
10- <i>Astronium</i>	<i>urundeuva</i> (Fr.All.) Ex.	Barkley, 1968
11- <i>Ayenia</i>	<i>tomentosa</i> L. [Bolivia]	Cristóbal, 1960
12- <i>Balfourodendron</i>	<i>riedelianum</i> (Engl.) Engl.	Cabrera, 1976
13- <i>Bauhinia</i>	<i>forficata</i> Link	Fortunato, 1986
14- <i>Brasiliopuntia</i>		Castellanos, 1944

15- <i>Bromelia</i>		Smith & Downs, 1974-79
16- <i>Brunfelsia</i>		Plowman, 1979
17- <i>Byttneria</i>	<i>scabra</i> L.	Cristóbal, 1976
18- <i>Caesalpinia</i>		Burkart, 1952
19- <i>Calliandra</i>		Burkart, 1952
20- <i>Calopogonium</i>		Burkart, 1952
21- <i>Campomanesia</i>		Landrum, 1986
22- <i>Canavalia</i>		Burkart, 1952
23- <i>Capparis</i>		Gómez, 1953
24- <i>Carica</i>	<i>quercifolia</i> (St.-Hil.) Hier.	Badillo, 1971
25- <i>Ceiba</i>		Gibbs (pers. comm.)
26- <i>Celtis</i>	<i>pubescens</i> (Kth.) Spreng.	Romanczuk & Mart., 1978
27- <i>Cereus</i>		Cabrera, 1976
28- <i>Chamaecrista</i>	<i>desvauxii</i> (Coll.) Killip	Irwin & Barneby, 1982
<i>Chamaecrista</i>	<i>rotundifolia</i> (Pers.)Gre en.	herbarium specimens
29- <i>Cnidoscolus</i>		Pax, 1958
30- <i>Combretum</i>	<i>fruticosum</i> (Loefl.)Stuntz	Exell, 1953
<i>Combretum</i>	<i>lanceolatum</i> P. e x Eichl.	Exell, 1953
<i>Combretum</i>	<i>laxum</i> Jacq.	Exell, 1953
<i>Combretum</i>	<i>leprosum</i> Mart.	Exell, 1953
31- <i>Copaifera</i>	<i>langsдорffii</i> Desf.	Burkart, 1952
32- <i>Copernicia</i>		Dahlgren & Glass., 1961
33- <i>Cordia</i>	<i>trichotoma</i> (Vell.) Arrab. ex Steud.	Cabrera, 1976
34- <i>Coursetia</i>		Lavin, 1988
35- <i>Coutarea</i>	<i>hexandra</i> (Jacq.)Schum.	Devoto & Rothkugel, 1942
36- <i>Crateva</i>	<i>tapia</i> L.	Gómez, 1953
37- <i>Cratylia</i>		Burkart, 1952
38- <i>Croton</i>		Cabrera, 1976



39- <i>Dalbergia</i>	<i>frutescens</i> (Vell.) Britt.	Burkart, 1952
40- <i>Dasyphyllum</i>		Cabrera, 1953 & 1959
41- <i>Desmanthus</i>	<i>virgatus</i> (L.) Willd.	Burkart, 1952
42- <i>Dicella</i>	<i>bracteosa</i> (A.Juss.) Gris.	Nieden zu, 1928
43- <i>Dioclea</i>		Burkart, 1952
44- <i>Discolobium</i>		Burkart, 1952
45- <i>Ditaxis</i>		Pax & Hoffmann, 1958a
46- <i>Dyckia</i>		Smith & Downs, 1974- 79
47- <i>Enterolobium</i>	<i>contortisiliquum</i> (Vell.) Morong	Burkart, 1952
48- <i>Erythrina</i>		Cabrera, 1976
49- <i>Erythroxyllum</i>		Cabrera, 1976
50- <i>Euphorbia</i>		Subils, 1977
51- <i>Galphimia</i>	<i>brasiliensis</i> (L.) A.Juss.	Nieden zu, 1928
52- <i>Geoffroea</i>	<i>striata</i> (Willd.) Morong	Burkart, 1949
53- <i>Guettarda</i>		Boelcke, 1981
54- <i>Heteropterys</i>	<i>syringifolia</i> Griseb.	Nieden zu, 1928
55- <i>Hymenaea</i>	<i>courbaril</i> L. var. <i>stilbo-</i> <i>carpa</i> (Hayne) Lee & Lang.	Lee & Langenheim, 1975
<i>Hymenaea</i>	<i>martiana</i> Hayne	Lee & Langenheim, 1975
56- <i>Ipomoea</i>	<i>asarifolia</i> (Desr.) Roem. & Schult.	O'Donell, 1959
<i>Ipomoea</i>	<i>carnea</i> Jacq. subsp. <i>fis-tulosa</i> (Mart. ex Ch.) Aust.	O'Donell, 1959
57- <i>Jacaratia</i>		Badillo, 1971
58- <i>Jatropha</i>		Pax, 1959
59- <i>Lagascea</i>	<i>mollis</i> Cav.	Stuessy, 1978
60- <i>Lantana</i>		Devoto & Rothkugel, 1942

61- <i>Lippia</i>		Devoto & Rothkugel, 1942
62- <i>Lonchocarpus</i>		Burkart, 1952
63- <i>Luehea</i>		Cabrera, 1976
64- <i>Machaerium acutifolium</i> Vog.		Burkart, 1952
65- <i>Maciura tinctoria</i> (L.) Don ex Steud		Vázquez Ávila, 1985
66- <i>Manihot</i>		Rogers & Appan, 1973
67- <i>Maytenus</i>		herbarium specimens
68- <i>Melochia</i>		Golberg, 1967
69- <i>Mimosa hexandra</i> Micheli		Burkart, 1952
	<i>pigra</i> L.	Burkart, 1952
70- <i>Opuntia</i>		Kiesling, 1975
71- <i>Parapiptadenia</i>		Cabrera, 1976
72- <i>Patagonula</i>		Cabrera, 1976
73- <i>Paonia</i>		herbarium specimens
74- <i>Peltophorum dubium</i> (Spr.) Taub.		Burkart, 1952
75- <i>Pentapanax</i>		herbarium specimens
76- <i>Pereskia</i>		Leuenberger, 1986
77- <i>Petiveria alliacea</i> L.		Franceschi et al., 1985
78- <i>Phyllostylon</i>		Cabrera, 1976
79- <i>Phytolacca dioica</i> L.		Lewis & Fire, 1981
80- <i>Pisonia</i>		Prado et al., in press a
81- <i>Pithecellobium</i>		Hoc, 1981
82- <i>Platypodium elegans</i> Vog.		herbarium specimens
83- <i>Poecilanihe</i>		Burkart, 1952
84- <i>Pouteria Gardneriana</i> (DC.) Radlk.		Pennington, 1990
85- <i>Pterocarpus</i>		Burkart, 1952
86- <i>Pterogyne nitens</i> Tul.		Cabrera, 1976
87- <i>Randia armata</i> (Sw.) DC.		Boelscke, 1981
88- <i>Ruprechtia laxiflora</i> Meissn.		Cabrera, 1976
89- <i>Scapindus saponaria</i> L.		Prado et al., in press a
90- <i>Sapium</i>		Cabrera, 1976
91- <i>Schinopsis brasiliensis</i> Engler [Bol.]		Meyer & Barkley, 1973

92- <i>Schoepfia</i>	<i>brasiliensis</i> DC.	Sleumer, 1984
93- <i>Sebastiania</i>		Cabrera, 1976
94- <i>Seguieria aculeata</i> Jacq.		Rohwer, 1982
95- <i>Senna</i>		Irwin & Barneby, 1982
96- <i>Serjania glabrata</i> Kunth		Radlkofer, 1956
97- <i>Sesbania exasperata</i> Kunth		Burkart, 1952
98- <i>Sida cordifolia</i> L.		herbarium specimens
99- <i>Sideroxylon obtusifolium</i> (Roem. & Schult.) Pennington		Pennington, 1990
	<i>subsp. obtusifolium</i>	
100- <i>Solanum granuloso-leprosum</i> Dunal		Prado et al., in press a
101- <i>Stachytarpheta</i>		herbarium specimens
102- <i>Sterculia striata</i> S.H. & Naud.		herbarium specimens
103- <i>Stigma phyllium</i>		Niedenau, 1928
104- <i>Tabebuia caraba</i> (Mart.) Bur.[Bol.]		herbarium specimens
	<i>impetiginosa</i> (Mart. ex DC.) Standley	Gentry, 1979
105- <i>Terminalia</i>		Exell, 1940
106- <i>Tournefortia rubicunda</i> Salzm. ex DC.		Devoto & Rothkugel, 1942
107- <i>Trichilia hirta</i> L.		Pennington, 1981
108- <i>Vitex</i>		Troncoso, 1974
109- <i>Ziziphus</i>		Escalante, 1946

nucleus' of the Pleistocenic Arc: 11.77% of Caatingas species appear in the piedmont deciduous forests of 'Palo blanco' and 'Tipa-Pacar\'a' in SW Bolivia-NW Argentina, and about 55% of the genera, whereas the '2<sup>nd</sup> nucleus' shares about 15% and 55% respectively. While there are no differences at generic level in the last two cases, there is a sizeable difference at specific level. However, it should be emphasized that the '2<sup>nd</sup> nucleus' is basically an artifact devised here to facilitate the analysis, since it comprises an area which although subjected to a single type of climate, groups very different geological substrata - Pre-Cambrian rocks in Misiones and E Paraguay, alluvial and æolian sedimentary areas, and calcareous outcrops as those of Corumbá and N Paraguay in the Apa river region- and also fundamentally different types of plant communities. It is beyond the scope of this study to try to analyze the vegetation of this sector to delimit the units enclosed and consequently pinpoint those which are floristically closer to the Caatingas, although obviously those on calcareous outcrops show the stronger links (Ratter et al., 1988b). In contrast, the Subandean Piedmont Forests comprise only two forest subtypes: the 'Palo blanco' and 'Tipa-Pacar\'a' Forests. These are floristically very close to each other and only distinguishable because of a latitudinal impoverishment. Together they constitute a well-defined phytogeographic unit (Cabrera, 1976), clearly detached from the Chaco s.s. vegetation and the upland wetter subtropical forest (Meyer, 1963; Vervoorst, 1982). In this case, therefore, the comparison with the Caatingas flora is more realistic since the '3<sup>rd</sup> nucleus' involves a much smaller area and only one definite formation.

The phytosociological analyses undertaken in the present study (Ch. 6) agree with Cabrera (1953 & 1976) and confirm that the Subandean Piedmont Forests (*sub* 'Transitional Forests' or 'Bosques de Transición' in the Argentine literature) cannot pertain to the Chaco province, and indeed Cabrera & Willink (1980) grouped them in their Amazonian Dominion. Since, however, the Caatingas province is floristically closer to the Subandean Piedmont Forests than to the Chaco, having in common with the former not only an appreciable number of woody species, but also some that are very important and sometimes dominant in both formations (i.e. *Anadenanthera colubrina* var. *cebil*, *Pterogyne nitens*, *Tabebuia impetiginosa*, *Astronium urundeuva*, *Myroxylon balsamum*,

**TABLE 8.4: Number of species and genera in common between the Caatingas and the Chaco s.s., the Subandean Piedmont Forests and the vegetation of the Paraguay-Paraná river system. Figures of species and genera in common are also expressed as percentages of the Caatingas totals.**

CAATINGAS	CHACO s.s.		SUBANDEAN PIEDMONT FORESTS (3rd nucleus)		PARAGUAY-PARANA RIVER SYSTEM (2nd nuc.)	
	Nº common	%	Nº common	%	Nº common	%
SPECIES (433)	3	0.69	51	11.77	66	15.24
GENERA (199)	42	21.11	109	54.77	109	54.77

*Amburana cearensis*, *Piptadenia viridiflora*, etc.), it can be concluded that there is no reason to retain the Caatingas province within the Chaquenian Dominion, as proposed by Cabrera & Willink (1980). On the contrary, on this evidence, it should logically be grouped within their own concept of the Amazonian Dominion (*sensu* Cabrera & Willink, 1980). Consequently, these authors hierarchical classification of Latin America vegetation should be modified as follows:

## II- Región Neotropical

### C- Dominio Amazónico

- 1- Provincia Amazónica
- 2- Provincia Pacífica
- 3- Provincia de los Yungas<sup>4</sup>
- 4- Provincia Venezolana
- 5- Provincia de los Cerrados
- 6- Provincia Paranense<sup>5</sup>
- 7- Provincia de los Llanos<sup>6</sup>
- 8- Provincia Atlántica
- 9- Provincia del Páramo
- 10- Provincia de las Caatingas

### E- Dominio Chaqueño

- 1- Provincia Chaqueña (s.s.)
- 2- Provincia del Espinal
- 3- Provincia Prepuneña
- 4- Provincia del Monte
- 5- Provincia Pampeana

## II- Neotropical Region

### C- Amazonian Dominion

- 1- Amazonian Province
- 2- Pacific Province
- 3- Yungas Province
- 4- Venezuelan Province
- 5- Cerrados Province
- 6- Paranense Province
- 7- Llanos Province
- 8- Atlantic Province
- 9- Paramo Province
- 10- Caatingas Province

### E- Chaquenian Dominion

- 1- Chaco Province (s.s.)
- 2- Espinal Province
- 3- Prepuna Province
- 4- Monte Province
- 5- Pampean Province

In this respect, the position sustained in this thesis finds further strong support in the numerical analyses performed in Sect. 6.2, at both specific and generic level. The Caatingas have never been

<sup>4</sup> 'Yungas' is used in masculine rendering by the Bolivian population who coined the term (Cárdenas, 1945; Braun, 1956), instead of feminine as employed by Cabrera (1976) and Cabrera & Willink (1980).

<sup>5</sup> Includes the 'Selva de Ribera' and the Austro-Brazilian Transitional Forest units.

<sup>6</sup> 'Sabana' province in the original; 'sabana' (=savanna) is a generic term that denominates a particular formation (*sensu* Beard, 1953), and its use for a phytogeographical province is not advisable, as it could be employed e.g. for the Cerrados province as well. 'Llanos', the autochthonous name in Colombia and Venezuela for the Orinoco plains savannas, is here recommended (see Sarmiento, 1983).

grouped with the representatives of the Chaquenan Dominion included in the analysis. On the contrary, they appear very closely related to the Subandean Piedmont Forests, and both of them to the rest of the seasonal formations of the Amazonian Dominion, with which they have formed fairly consistent clusters. There are also profound contacts between the Caatingas and the vegetation of the Guajira province.

### 8.3- The origin of the Caatingas flora:

It can be postulated that the Caatingas vegetation has been in the present position for a very long period, as indeed some geological evidence seems to indicate (Tricart, 1961). Nevertheless, it was also subject to the Pleistocenic wet-dry cycles, particularly in the Mata de Cipó area and central San Francisco valley, which were even drier during certain periods (Tricart, 1961 & 1985). If the Caatingas have been firmly established since the end of the Tertiary (Ab' Sáber, 1974), a marked degree of endemism would be expected in the flora and fauna. This is the case as regards plants (see preceding discussion), and although the picture is much more obscure with respect to mammals (Mares et al., 1985), it is also true for the rich endemic bird fauna (see Ch. 7). The particularly numerous endemic genera and species in the Cactaceae, a family nearly restricted to South America, also supports the hypothesis of long established Caatingas.

Nevertheless, both endemic and non-endemic plant taxa may have an alien origin within the continent. Some migratory routes (Fig. 8.3) can be postulated for the Caatingas flora from the available information in taxonomic monographs and the distribution maps presented in this thesis (Ch. 5).

**a- The African connection:** although the African-South American angiosperm connection is rather polemical (compare Raven & Axelrod, 1974, *vs.* Thorne, 1978), a number of pantropical genera could have entered South America via the Caatingas (or viceversa!) at the time of a closer relative position to Africa (Raven & Axelrod, 1974; Gillet, 1979), such as *Ziziphus*, *Cochlospermum*, *Parkinsonia*, etc.; two potential examples are analyzed below. The only known American species of *Commiphora*, a genus of some 185 species otherwise almost entirely African (a few species occur in Arabia and India), is *C. leptophloeos*,



**Fig. 8.3:** Postulated migratory routes reputable for the origin of the Caatingas flora (see explanation in text).

previously recognized as *Bursera* simply because it had been collected in South America and not in Africa (Gillet, 1979). It is practically restricted to the Caatingas (Fig. 5.35) save for three clear-cut outposts indicating a previous more expanded range of the species, or even probable ancient expansions of the Caatingas themselves (see maps in Hester, 1966, *sub* 'Deciduous Forest', and Ab' Sáber, 1977b). The specimen collected by Ratter et al. in Corumbá area shows a certain degree of morphological differentiation which may result in a new taxon at varietal or subspecific level (Gillet, *in sched.* & pers. comm.). A counter-hypothesis could be raised suggesting that *C. leptophloeos* evolved independently of the African members of the genus from the *Bursera* floristic stock present in Mesoamerica and N South America. In the genus *Erythrina*, the subgenus *Erythraster* comprises 13 species, of which 11 species occur in the Old World tropics (Krukoff & Barneby, 1974). The other two consist of a Cuban endemic and *Erythrina velutina*, which occurs in the Caatingas, W Ecuador and the dry Caribbean coast and could have arrived to South America via the African representatives of the subgenus.

**b- The Caribbean connection:** certain species of the Caatingas seem to have derived from a close relative in the dry Caribbean coast of N Colombia and Venezuela (the Guajira province of Cabrera & Willink, 1980), with some probable cases of vicariance. This hypothesis finds support in Sarmiento (1975), who studied the arid biomes of South America and made a comparison at generic level, and concluded that the strongest floristic relationships of the Caatingas refer to the Guajira province together with the Northern Andean Valleys of Colombia. Such is the case of *Copernicia tectorum*-*C. cerifera*, later deriving into the southern *C. alba* (see Sect. 8.2); *Licania rigida* of the Caatingas has its closest relative in the Colombian and Venezuelan *L. arborea* (Prance, 1972), which also extends into Central America; *Spondias tuberosa*, the resourceful 'umbú' of the sertão encounters its homologous species in *S. mombin* from the dry Caribbean sector of N South America. In the Cactaceae family, the Caatingas endemic *Pereskia aureiflora* is closest to *P. guamacho* of the dry Guajira province (Leuenberger, 1986), despite the fact that for this genus an Andean route might seem more likely if the distribution of all of its species is considered. Some species seem to follow a Caatingas-Guajira disjunction in their range, such as *Mimosa*



*tenuiflora* and *Chloroleucon mangense*, perhaps indicating that they did not have enough evolutionary time to speciate in either area; other species would be Caatingas endemics if it were not for isolated collections in N South America, such as *Sebastiania catingae* (disjunct in Sabanilla, Colombia; see Pax & Hoffmann, 1958b) and *Mimosa gemmulata* (disjunct in Lara, Venezuela; see Barneby, 1985).

Some other examples could be provided, but sometimes the connection Guajira-Caatingas is not so clear-cut. For instance, the present author has been unable to find any literature on the genus *Cavanillesia*, or confirmation via herbarium specimens at K, but it seems most likely that *C. arborea* of the Caatingas, Mata de Cipó and forests in Espírito Santo, must be a vicariad of *C. platanifolia*, the 'macondo' of the Caribbean coast of South America, but there also appears to be a third species in Amazonian localities (Rizzini, 1963) of unknown status. Harley (in press) shows two Labiatae which link the Caatingas to Venezuela, i.e. the monotypic *Eriopidium strictum* (occurring only in NE Brazil and the Orinoco river valley), and the caatinga species *Hyptis salzmanii* with disjunction in NE Venezuela but with one collection in Guyana close to the Rio Branco area.

**c- The Andean route:** it is likely that some species have reached the Caatingas via the west of the continent, as the extant fragments of a previously continuous distribution indicate. The main stepping stones of this route – dry Caribbean area, coastal western Ecuador, piedmont forests of Bolivia and Argentina, and the rest of the Pleistocenic Arc – are linked via dry interandean valleys mainly in Colombia and Peru, also postulated to have been used as migratory pathways by animals (Müller, 1973). The complex *Geoffroea striata/spinosa* (Fig. 5.58), and the trees *Senna spectabilis* (Fig. 5.62), *Parkinsonia aculeata* (Fig. 5.74) and *Sideroxylon obtusifolium* (Fig. 5.75) seem to follow this pattern.

A more complex matter is to determine the direction followed by the proposed taxa for this migratory route. For instance, Haynes & Holm-Nielsen (1989) argue for the Caatingas as the possible center of origin of the genus *Hydrochleys* (Limnocharitaceae), where the greatest concentration of primitive characters is found, and postulate a southerly migration which resembles very much the Pleistocenic Arc proposed

here. Subsequently, the genus must have joined the Andean route up to the Caribbean coast of South America, and from here diverging SE to the Guianas and NW to Central America. Haynes & Holm-Nielsen (1989) point out the striking fact of the absence of Alismatidae from the Amazon basin, as most taxa are restricted to areas with wet and dry seasons, specially in ephemeral ponds and forests with flood-drought cycles. Although the Andean route in the genus *Hydrochleys* is well supported by the evidence provided, there is still a chance that a Trans-Amazonian route could also have existed, whereas any suitable environment for these aquatic plants has disappeared along the migratory pathway across eastern Amazonia. Only fossil or pollen evidence could prove this point.

Exactly the opposite direction seems to have occurred with the genus *Coursetia* sect. *Cracoides* (Leguminosae), particularly in the final leg NW Argentina-Caatingas when it runs a SW-NE orientation as proposed by Andrade-Lima (1982) but for the wrong floristic stock. Lavin (1988), in his impressive monographic treatment of *Coursetia*, makes very valuable comments on its phytogeography. He postulates that the caatinga species *C. vicioides*, the closest to the perichaquenian *C. hassleri*, must have arrived (or its ancestors) to the Caatingas from the south, migrating from N Argentina and S Bolivia where there are a number of species pertaining to the same sect. *Cracoides*. This section has two primary centers of diversity in the cordilleras of central and southern Mexico and in the Andes of Colombia to N Peru, basically following the Amphitropical Seasonal Forests Pattern shown in Sect. 5.3.3. Lavin found the presence of *Coursetia rostrata* (sect. *Coursetia*) in the Caatingas rather puzzling since it is here very distant from its closest relatives, the *C. glandulosa* group in Mexico, and he suggested it must have migrated into NE Brazil via N Argentina and S Bolivia. However, an alternative scenario is that a common ancestral stock could have migrated together with other members of the flora of Mexico, either elements of the Sonora desert (*Parkinsonia aculeata*, *Sideroxylon obtusifolium*) or deciduous forests communities (*Tabebuia impetiginosa*, *Coutarea hexandra*, *Crateva tapia*, *Myroxylon balsamum*, *Poeppegia procera*, etc.; see Sect. 5.3.3), via a Trans-Amazonian route (see below).

**d- The Trans-Amazonian route:** a number of Caatingas species probably have arrived there via the Atlantic side of the continent, crossing the Amazonian plains at a time when the rainforests had receded because of the wet-dry cycles during the Pleistocene. Originally coming from Mexico, Central America and/or the Caribbean area, the main stepping stones of this route seem to be: 1- the Guajira province in N Colombia and Venezuela, and the Orinoco delta in some cases; 2- the Guianas as a whole, or the SW sector of Guyana and adjoining Rio Branco in Brazil, i.e. the Roraima-Rupununi area where *Commiphora leptophloeos*, *Brunfelsia uniflora* and *Coursetia ferruginea* have been collected; 3- the Faro-Monte Alegre area near Santarém in Pará, Brazil, where species such as *Tabebuia impetiginosa* (Fig. 5.70), *Myroxylon balsamum* (Fig. 5.71), *Aspidosperma pyrifolium* (Marcondes-Ferreira, 1988) and *Cereus* cf. *jamacaru* (Andrade-Lima, 1959 & 1966c) have been collected or cited; 4- several localities in Maranhão state, such as the alleged caatinga vegetation in the Coroatá-Vargem Grande area (Bigarella et al., 1975); and 5- finally the province of the Caatingas. Some of these species would extend from there to the south into SE Brazil or E Paraguay, therefore overlapping in part the Pleistocenic Arc (see Sect. 5.3.1), and in some cases even reaching the savannas of NE Bolivia (Llanos de Mojos).

The present author must disagree with Lavin (1988) when he denies the possibility of an ancient E Amazonian extension of the Caatingas during a drier climatic phase. On the contrary, several distribution maps shown in this thesis present basically the evidence of such an expansion, of which only relictual isolated populations are extant at present. This does not invalidate his hypothesis of the arrival of *Coursetia rostrata* via the Andean route (see above), but it is here considered as more likely that the Trans-Amazonian route was taken instead, even though the evidence for this has been wiped out by the expansion of the rainforests. Perhaps significantly, there is also mounting evidence from animal distribution patterns for Amazonian cross-connections (see Ch. 7, and Müller, 1973).

The most relevant species following this route apparently also migrated via the Andean route, and they are commented upon below (point e). Some other examples probably are the distribution ranges of *Crateva tapia* (Fig. 5.68), *Hymenaea courbaril* var. *courbaril* (Fig. 5.69),

*Albizia polyantha* (Fig. 5.91), and *Aspidosperma discolor* (Fig. 5.92). Iltis (1959) in his landmark paper on the taxonomy and evolution of *Cleome* sect. *Physostemon* provided further evidence for this route. The Caatingas species, *C. tenuifolia* and *C. rotundifolia*, are considered highly evolved taxa, and their ancestral stock in all likelihood has come from W Mexico via this Trans-Amazonian route, as *C. guianensis* (a wide ranging species in the Americas, collected in Monte Alegre, Pará, and in the driest 'seridó' of Paraíba) and *C. lanceolata* clearly suggest, the latter species with three subspecies in Oaxaca (Mexico), the Caatingas and E Paraguay.

e- The pincers movement (Andean/Trans-Amazonian route): a group of species of deciduous seasonal forests seem likely to have migrated following both preceding pathways, unless some sectors of their present distribution consist of much more recent arrivals which could not be attributed to Pleistocenic climatic fluctuations. Such are the cases of the amphitropical trees *Tabebuia impetiginosa* (Fig. 5.70), *Myroxylon balsamum* (Fig. 5.71), *Coutarea hexandra* (Fig. 5.67), the shrub *Ipomoea carnea* ssp. *fistulosa* (Fig. 5.59), and the South American complex *Cordia alliodora/trichotoma* (Fig. 5.64). Probably *Solanum granuloso-leprosum* (Fig. 5.63) could be added to this list, and also the genus *Loxopterigium* (Anacardiaceae) since it fragments into five species along both sides of the continent, although there is no proof that both arms of the distribution ever met in the intervening Pleistocenic Arc (Fig. 5.61).

*Cochlospermum vitifolium*, regarded as the most primitive species of the genus, also seems to have followed both routes (see map in Poppendieck, 1981). The cerrado species *C. regium* (an hexaploid with  $2n=36$ ; Morawetz, 1986) may have evolved from *C. vitifolium* ( $2n=24$ ), and a corridor of transitional forms between them occurs to the west of the Caatingas. Meanwhile, both species meet again in Bolivia, but in this case they are in distinct habitats and do not appear to hybridize. This is taken here as an indication that both routes were followed independently, although not necessarily simultaneously. Thus the eastern arm gave rise to *C. regium* when it had to face the very different environment of the Cerrados, and it thereby spread south until eventually meeting the disjunct populations of *C. vitifolium* in Bolivia. This agrees with

Poppendieck's view (op. cit.) that these latter populations are a relict of a once continuous distribution previous to the evolution of *C. regium*, and also with Morawetz (1986) who postulates the origin of polyploidy in *Cochlospermum* as a result of repeated migrations and/or changes of ecological niche.

The section *Franciscea* in the genus *Brunfelsia* (Solanaceae) recognizes two major centres of speciation: the eastern Andes, with the more primitive species, and SE Brazil, with the greatest number of species (Plowman, 1979). The bridge between both areas is *Brunfelsia uniflora* (Fig. 5.56), which migrated either East from the Andes in the Piedmont Forests to SE Brazil and later the Caatingas, or from SE Brazil westwards and northwards, but in any case the corridor must have been available through the wet-dry arc of seasonal vegetation. From the Caatingas this species very probably extended north to the dry Guajira province in the Caribbean coast of South America through E Amazonia, leaving extant populations in the Rio Branco-Roraima region. The latter "are morphologically distinct and appear to have been isolated in this endemic area for some time" (Plowman, op. cit., p.488). Thus, the section *Franciscea* seems to adjust well to the pincers movement, while the particular case of *B. uniflora* can be taken as further evidence of the Trans-Amazonian route, in this case probably in S-N direction.

Another group of Caatinga species seems to have moved along this proposed migratory route but either failed to complete the pincers movements or they became extinct in certain parts of it. Such is the case of *Aspidosperma cuspa* and *A. polyneuron* (Fig. 5.54 & 5.55), which in the west side of the continent spread through dry Andean valleys in Colombia but only reaching Ecuador or N Peru, and both are absent from Bolivia or the Subandean Piedmont Forests. Also *Erythrina velutina* can be mentioned, which reaches as far south as W Ecuador in the west, and the Caatingas in the east (see distribution map in Bigarella et al., 1975). Another example is provided by the Composite herbaceous genus *Isocarpha*, which presents five species arranged in two sections (Keil & Stuessy, 1981). Section *Isocarpha* holds four of the species, two occurring from Mexico to N Colombia and Venezuela through Central America and the West Indies, while the other two appear at different altitudes in the lowlands of W Ecuador (*I. microcephala*, confined to the

strongly Caatingas-linked vegetation of this area) and the mountains of N Peru. The sect. *Cylindriflorae* contains only the Caatingas endemic *I. megacephala*, which has substantially differentiated evolutionarily from the rest of the genus (Keil & Stuessy, 1981). The latter species and section would be totally isolated and disjunct if it were not for two exsiccata of *I. atriplicifolia* var. *atriplicifolia* in N Piauí and N Maranhão, at the edge of the Caatingas, while the nearest collections of this variety are located in the Maracaibo Lake in Venezuela and dry coastal Colombia (the Guajira province).

f- The Pleistocenic Arc as a migratory route: a considerable group of woody species, comprising some of the more important members of the Caatingas, follow this pattern of distribution across central South America, as discussed at length in Sect. 5.3.1. This arc of formations must have been used as a migration corridor by other amphitropical and South American species (see routes **c**, **d** and **e**). *Anandenanthera colubrina* var. *cebil* (Fig. 5.38), the paradigm of this kind of distribution, is complemented by *A. colubrina* var. *colubrina* (Fig. 5.39) which is supposed to have arisen from var. *cebil* or an ancestral form (Altschul, 1964) in the Planalto of central Brazil, where the greatest variability of this small genus concentrates. The other species of the genus, *A. peregrina*, must have originated at an earlier time than *A. colubrina* itself (Altschul, 1964) in the same area, and it seems to have migrated northwards via the Pleistocenic Arc and either the Trans-Amazonian route or 'campos' expansions amid the then contracted Amazon rainforests, to finally arrive in N Venezuela and the West Indies.

The extra-Amazonian Phytolaccaceous genera *Seguieria* and *Gallesia* seem to have their centre of diversity and probably of origin in SE Brazil, although Rohwer (1982, p. 243) has misgivings about this view. Five of the six species of *Seguieria* seem to fall within the scope of the Pleistocenic Arc, from wetter areas in the Caatingas to N Peru, particularly *Seguieria aculeata* which also extends beyond this arc to the Guajira province (see Rohwer, 1982, Fig. 11). Some of these species, or their ancestors, must have used the seasonal formations as a corridor to finally speciate in NW Bolivia (*S. brevithyrsa*) or N South America (*S. macrophylla*).

**g- The Amazonian encroachment:** a more reduced group of species pertaining to genera which have the bulk of their distribution in the Amazon rainforests and related formations (such as gallery forests in the Cerrados), can also be found well into the semiarid NE Brazil. Examples are *Couepia uiti* (Fig. 5.93), and in the mainly Amazonian genus *Sterculia* (Taroda, 1984), *S. striata* occurs in arboreal caatinga (Andrade-Lima, 1975; Ratter et al., 1978) and also in W Bahia, N Minas Gerais and the Corumbá calcareous outcrops (Fig. 5.53). The Leguminous tree *Poeppegia procera* extends from Mexico and Central America to Andean South America, but instead of following the usual pattern of seasonal formations seems to take a shortcut through the Amazon (Fig. 5.72) to later reappear in the Caatingas. The small Amazonian genus *Martiodendron* (Leguminosae) comprises mostly majestic canopy trees but also a shrub to treelet which has evolved in northern areas of the Cerrados and in the Caatingas, *M. mediterraneum* (Koeppen & Iltis, 1962).

**h- The Atlantic forest encroachment:** in Rizzini's view (1963, 1979) half the floristic stock of the Caatingas is derived from the Mata Atlântica rainforests. It is not possible with the available taxonomic and evolutionary information to ascertain the correctness of this view, but there exist evidence indicating that certain species could possibly have resulted from adaptation of taxa from more humid environments. Lee & Langenheim (1975) suggest that the genus *Hymenaea* (Fabaceae) has originated in rainforests in the New World, probably with *H. oblongifolia* in the center of diversification of present-day species. One of the varieties of that species, var. *latifolia* of the 'Hylaea Bahiana' (Andrade-Lima, 1966a), probably gave rise to the caatinga endemism *H. eriogyne*, together with other species. Likewise, the Caatingas endemics *Pereskia bahiensis* and *P. stenantha* (Cactaceae) are very close to, and probably derived from, *P. grandifolia* of coastal Brazil (Leuenberger, 1986). Also in the Fabaceae, the caatinga endemic *Parapiptadenia zehntneri* is closest to *P. pterosperma* of the Atlantic rainforests in Espírito Santo and Rio de Janeiro (Lima & Lima, 1984); a parallel situation is reported for *Luetzelburgia* (Lima, 1984), where the Caatingas endemic *L. andrade-limae* is the nearest to *L. guaissara* from Mata Atlântica in Rio de Janeiro, São Paulo, Paraná and Santa Catarina. A number of species accepted here as albeit rather dubious members of the Caatingas have

very probably edged into that province from the Atlantic forests or the local 'brejos' in wetter years or taking advantage of somewhat more humid pockets. Such taxa are *Phyllosthylon brasiliense*, *Gallesia integrifolia*, *Seguieria aculeata*, *Myroxylon balsamum*, *Pisonia tomentosa*, etc.. The Atlantic forest- Caatinga link has not been explored intensively in the present study.

i- The Cerrados expansions: some species whose distribution is basically centered in the Cerrados savannas of central Brazil, can also extend to NE Brazil and become relevant members of the Caatingas, such as *Tabebuia caraiba* (Fig. 5.52). Nevertheless, in most such cases their presence in the thorn forests seems to be more occasional, e.g.: *Machaerium acutifolium* (Fig. 5.80), *Platypodium elegans* (Fig. 5.65), *Hymenaea martiana* (Fig. 5.79), *Copaifera langsdorfii* and *Aspidosperma discolor* (Fig. 5.92), the latter also extending into the Amazon forests. Also *Riedeliella graciliflora* is a cerrado shrub with disjunct populations in the Caatingas of SW Bahia (Lima & Vaz, 1984).

j- Some curious distributions: two perplexing cases of disjunction have been found during the course of this study. The Apocynaceae *Skytanthus hancornifolius* has been recorded in the Caatingas (Harley & Mayo, 1980), whereas the other species of this genus are known to occur in the N Chilean desert. Very similar to this pattern is the distribution of *Hyptis* sect. *Leucocephala* (Harley, in press) which comprises three species: *H. leucocephala* is a small herb endemic to the Caatingas, *H. stachydifolia* is a shrub of 'campo rupestre' upland areas in N Bahia, while on the other side of the continent their closest relative, *H. elongata*, occurs in coastal Peru. These enormous disjuncts Caatingas-coastal Pacific desert of Peru and Chile are regarded here as very puzzling, and no discussion to this kind of disjunction has been encountered. It could be, obviously, the result of somewhat modern long-distance dispersal (migratory birds carrying their seeds?, across the Andes??), or both areas had been connected somehow before the final uplift of the Puna Altiplano in the late Tertiary (Pliocene, see Solbrig, 1976), or they are relictual fragments at the extremes of some of the NE Brazil-Andean Cordillera distributions previously discussed.



#### 8.4- Distribution patterns and palæoclimates:

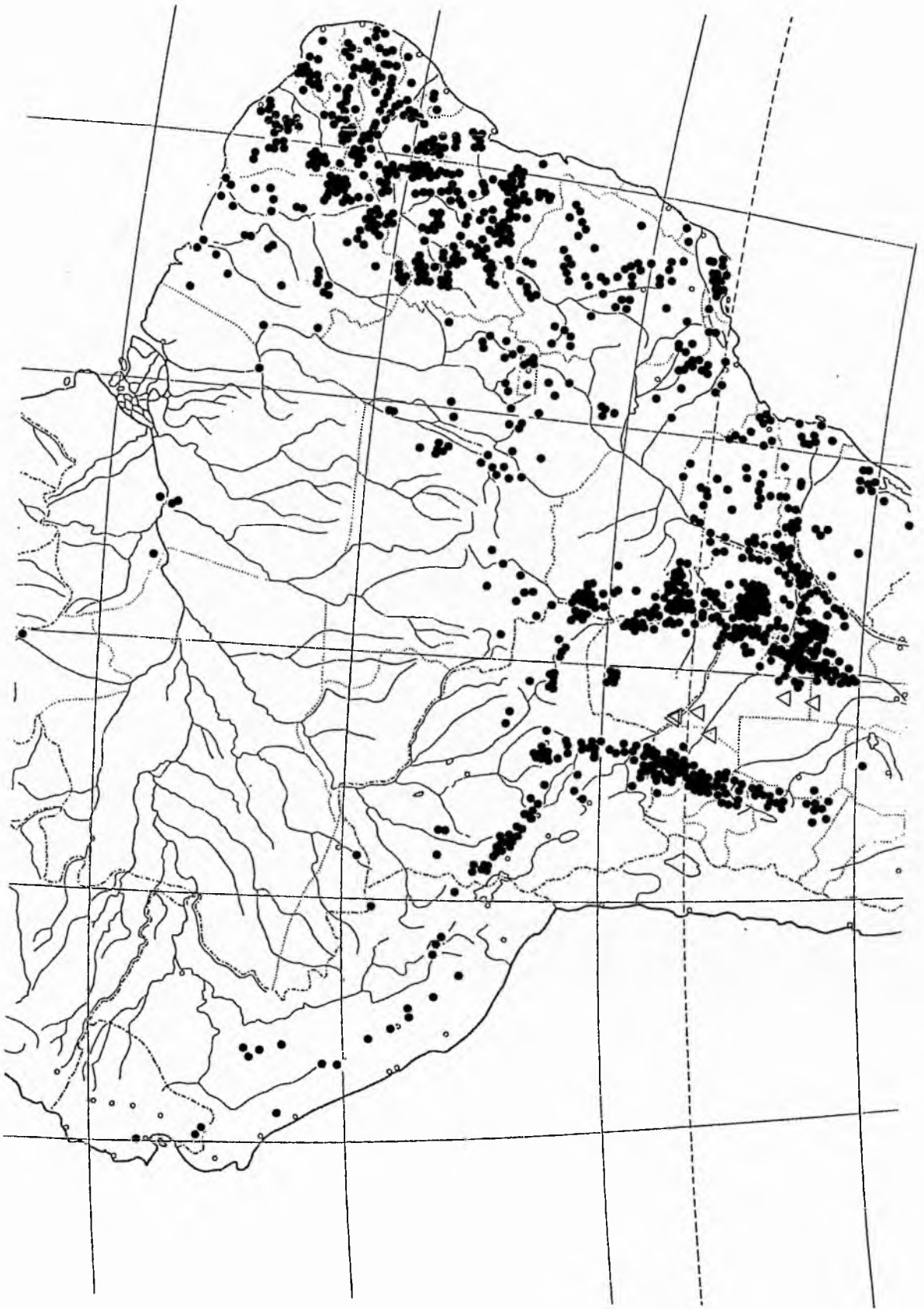
The individual species distribution dot maps presented in sections 5.3.1, 5.3.2 and 5.3.3 have been superimposed to produce two compound maps (Fig. 8.4 & 8.5) which aim to show the main distribution patterns which are at the heart of the discussion and analyses presented in this thesis. Fig. 8.4 maps the distribution 'tendencies' or patterns of those 36 species judged to comprise what has been called here the 'Residual Pleistocenic Seasonal Formations Arc', or Pleistocenic Arc (see legend for list of species involved, and their individual distribution maps in Sect. 5.3.1). Three concentrations or 'nuclei' of distributions can be discerned: (1) the Caatingas of NE Brazil, (2) the Paraguay-Paraná river system, and (3) the Subandean Piedmont Forests of SW Bolivia and NW Argentina. Less dense dotting is visible expanding to the west of the 1<sup>st</sup> nucleus into Maranhão state, where the presence of relictual caatinga outposts is still a controversial matter (cf. Galvão, 1955, and Bigarella et al., 1975, vis-à-vis Eiten, 1965 & 1972, p. 288). This area in turn can be hypothesized as linking to the Faro/Monte Alegre area in Pará, and further north to the Roraima-Guyana border area. The single dot shown in the latter region corresponds to the very significant exsiccatum of *Commiphora leptophloeos* by E. Ule.

The first nucleus is somewhat less loosely connected to the second through two 'tracks'<sup>7</sup>: the northern and the southern routes. The northern track seems to cut present-day Cerrados in two halves, extending as a narrow strip from W Bahia (probably getting into Goiás via the Rio Grande valley) to the calcareous outcrops in the Federal District and surrounding areas (see Ratter et al., 1978). The deciduous forests of the so-called Mato Grosso de Goiás (beginning somewhat to the E of the city of Goiânia) are part of this track, which crosses the Araguaia river at the height of Aragarças, presumably here branching north to the Xavantina/Cachimbo and Ilha do Bananal areas, and west to the Cuiabá-N Pantanal area, later reaching the calcareous hills around Corumbá and Urucúm in Mato Grosso do Sul (Kanter, 1936; Kuhlman, 1954; Ratter et al., 1988b).

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<sup>7</sup> The present author is aware that some of the proposed 'tracks' might simply overlap with well collected areas or routes, instead of indicating an adjusted pattern of distribution. However, it is here believed that these tracks do suggest ancient connections between the nuclei of distribution.

**Fig. 8.4:** Compound map of the 36 woody species following wholly or in part the Pleistocene Arc of distribution. Open triangles indicate the few intrusions of tropical elements into the Chaco plains. The species mapped are: *Alseis floribunda*, *Amburana cearensis*, *Anadenanthera colubrina* var. *cebil* and var. *colubrina*, *Aspidosperma pyriforme*, *Aspidosperma riedelii* ssp. *riedelii* and ssp. *oliganthum*, *Astronium balansae*, *A. concinnum*, *A. urundeuva*, *Athyana weinmannifolia*, *Balfourodendron riedelianum*, *Brunfelsia australis*, *Calycophyllum multiflorum*, *Carica quercifolia*, *Celtis pubescens*, *Combretum leprosum*, *Commiphora leptophloea*, *Diatenopteryx sorbifolia*, *Diplokeleba floribunda*, *D. herzogii*, *Enterolobium contortisiliquum*, *Hymenaea martiana*, *H. velutina*, *Machaerium acutifolium*, *Maytenus ilicifolia*, *Mimosa caesalpinifolia*, *Patagonula americana*, *P. bahiensis*, *Phytolacca dioica*, *Piptadenia viridiflora*, *Pouteria gardneriana*, *Pterogyne nitens*, *Ruprechtia laxiflora*, *Schinopsis brasiliensis*, *S. peruviana*, *Ziziphus guaranitica*, *Z. oblongifolius*.



The southern track extends at first along the São Francisco and Jequitinhonha river valleys, and south in a wide band along the Rio das Velhas up to Belo Horizonte area and the Rio de Janeiro state. The latter region has been subject to intense wet-dry climatic fluctuations during the Pleistocene (Cailleux & Tricart, 1959; Tricart, 1961). The southern track then goes through the states of São Paulo, Paraná and Santa Catarina, mostly via the Planalto and river Uruguay basin forests, until meeting the 2<sup>nd</sup> nucleus of distribution in NE Argentina, E Paraguay and SW Mato Grosso do Sul.

The 2<sup>nd</sup> nucleus, with a central axis in the Paraguay-Paraná system is nowadays linked to the 3<sup>rd</sup> nucleus only through the Santiago and Chiquitos Sierras in Bolivia. This connection is interrupted between Chiquitos and Santa Cruz de la Sierra by a moderate northwards protrusion of the Chaco s.s. (see Fig. 8.2), which seems to encounter or to give way to tropical forests of direct Amazonian influence with no intervening communities of species of the Pleistocenic Arc. It is likely, however, that there were almost certainly additional links in the past between the 2<sup>nd</sup> and 3<sup>rd</sup> nuclei, as is today exemplified by the vegetation of the Cerro León in the middle of the Paraguayan Chaco plains. Spichiger & Ramella (1989) and Ramella & Spichiger (1989) describe some communities on these hills and along the Timane/Lagerenza river valley, which very closely resemble the physiognomy and floristics of both the 'Palo blanco' forest and arboreal caatinga, being also very similar to the 'caatinga' forest of calcareous hills around Corumbá (Ratter et al., 1988b). It is likely that when the flora and vegetation of Cerro León becomes better known, stronger links with calcareous and Caatingas vegetation will emerge. Indeed, one would predict the presence of at least some species, such as *Schinopsis brasiliensis*, *Commiphora leptophloeos*, *Tabebuia impetiginosa*, *Piptadenia viridiflora*, *Senna spectabilis* var. *spectabilis*, *Ruprechtia laxiflora*, *Enterolobium contortisiliquum*, *Patagonula americana*, one of the species of the genus *Loxopterigium* (or a new taxon), the complex *Cordia alliodora/trichotoma*, *Phyllostylon rhamnoides*, or even *Brunfelsia uniflora*, *Myroxylon balsamum* or *Aspidosperma polyneuron*, none of which have been cited for the area yet. Any of these taxa would add to the already known presence there of *Anadenanthera colubrina* var. *cebil*,

*Astronium urundeuva*, *Amburana cearensis*, *Pterogyne nitens*, *Geoffroea striata*, *Aspidosperma pyriformis*, *Albizia polyantha*, *Maclura tinctoria*, *Pisonia zapallo*, *Sideroxylon obtusifolium* and *Calycophyllum multiflorum* (Spichiger & Ramella, 1989; Ramella & Spichiger, 1989). It is also likely that specific and even generic endemisms would be encountered in the Cerro León or other isolated hills of the Paraguayan Chaco, such as the recently described and puzzling *Sphingiphila* (Bignoniaceae), known only from the type collection in the Cerro Chovoreca in N Paraguay (Gentry, 1990).

The 3<sup>rd</sup> nucleus stretches continuously from SE Catamarca in NW Argentina to Santa Cruz de la Sierra in Bolivia as a narrow strip of deciduous forests. It extends tenuously but persistently along the foothills of the Andes in NW Bolivia, and enters Peru to be present in dry interandean valleys and just reach western Ecuador. The Acre state in Brazil has two species of the Pleistocenic Arc (*Amburana cearensis* var. *acreana* and *Celtis pubescens*) and, not unexpectedly, other more widespread species have also been collected in this area, e.g. *Myroxylon balsamum* and *Poeppigia procera*.

The composite map of Fig. 8.4 also shows a conspicuous blank area between the 2<sup>nd</sup> and 3<sup>rd</sup> nuclei, which corresponds to the Chaco s.s. as here defined (see Fig. 8.2). This is further striking evidence of the virtual lack of floristic links between the Chaco and the Caatingas. There are, however, six exsiccata within the Chaco (indicated with open triangles in Fig. 8.4) which correspond to some of the few intrusions of tropical elements in the Chaco plains via the gallery forests in the west (*Enterolobium contortisiliquum*, *Calycophyllum multiflorum*, *Albizia polyantha*, *Anadenanthera colubrina* var. *cebil*), and via gallery forest or relictual stands of richer forest in the east (*Ruprechtia laxiflora*, *Patagonula americana*, *Phytolacca dioica*, *Astronium balansae*). The scanty presence of these elements within the Chaco plains, together with those cited in Morello (1967), Adámoli et al. (1972) and Morello & Adámoli (1974), were regarded by the same authors as 'species of non-chaquenan lineage' (Adámoli et al., 1972) or 'transchaquenan elements of subtropical forests' (Morello & Adámoli, 1974, p. 44). In Table 8.5 are listed some species of the 'Palo blanco' and 'Tipa-Pacará' forests whose

**TABLE 8.5: List of woody species of the Subandean Piedmont Forests also occasionally occurring in Western Chaco.**

*Anadenanthera colubrina* (Vell.) Bren. **var. cebil** (Griseb.) Altschul  
*Basistemon spinosus* (Chodat) Moldenke  
*Calycophyllum multiflorum* Grisebach  
*Carica quercifolia* (St.-Hil.) Hieron.  
*Ceiba chodatii* (Hassler) Gibbs & Semir comb. ined.  
*Coursetia hassleri* Chodat  
*Enterolobium contortisiliquum* (Vell.) Morong  
*Jacaratia corumbensis* Kuntze  
*Maclura tinctoria* (L.) Don ex Steudel **subsp. mora** (Griseb.) V.Ávila  
*Manihot guaranitica* Chodat & Hassler **subsp. guaranitica**  
*Patagonula americana* L.  
*Pereskia sacharosa* Grisebach  
*Phyllostylon rhamnoides* (Poisson) Taubert  
*Pterogyne nitens* Tul.  
*Ptilochaeta nudipes* Grisebach  
*Quiabentia pflanzii* (Vaupel) Berger

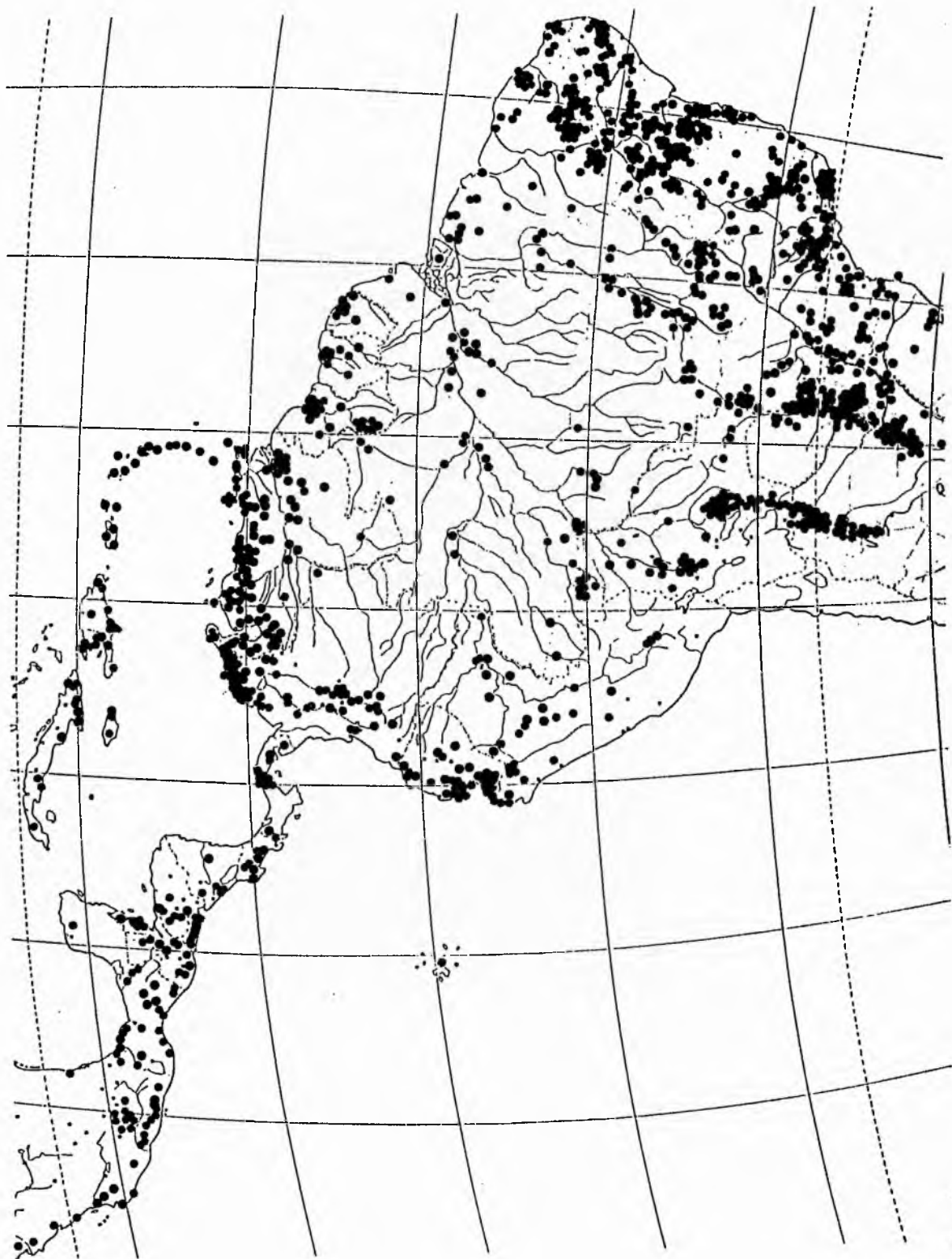
presence within the Western Chaco are further evidence that these forests were more extended to the east of their present position during the climatic fluctuations of the Pleistocene (Vuilleumier, 1971; Ab' Sáber, 1977b). These forests must have extended further south as well, as the relictual presence of *Anadenanthera colubrina* var. *cebil* in the Córdoba hills (Hunziker, 1973) seems to indicate.

Figure 8.5 presents another composite map of species relevant to the Caatingas with more ample distributions (see legend for list of species, and individual maps in Sect. 5.3.2 & 5.3.3). This map still permits a clear delimitation of the Pleistocenic Arc, and although the three nuclei of distribution are still discernible, this aggregation of species emphasizes the connecting tracks between them and also highlights links to the Caribbean and W Ecuador areas. Some of these additional species emphasize the importance of the Acre region in the west of Amazonia, whilst in the east the Faro/Monte Alegre and the Rio Branco/Roraima areas are better defined as a potential connecting route Caatingas-Guajira province; there is also an alternative route via the Guianas. A nucleus in W Ecuador is seen as linked to N Colombia through the Magdalena and Cauca valleys, as also postulated for animal distributions by Müller (1973). A number of elements reach the dry Caribbean area through Mesoamerica, coming from as far Mexico and W Central America, while others arrive to South America through the West Indies (e.g. *Hymenaea courbaril* var. *courbaril* ).

It can be noted at this point that there is a close correspondence between these two synthetic maps (Fig. 8.4 & 8.5), and the hypotheses of past climatic events occurring during the Pleistocene, as exemplified in the maps and hypotheses presented by Ab' Sáber (1977b & c). Firstly, the Ab' Sáber map (Fig. 8.6; Ab' Sáber, 1977c) of Morphoclimatical and Phytogeographical Dominia of South America shows, to a certain extent, the pattern of the Pleistocenic Arc. Ab' Sáber delimited the main core areas in South America as those with homogeneous geomorphological and climatological features which correlated with known floristic provinces. His 'Domínio do Chaco Central' is then a perfect match to the Chaco s.s. (cf. Fig. 8.2 & 8.6), even to the extent of leaving the so-called Eastern Chaco as a transitional sector. He also regarded the 'Domínio das Caatingas' core area as perfectly defined because of its homogeneity

**Fig. 8.5:** Compound map of the woody species following wholly or in part the South American and Amphitropical Seasonal Forests patterns of distribution. The species mapped are: *Aspidosperma cuspa*, *A. polyneuron*, *Astronium fraxinifolium*, *Brunfelsia uniflora*, *Cordia alliodora/trichotoma* complex, *Coutarea hexandra*, *Crathea tapia*, *Geoffroea striata/spinosa* complex, *Hymenaea courbaril* var. *courbaril* and var. *stilbocarpa*, *Ipomoea carnea* ssp. *fistulosa*, the genus *Loxopterygium*, *Myroxylon balsamum*, *Peltophorum dubium*, the genus *Phyllostylon*, *Platypodium elegans*, *Poeppigia procera*, *Senna spectabilis* var. *spectabilis* and var. *excelsa*, *Solanum granuloso-leprosum*, *Tabebuia impetiginosa*.







in landscape, ecology and hydrology (Ab' Sáber, 1977c, p. 13); he also left a number of areas unmarked because they would not fit into any of the core areas, and these he regarded as transitional. In this category Ab' Sáber included the 'agreste', the 'mata de cipó' in S Bahia, and parts of Maranhão and Piauí. These transitional belts are continuous from the Caatingas, all around north and south of the Cerrados core area, to reach the Pantanal, Eastern Chaco, the areas north of the Santiago and Chiquitos Sierras, and the Subandean Piedmont Forests in Bolivia and NW Argentina. From the so-called Eastern Chaco finger-like protrusions extend along the Uruguay, Paraguay and Paraná river valleys. This sequence effectively traces the Arc of Residual Pleistocenic Seasonal Formations (compare Fig. 8.4 & 8.6), with some differences in what Ab' Sáber refers to as the Planalto forests, and with the detail that the calcareous enclaves within the expanse of the Cerrados are omitted. However, Ab' Sáber (1977c) pointed out that because of the scale of his map no attempt was made to indicate the presence of enclaves within the core areas.

Much the same close correspondence can be observed with the Ab' Sáber (1977b) map of natural dominia in South America between 13,000 to 18,000 years BP (Fig. 8.7). Based mainly in geomorphological evidence he proposed that the Caatingas-like vegetation and habitats were much more widespread at the time of glacial phases (Würm-Wisconsin), when the climate of South America must have been increasingly drier and somewhat colder than present (Damuth & Fairbridge, 1970; Vuilleumier, 1971; Bigarella et al., 1975; Ab' Sáber, 1977b). A 'Caatingas type' vegetation would at that time have extended south from its present position as a wide band across Minas Gerais and Rio de Janeiro, presumably also enclosing those areas of the continental shelf uncovered by the retreating sea waters along SE Brazil (see Ab' Sáber's map, and Vuilleumier, 1971, Fig. 2). The 'Caatingas area' also extended west through Piauí and Maranhão, encircling completely the Cerrados and stretching SW across N Goiás, Ilha do Bananal, the Federal District, mid-Araguaia river, the Cuiabá pediplane, the Pantanal, and finally encasing the Chaco in a much more reduced extension than that of present-day, limiting it in its north, east and west borders. At this time, under the prevailing climatic regime, it is also

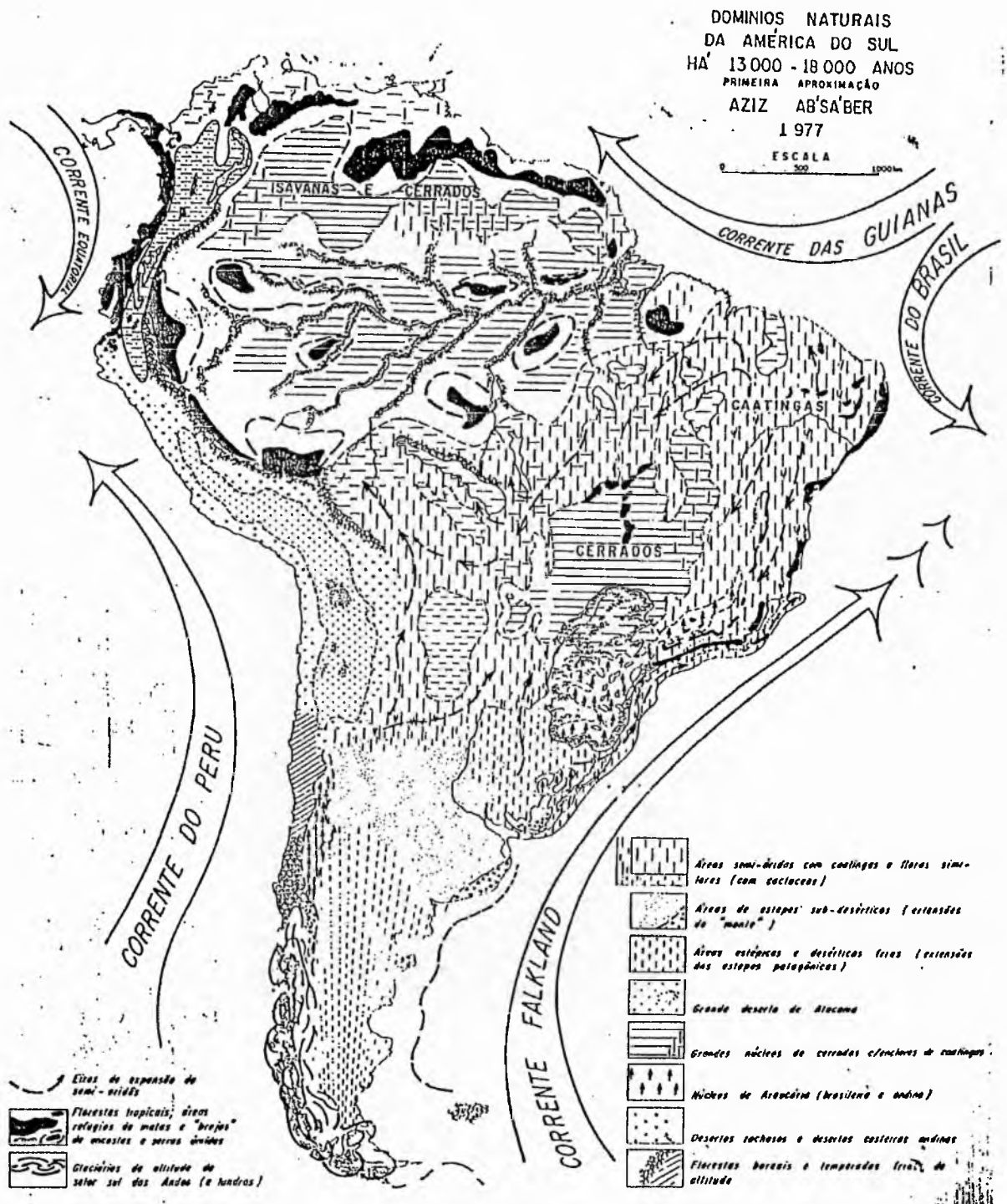


Fig. 8.7: Natural Domina in South America between 13,000 to 18,000 years BP, according to Ab' Sáber, 1977b.

likely that the Subandean Piedmont Forests extended east into the Chaco plains.

The distribution maps of caatinga species shown in this study, and particularly the composite ones of Fig. 8.4 & 8.5, are again in close accord with Ab' Sáber hypothesis as shown in his map (Fig. 8.7). The resemblance is sustained even to the extent of precise localities (as opposed to broad regions), which were in his view, and it is here agreed, part of the Caatingas tracks not only crossing the Cerrados but also the Amazon (such as the depressions in the Rio Branco/Roraima area). There is some lack of agreement between modern distributions and these Pleistocene reconstructions. Thus, present-day plant distributions do not show strong evidence to support the wide western arm of the circum-cerrado extension of the 'Caatingas-type' vegetation as proposed by Ab' Sáber (1977b), although it could have been wiped out by climatic change and the subsequent expansion of the Cerrados and rainforests. Rather, the distribution patterns suggest that the western expansion of the Caatingas across Maranhão must have continued along eastern Amazonian areas such as Faro/ Monte Alegre, to link with the Rio Branco/Roraima depressions, SE Orinoco river delta, and finally reaching the dry Caribbean coast of N Venezuela and Colombia. In this scenario the Cerrados would have been cut into two segments, a northern one in N Goiás, S Maranhão, SW Piauí and parts of W Bahia, and a southern one in SW Goiás, S Mato Grosso, W São Paulo, and the eastern three-quarters of Mato Grosso do Sul (see Fig. 8.4). This presumably must have had an effect on the floristics of the Cerrados, and could possibly explain the N-S floristic gradient recently reported by Ratter & Dargie (in press). There would also most likely have been a track of seasonal vegetation along the Santa Catarina state, linking the coastal Caatingas and the Ilha Santa Catarina to the Paraguay-Paraná river system and cutting through the pre-existing *Araucaria* forests, via the Rio do Sul area and the upper river Uruguay, as shown here in distribution maps and also proposed by Klein (1975), together with a more southern route through Torres in Rio Grande do Sul (Klein, 1975; Ab' Sáber, 1977b). Ab' Sáber also overlooked the links that must have existed with dry western Ecuador, via dry interandean valleys both through Peru and Colombia (the Magdalena, Marañón, Huállaga, etc., river valleys),

although the Acre state area is nearly reached by one of his proposed expansions of the Caatingas.

During the interglacial episodes in the Pleistocene, temperatures were seemingly warmer than today (Vuilleumier, 1971), and the sea level rose inundating the Amazon basin and particularly the area of the Paraguay-Paraná system (see Vuilleumier, op. cit., Fig. 2).. This surely caused pronounced environmental modifications in the substratum which would have been encountered by the elements of seasonal formations reaching the latter area in the following glaciation phase, and consequently there could have been either specific differentiation or extinction for some of those elements. This view is supported by the idiosyncracies in the distributions of some taxa, e.g. *Myroxylon balsamum* and *Piptadenia viridiflora* (Fig. 5.71 & 5.48) are completely absent from the 2<sup>nd</sup> nucleus of distribution from Corumbá to Argentina, and it is also noteworthy that of all the areas of seasonal woody formations this is the only one where the genus *Loxopterigium* has not been recorded (Fig. 5.61). The shrub *Brunfelsia uniflora* (Fig. 5.56) is also absent from this area, but its place is occupied by its derivative *B. australis* (Fig. 5.57, and Plowman, 1979). Both *Amburana cearensis* (Fig. 5.40) and *Senna spectabilis* var. *spectabilis* (Fig. 5.62) seem to be suddenly interrupted in their southern expansion in the northern border of Paraguay (Apa river region). The tree *Astronium urundeuva* (i.e. = *Myracrodruon urundeuva* , Fig. 5.41) reaches Argentina along this area allegedly submitted to past marine transgressions, but it appears to be here far less frequent than in the Subandean Piedmont Forests, and ultimately it is replaced by its very close relative *A. balansae* (i.e. = *Myracrodruon balansae* , Fig. 5.83), which sometimes extends deeply into the Chaco s.s.. If the reinstated genus *Myracrodruon* is accepted, it would constitute a new endemism to the Pleistocenic Arc, to be added to *Amburana* , *Pterogyne* and *Patagonula* .

### 8.5- Tail-end:

There are still, of course, many unanswered questions. For example, if the climate was colder and drier during glacial episodes, how is it possible that caatinga-like vegetation could have extended south to NE and NW Argentina, with species which are limited by frost

occurrence?. It is possible that the same climatic features did not prevail throughout the area at the same time (Markgraf, 1989). For example, the western face of the Andes had opposite conditions to those in the east (Vuilleumier, 1971). Furthermore, it is possible that within the tropics it was relatively colder (by about 4 to 5°C) and drier, whilst the climate in NW Argentina might have been less subject to frosts and somewhat more humid than the present climate encountered in the driest parts of the Chaco s.s., so permitting the Subandean Piedmont Forests to extend their range. Markgraf's studies (1989) support this hypothesis since, according to her, moisture patterns showed regional differentiation in

South America, and "the southern subtropics were substantially moister than today during full- and late-glacial times, whereas everywhere else conditions were far drier than today". In principle there seems to exist evidence that this was likely so; there are patches of lateritic palæosoils within the dry subtropical western Chaco in Formosa (Groeber, 1958), which would correspond to a past period under a humid tropical climate, which in turn left a palæofluvial system recognizable in aerial photography (Adámoli et al., 1972). On the other hand, there are dune fields in SE Bolivia, W Paraguayan Chaco and central Formosa in Argentina, nowadays immobilized and covered with vegetation, which indicate that at some stage the climate was much drier than at present (Putzer, 1962).

In the study of the distribution patterns of the Caatingas floristic elements another paradox is apparent: how do woody species such as *Albizia polyantha*, *Ipomoea carnea* ssp. *fistulosa*, *Enterolobium contortisiliquum*, *Geoffroea striata/spinosa*, *Crateva tapia*, etc., survive the capricious drought cycles of the Caatingas, whilst they are also common in areas such as the Amazon basin or the Paraguay-Paraná river system where flooding is the rule?. In this context, some results emerging from studies by F. Scarano (St. Andrews University) on anoxia tolerance are perhaps significant. Working on flooding-tolerant plants such as *Enterolobium contortisiliquum*, he established that drought causes hypoxia (low oxygen levels) in root tissues, which in turn enables the plant to prolong its flooding tolerance period (Scarano, pers. comm.).

The present study set out to critically evaluate the alleged floristic links between Chaco and Caatingas vegetation in South

America. Such links turned out to be very weak indeed, particularly when they are compared to the actual affinities between the Caatingas and other seasonal communities in the continent (the Subandean Piedmont Forests in NW Argentina and SW Bolivia, the Guajira province in N Colombia and Venezuela). Indeed, the links are so weak that it suggested that the Caatingas should be removed from the Chaquenan Dominion. Moreover, the prevailing concept of the Chaco itself, as a result of this analysis, proved to be a broad geographical entity rather than a well defined geobotanic unit in vegetational terms. The detailed study of the patterns of distribution of most of the more important species involved provides new evidence of probable ancient connections across the continent between present-day seasonal woody communities, such as what has been called here the 'Pleistocenic Arc'. These corridors of semiarid to strongly seasonal formations seem likely to have functioned as migratory routes by plant species, and this scenario provides a logical explanation for the patterns of speciation and degree of diversity found in such taxa when subsequent climatic changes broke up their previously more continuous distributions.



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