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What is the Gran Chaco vegetation in South America? II. A redefinition
Contribution to the study of the flora and vegetation of the Chaco. VII

DARIÉN E. PRADO

ABSTRACT

PRADO, D. E. (1993). What is the Gran Chaco vegetation in South America? II. A redefinition. Contribution to the study of the flora and vegetation of the Chaco. VII. *Candollea* 48: 615-629. In English, English and Spanish abstracts.

The twenty-three more relevant woody communities of the Gran Chaco are studied following classical phytosociological and numerical analysis techniques (PCA and CLINK), in an attempt to redefine the present concept of the Chaco province in South America. The congruence between the different results is striking. On this basis, the communities Gallery Forest, "Selva de Ribera", "Tipa-Pacará" Forest, "Palo blanco" Forest and the Calcareous Forest of Mato Grosso do Sul cannot be regarded as chaquenian, while the Austro-Brazilian Transitional Forest and three different communities from Mato Grosso are considered transitional. A new map of the Chaco *sensu stricto* is presented, with a wide belt of transitional vegetation on the east of the region, whereas gallery forests and hills vegetation are completely excluded.

RESUMEN

PRADO, D. E. (1993). ¿Qué es la vegetación del Gran Chaco de Sudamérica? II. Redefinición. Contribución al estudio de la flora y de la vegetación del Chaco. VII. *Candollea* 48: 615-629. En español, resúmenes en inglés y en español.

Las veintitrés comunidades leñosas más relevantes del Gran Chaco fueron estudiadas siguiendo técnicas de análisis fitosociológico clásico y númerico (PCA y CLINK), tratando de redefinir el concepto actual de la provincia del Chaco en Sud América. La congruencia entre los distintos resultados es sorprendente. Sobre esta base, las comunidades Bosque en Galería, Selva de Ribera, Bosque de Tipa y Pacará, Bosque de Palo Blanco y los Bosques Calcáreos de Mato Grosso do Sul no pueden ser aceptadas como chaqueñas, mientras que el bosque Transicional Austro-Brasileño y tres comunidades diferentes de Mato Grosso son consideradas transicionales. Se presenta un nuevo mapa del Chaco *sensu stricto,* que muestra una amplia faja de vegetación transicional en el este de la región, al tiempo que los bosques en galería y la vegetación de los cerros son totalmente excluídos.

KEY-WORDS: Chaco — Classical phytosociology — Floristics groups — Numerical analysis — Vegetation — Woody communities.

Introduction

In a previous contribution a review of the available knowledge on the Gran Chaco vegetation of Bolivia, Paraguay and Argentina was presented (PRADO, 1993). In studying this problem the need of a thorough analysis of the present day notion of the Chaco arose, since in the literature available the concept of the Chaco as a phytogeographical province has simply been equated with the Chaco as a geographical region (see review in PRADO, 1993), an established view that has prevailed unchallenged so far. The comparative study showed that the geographical region known as

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the "Gran Chaco" in fact includes rather different kinds of vegetation, and there is a number of floristic elements of widely different lineages in the woody communities still regarded as chaquenian. Such studies then provide the basis for an attempt to redefine the "Chaco proper" by more objective techniques.

The twenty-three woody vegetation units encompassed in the analysis have been regarded as pertaining to the Gran Chaco by different authors. These include the Gallery Forests in the islands of the river Paraná and tributaries, considered chaquenian by RAGONESE (1941) and RAGONESE & CASTIGLIONI (1970), and often confused with the next one, the "Selva de Ribera" (SCHULZ, 1967; PRADO & al., 1989), as in REBORATTI & NEIFF (1986). The Subandean Piedmont Forests of NW Argentina and SW Bolivia (PRADO, 1991), bordering the western limit of the Chaco and included in it by HUECK (1959, 1972) and UNZUETA (1975), consists of two different units: the "Tipa-Pacará" and the "Palo blanco" forests. The Austro-Brazilian Transitional Forest (PRADO, 1991) and the nearby "quebrachales" of *Schinopsis balansae* have, more often than not, been confused as a single vegetation type (e.g. HUECK, 1972; CABRERA, 1976). Also arguable is the phytogeographical position of the five communities described by PRADO & al. (1992) for a sector of alleged Chaco vegetation in Mato Grosso do Sul (HUECK, 1955). There is little argument, in contrast, about the chaquenian character of the "quebrachales" of three "quebrachos" dominated by *Schinopsis quebracho-colorado,* of white "quebracho" *(Aspidosperma quebracho-blanco),* and of two "quebrachos" in the drier western Chaco; the same is true for the "Palosantales" of *Bulnesia sarmientoi,* the white "quebracho" dominated Arid Chaco Woodland of SW Chaco (SARMIENTO, 1972), together with the main four azonal woody communities ("Algarrobales", "Cardonales", two variants of "Palmares", and "Vinalares"; PRADO, 1993). Also enclosed in the analysis are the Pampean and Subandean varieties of the Sierra Chaco Forests.

Methods

In order to assess to what an extent the woody chaquenian communities and neighbouring seasonal formations are interrelated, 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 analyses 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 be interpreted as representing one particular environmental or ecological factor. The individuals are then displayed in succesive two-dimensional plots ("scattergrams"), of which only the Axis I-Axis II coordinates are shown and discussed here.

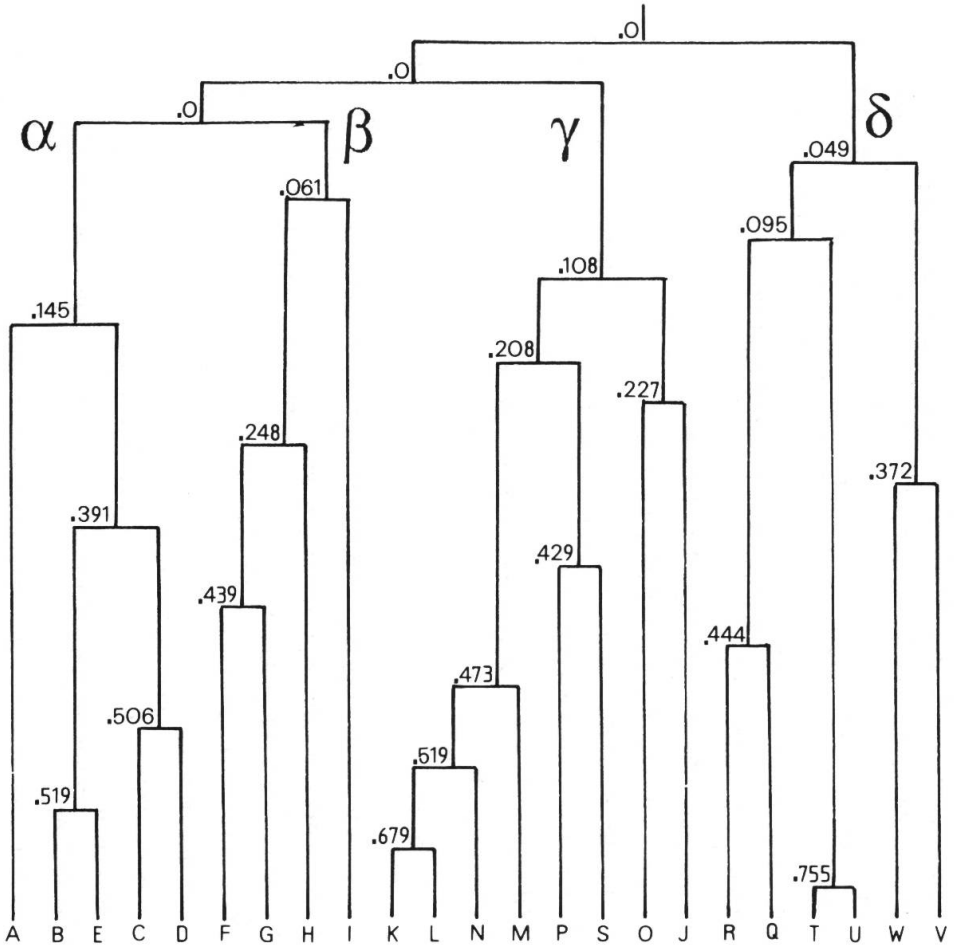

Fig. 1. — Dendrogram resulting from Clink classification analysis of the main woody communities of the Chaco and neighbouring formations. Letters at the bottom indicate the communities studied (see Table 1 for key), and figures in the horizontal lines the similarity index value at each level of fusion.

Results

All the vegetation types described by PRADO (1993) and usually regarded as part of the Gran Chaco region have been analyzed in Table 1. A number of FG, namely II, V, VI and XII 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-Pacará" Forest), D ("Palo blanco" Forest) and the Austro-Brazilian Transitional Forest (E), alongside the communities described by PRADO & al. (1992) for Mato Grosso do Sul (F, G, H, I and J). Apart from FG XXI, which comprises species with a wide ecological plasticity, there are scarce connections between communities A to J and what will be here regarded as Chaco s.s. (communities K to W). The FG XXII comprises the species that relate the Austro-Brazilian Transitional Forest (E) to the Chaco proper, which are on the one hand of scarce importance here and sometimes accidental, and on the other

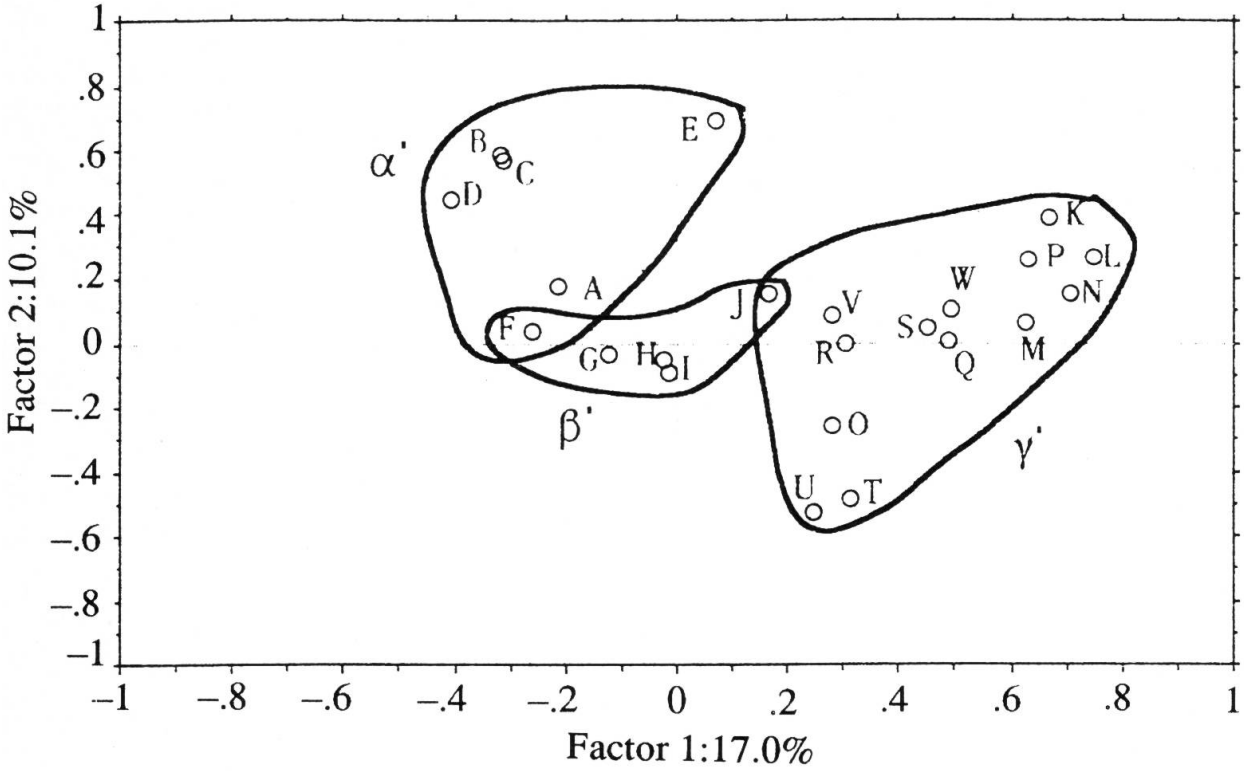

Fig. 2. — Scattergram from PCA analysis of the main woody communities of the Chaco and neighbouring formations.

are overweighed by the much more relevant links to communities A to D. The Chaco forest at 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 1 and coinciding with PRADO & al. (1992). The FG XXIII, XXIV, XXV, XXVI, XXVII, XXVIII, XXXIII and XXXIV illustrate the strong internal homogeneity of the Chaco s.s. woody communities.

Fig. 1 shows the dendrogram resulting from the CLINK classification analysis applied to the same set of communities shown in Table 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 (J). Group α comprises communities A to E, while β those of Mato Grosso do Sul (F to I). Meanwhile, groups γ and δ consist of all the communities of the 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. 2 present three basic clusterings of communities: the wetter ones (A to F) are together in cluster α', the Mato Grosso do Sul communities are grouped in another one (β'), while the bulk of the Chaco s.s. in cluster γ' shows stronger links within itself than with the rest of the neighbouring formations. Once again the Chaco of Porto Murtinho (J) 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.

Discussion

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 PRADO, 1993 and Table 1), five

Table 1. — Classical phytosociological analysis of the main woody communities of the Chaco and neighbouring formations. Source of the floristic lists is indicated.

Column: **A,** Gallery forest, Paraná River (FRANCESCHI & LEWIS, 1979). **B,** "Selva de Ribera" (PRADO & al., 1989; MORELLO & ADÁMOLI, 1974). **C,** "Tipa-Pacará" forest (MEYER, 1963; DIGILIO & LEGNAME, 1966; BROWN & al., 1985). **D,** "Palo blanco" forest (MEYER, 1944; CORO, 1956; ADÁMOLI & al., 1972; CABRERA, 1976). **E,** Austro-Brazilian Transitional Forest (LEWIS & PIRE, 1981, and author's field experience; also MORELLO & al., 1971, MORELLO & ADÁMOLI, 1974, and CABRERA, 1976). **F,** Calcareous woodlands, Mato Grosso do Sul (PRADO & al., 1992). **G,** *Schinopsis balansae* parkland, M. Gr. do Sul (PRADO & al., 1992). **H,** *Aspidosperma-Mimosa* scrubland, M. Gr. do Sul (PRADO & al., 1992). **I:** *Diplokeleba-Tabebuia-Capparis* scrubland, M. Gr. do Sul (PRADO & al., 1992). **J,** Chaco forest, Pto Murtinho, M. Grosso do Sul (PRADO & al., 1992). **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 & al., 1972, and author's field experience). **N,** "Quebrachal" of white "quebracho" (MORELLO & al., 1971; LEWIS & PIRE, 1981). **O,** "Palosantal" of *Bulnesia sarmientoi* (MORELLO & al., 1971, and ADÁMOLI & al., 1972). **P,** "Algarrobal" of *Prosopis* spp. (MORELLO & al., 1971). **Q,** "Vinalar" of *Prosopis ruscifolia* (MORELLO & 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	Selv	Tipa	Pab	AuG	Calc	Sbll	AsM	DiTn	ChPM	QCh	Q x 3	Q x 2	VNQ	Pasa	Alg	Vin	Pmw	PmE	ACW	Card	NSCn	SSCn	
	Family	Genus	Species																								
1	LAUR	Nectandra	falcifolia	1																							
2	LEGM	Albizia	polyantha	1																							
3	MYRT	Hexachlamis	edulis	1																							
4	CAPP	Crateva	tapia	1																							
5	APOC	Peschiera	australis	1																							
6	LEGM	Inga	uruguensis	1																							I
7	LEGM	Acacia	monacantha	1																							
8	ULMA	Celtis	iguanaea	1																							
9	EUPH	Croton	urucurana	1																							
10	FLAC	Banara	arguta	1																							
11	AREC	Arecastrum	romanzoffianum	1																							
12	LEGP	Geoffroea	striata	1																							
13	ANNO	Rollinia	emarginata	1																							
14	POLY	Ruprechtia	laxiflora		1	1	1	1	1																		II
15	LEGM	Enterolobium	contortisiliquum		1	1	1	1	1																		
16	MYRT	Eugenia	uniflora		1	1	1	1	1																		
17	RUTA	Fagara	naranjillo		1	1	1	1																			
18	COMB	Terminalia	triflora		1		1	1																			III
19	MYRS	Rapanea	laetevirens		1	1	1																				
20	SAPO	Pouteria	gardneriana		1	1																					
21	LEGC	Holocalyx	balansae			1																					
22	MORA	Ficus	luschnathiana			1																					
23	SAPI	Sapindus	saponaria			1																					
24	MORA	Sorocea	sprucei			1																					
25	MELI	Trichilia	elegans			1																					IV
26	NYCT	Pisonia	aculeata			1																					
27	CEL	Schaefferia	argentinensis			1																					
28	PTER	Acrostichum	aureum			1																					
29	CECR	Cecropia	adenopus			1																					
30	RUTA	Pilocarpus	pennatifolius			1																					
31	STER	Guazuma	ulmifolia			1																					
32	TILI	Luehea	divaricata			1																					
33	LEGC	Peltophorum	dubium			1																					
34	ULMA	Phyllostylon	rhamnoides			1	1	1	1	1																	V
35	ULMA	Celtis	sp			1	1	1	1	1			1													1	
36	BIGN	Tabebuia	impetiginosa			1	1	1	1	1	1																
37	LEGM	Anadenanthera	colubrina v cebil			1	1	1		1																	
38	ANAC	Astronium	urundeuva					1		1	1	1															
39	RUTA	Fagara	rhoifolia				1	1	1		1															1	
40	CAPP	Capparis	aff retusa ?			1																	1			1	
41	SAPI	Diplokeleba	floribunda						1														1				
42	BORA	Patagonula	americana			1	1	1	1																		
43	MYRT	Myrcianthes	pungens			1	1	1	1																		
44	SAPI	Allophyllus	edulis			1	1	1	1																		
45	NYCT	Pisonia	zapallo			1	1	1	1																		VI
46	LEGC	Gleditsia	amorphoides			1		1	1																		
47	SAPO	Chrysophyllum	gonocarpum			1		1	1																		
48	MORA	Maclura	tinctoria			1		1	1																		
49	LEGM	Pithecellobium	scalare					1	1																		
50	ARAL	Pentapanax	angelicifolius			1	1	1																			
51	CARI	Carica	quercifolia			1	1		1																		
52	PHYT	Phytolacca	dioica			1			1																		
53	SOLA	Brunfelsia	australis			1			1																		
54	ANAC	Astronium	balansae			1			1																		VII
55	LEGC	Pterogyne	nitens			1		1																			
56	SAPI	Cupania	vernalis			1	1																				
57	SAPO	Chrysophyllum	marginatum			1	1																				VIII
58	ULMA	Trema	micrantha			1	1																				
59	BIGN	Jacaranda	mimosifolia				1																				
60	MYRT	Myrcianthes	mato				1																				
61	BIGN	Tecoma	stans				1																				
62	PIPE	Piper	tucumanum				1																				IX
63	TILI	Heliocarpus	popayanensis				1																				

				A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	
				Gali	Selv	Tipa	Pab	Aug	Calc	Sbli	AsM	DiTn	ChPt	MOCh	Ox1	Ox2	whO	Pasa	Alg1	Vinl	Pmw	PmE	ACw	Carg	N5Ch	S5Ch	
64	LEGP	Tipuana	tipu				1	1																			
65	LEGP	Myroxylon	balsamum				1	1																			
66	LEGM	Paraptadenia	excelsa				1	1																			
67	URTI	Urera	baccifera				1	1																			
68	BOMB	Pseudobombax	argentinum					1																			
69	MELI	Cedrela	odorata					1																			
70	LEGP	Lonchocarpus	lilloi					1																			X
71	LEGM	Acacia	albicorticata					1																			
72	SAPI	Athyana	weinmannifolia					1																			
73	LEGC	Senna	spectabilis v. sp					1																			
74	BORA	Cordia	trichotoma/aillo					1																			
75	AREC	Acrocomia	chonta					1																			
76	MELI	Trichilia	claussenii					1																			
77	ELAE	Mutingia	calabura					1																			
78	RUBI	Pogonopus	tubulosus					1																			XI
79	COMP	Vernonia	fulta					1																			
80	COMP	Chlorothamnus	lorentzii					1																			
81	BUDD	Buddleja	albomaculata					1																			XII
82	RUTA	Fagara	hyemalis						1																		
83	BOMB	Ceiba	speciosa						1																		
84	RUBI	Calycophyllum	multiflorum				1		1																		XIII
85	LEGP	Amburana	cearensis				1		1																		
86	EUPH	Cnidoscolus	vitifolius v. chic				1		1																		
87	ANAC	Schinopsis	brasiliensis						1																		
88	STER	Helicteres	lhotskyana						1																		
89	EUPH	Sapium	sp						1																		
90	RUBI	Randia	armata						1																		XIV
91	STER	Sterculia	striata						1																		
92	LEGP	Machaerium	hirtum						1	1			1														
93	EUPH	Croton	sp 1						1					1													
94	RHAM	Ziziphus	oblongifolius							1	1	1															
95	POLY	Coccoloba	sp									1		1													
96	ERYT	Erythroxylum	sp							1				1													
97	CACT	Ceres	uruguayanus								1	1															
98	BORA	Cordia	glabrata						1	1	1																XV
99	AREC	Acrocomia	total						1	1	1																
100	CELA	Maytenus	ilicifolia						1	1																	
101	RHAM	Rhamnidium	elaeocarpum						1	1																	XVI
102	RUBI	Chomelia	obtusifolia						1	1																	
103	BOMB	Pseudobombax	sp						1	1																	
104	BIGN	Tabebuia	ochracea							1																	
105	RUBI	Tocoyena	formosa							1																	XVII
106	COMB	Terminalia	argentea							1																	
107	Undt	Pisonia ?	sp							1																	
108	LEGM	Mimosa	hexandra							1	1																XVIII
109	LEGM	Mimosa	sp							1	1																
110	LEGM	Prosopis	ruboriflora								1																XIX
111	EUPH	Jatropha	ribifolia								1																
112	LEGM	Prosopis	sp									1															XX
113	NYCT	Bougainvillea	sp									1															
114	LEGM	Goldmani	paraguensis									1															
115	EUPH	Aporosella	chacoensis										1														
116	RHAM	Scutia	buxifolia	1	1	1		1							1	1											
117	ACHA	Achatocarpus	praecox		1	1									1	1	1	1			1						
118	SAPO	Sideroxylon	obtusifolium		1			1					1		1	1		1									XXI
119	SANT	Acanthosyris	falcata		1			1								1				1							
120	MYRT	Myrcianthes	cisplatensis			1		1							1												
121	BOMB	Ceiba	chodatii			1	1										1									1	
122	EUPH	Sapium	haematospermum	1																		1					
123	LEGP	Geoffroea	decorticans					1							1	1	1	1		1	1	1	1	1	1		1
124	APOC	Aspidosperma	quebracho-blanco					1		1	1		1		1	1	1	1	1	1				1			1
125	RHAM	Ziziphus	mistol					1					1		1	1	1	1		1	1	1				1	1
126	LEGM	Prosopis	nigra					1							1	1	1	1		1			1	1			1
127	ANAC	Schinus	fasciculatus					1							1	1	1	1		1			1				1
128	LEGM	Acacia	praecox					1					1		1	1	1	1									
129	ANAC	Schinopsis	balansae							1			1		1	1											
130	LEGC	Caesalpinia	paraguariensis					1							1	1	1										
131	LEGC	Cercidium	praecox								1					1	1	1						1	1		1
132	BIGN	Tabebuia	nodosa									1	1				1			1			1				
133	CAPP	Capparis	tweediana									1			1	1					1	1					
134	CAPP	Capparis	speciosa									1					1	1									
135	SANT	Jodina	rhombifolia											1	1	1	1	1								1	1
136	LEGM	Acacia	aroma											1	1	1	1	1		1						1	1
137	CAPP	Capparis	retusa											1	1	1	1	1	1		1						
138	VERB	Aloysia	gratissima											1	1	1	1	1									1
139	SIMA	Castela	coccinea											1	1	1											
140	CELA	Maytenus	vitis-idaea											1	1		1	1			1			1	1		
141	ULMA	Celtis	spinosa											1			1			1			1				
142	LEGM	Acacia	caven													1		1		1			1			1	1
143	LEGM	Prosopis	alba													1	1	1		1			1				1
144	ULMA	Celtis	pallida													1	1	1	1	1	1						1
145	SOLA	Grabowskia	duplicata													1		1			1		1	1			
146	LEGC	Senna	aphylla													1								1			
147	ZYGO	Porlieria	microphylla													1											1
148	SOLA	Cestrum	parqui													1											
149	LEGM	Prosopis	affinis													1							1				
150	AREC	Trithrinax	campestris													1		1									1
151	CACT	Opuntia	spp.																				1				
152	CHEN	Holmbergia	tweediei															1			1						XXVI
153	LEGM	Acacia	furcatispina														1										1

				A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	
				Gall	SelV	TipJ	Pab	AuB	Calc	SpII	AsM	DiTn	ChPM	Q.Ch	Q.x3	Q.x2	WhG	Pasa	Algr	Vini	Pmw	PmE	ACW	Card	N5Ch	S5Ch	
154	ANAC	Schinopsis	quebracho-colorado												1	1		1									
155	CAPP	Capparis	atamisquea												1	1							1				
156	CELA	Maytenus	spinosa												1	1											
157	LEGM	Prosopis	kuntzei												1		1	1									
158	POLY	Ruprechtia	triflora											1		1	1	1									
159	CAPP	Capparis	salicifolia													1	1	1		1							
160	LEGC	Mimoziganthus	carinatus													1							1		1		
161	OLAC	Ximenia	americana													1							1		1		
162	CACT	Stetsonia	coryne													1		1					1		1		
163	CACT	Cereus	validus													1		1					1		1		
164	VERB	Aloysia	scorodonoides													1											
165	ZYGO	Bulnesia	foliosa													1											
166	LEGM	Mimosa	detinens													1											
167	NYCT	Bougainvillea	campanulata													1											
168	BROM	Bromelia	hieronymi													1											
169	BROM	Bromelia	serra													1											
170	CACT	Echinopsis	minuana														1	1									
171	CACT	Cleistocactus	smaragdiflorus														1	1									
172	CACT	Eriocereus	pomanensis														1	1									
173	CACT	Opuntia	colubrina															1									
174	COMP	Tessaria	dodoneaefolia															1									
175	CACT	Opuntia	chakensis															1									
176	CACT	Opuntia	sp															1									
177	CACT	Monvillea	cavendishii															1									
178	CACT	Eriocereus	tortuosus															1									
179	ZYGO	Bulnesia	sarmientoi											1					1								
180	APOC	Aspidosperma	triternatum											1					1								
181	CACT	Opuntia	discolor																1								
182	CACT	Opuntia	retrorsa																1								
183	CACT	Echinopsis	schaferi																1								
184	BROM	Dyckia	ferox																1								
185	BROM	Bromelia	urbaniana																1								
186	LEGM	Prosopis	sericantha																1								
187	COMP	Cyclolepis	genistoides															1			1			1		1	
188	SOLA	Lycium	sp															1				1	1	1		1	
189	LEGM	Prosopis	ruscifolia											1					1	1	1	1					
190	APOC	Vallesia	glabra																1		1	1					
191	LEGM	Prosopis	vinalillo																1		1	1					
192	AREC	Trithrinax	biflabellata																		1	1					
193	LEGM	Prosopis	hassleri																	1							
194	CHEN	Atriplex	sp																	1							
195	LEGC	Parkinsonia	aculeata																			1					
196	COMP	Baccharis	salicifolia																			1					
197	COMP	Hyalis	lancifolia																			1					
198	AREC	Copernicia	alba											1							1	1					
199	LEGM	Prosopis	torquata																				1	1	1	1	
200	NYCT	Bougainvillea	spinosa																				1		1		
201	PORT	Grahamia	bracteata																				1		1		
202	ZYGO	Larrea	divaricata																				1		1		
203	CELA	Maytenus	viscifolia																				1		1		
204	ZYGO	Plectrocarpa	tetracantha																				1		1		
205	LEGM	Prosopis	strombulifera																				1		1		
206	CHEN	Allenrolfea	vaginata																				1		1		
207	MALP	Tricomaria	usillo																				1		1		
208	LEGM	Prosopis	elata																					1			
209	ZYGO	Bulnesia	bonariensis																					1			
210	LEGM	Prosopis	pugionata																					1			
211	ZYGO	Larrea	cuneifolia																					1			
212	ZYGO	Bulnesia	retama																					1			
213	LEGC	Senna	acanthoclada																					1			
214	CACT	Cleistocactus	baumannii																					1			
215	VERB	Lippia	salsa																						1		
216	CHEN	Atriplex	cordobensis																						1		
217	BORA	Cortesia	cuneifolia																						1		
218	ANAC	Schinopsis	haenkeana																							1	1
219	RHAM	Condalia	microphylla																							1	1
220	ULMA	Celtis	tala																							1	1
221	ANAC	Schinus	bumelioides																							1	
222	ANAC	Schinus	molle																							1	
223	RUTA	Fagara	coco			1																					1
224	NYCT	Bougainvillea	stipitata			1																					1
225	POLY	Ruprechtia	apetala			1																					1
226	ANAC	Lythraea	ternifolia																								1
227	ROSA	Kageneckia	lanceolata																								1
228	RHAM	Condalia	montana																								1
229	LEGM	Prosopis	alba v. panta																								1
230	LEGM	Prosopis	chilensis																								1
231	LEGM	Acacia	atramentaria																								1
232	LEGC	Caesalpinia	mimosifolia																								1
233	COMP	Flourensia	campestris																								1
234	RHAM	Colletia	spinosissima																								1
235	COMP	Heterothalamus	alienus																								1

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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", the "Palosantal", "Algarrobal", "Vinalar", "Cardonal", the two "Palmares", both Sierra Chaco variants, the Arid Chaco Woodland and the Chaco Forest at Porto Murtinho. A brief discussion on the excluded and transitional communities follows.

a) Excluded communities

Between the communities listed in Table 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. 1 & 2) have shown that they are more closely inter-related, and linked to what has been called "Austro-Brazilian Transitional Forest" (PRADO, 1991), than to the Chaco s.s. communities. Therefore, none of these five vegetation types should be included in the Chaco phytogeographical province, as the more modern treatments have indicated (e.g. CABRERA, 1976; PRADO, 1991).

b) Transitional communities

The four transitional units consist of three from the Mato Grosso do Sul area studied by PRADO & al. (1992): the *Schinopsis balansae* parkland (G), the *Aspidosperma-Mimosa* scrubland (H), and the *Diplokeleba-Tabebuia-Capparis* scrubland (I), and finally the "Austro-Brazilian Transitional Forest" (E). The first three communities contain a very low percentage of true Chaco species (PRADO & al., 1992), 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. 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 PRADO, 1993). 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 it rather thrives on non-climatogenic saline soils, with high clay level, periodical waterlogging, elevated Na^{++} concentration and very strongly alkaline subsoils (ESPINO & 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 Chaco s.s. 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 widespred 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 (e.g. *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., such as the species listed above together with *Diplokeleba floribunda, Astronium balansae, Chrysophyllum gonocarpum, Pithecellobium scalare* and *Brunfelsia australis* (see Table 1, FGs II, V and VI). Seven of the most typical Chaco species[1] may also occur 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 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, 1966, 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 Dominium (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 against the chaquenian species pushing east in areas with less alkaline and less waterlogged soils.

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-Pacará" (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 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 & PÉREZ-MOREAU (1944) in their map of vegetation of Argentina.

c) The Eastern Chaco problem

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 Dominia, 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

[1]These are: *Geoffroea decorticans, Aspidosperma quebracho-blanco, Ziziphus mistol, Prosopis nigra, Schinus fasciculatus, Acacia praecox* and *Caesalpinia paraguariensis* (see Table 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.).

as Chaco species (see distribution map in PRADO & GIBBS, in press) 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 & al., 1977; FURLEY & RATTER, 1988; RATTER & al., 1988), 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 subregions map in MORELLO & ADÁMOLI, 1968; also HUECK & SEIBERT, 1981) seems to coincide roughly with a rainfall isoline somewhere between 950 to 1000 mm per year (PRADO, 1991), 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 Second 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. 4) matches very well with an equivalent narrow band along the river Paraná with C_2B_4'ra' climate (Fig. 3), and so does the zero isoline for the MI according to Thornthwaite's Second System (BURGOS & VIDAL, 1951, Fig. 7D). The similarities extend even to most of the chaquenian districts proposed by RAGONESE & CASTIGLIONI (1970), such as the "Pilaguense", "Matacense", and "Santiagueño" districts, to which the corresponding climate types are C_1A'da', DA'da' and DB_4'da' respectively, and the districts "Campestre", Mixed Forests & Savannas and Chaquenian Forest as a group with the corresponding climate type C_1B_3'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), RAMELLA & SPICHIGER (1989), SPICHIGER & RAMELLA (1989), and ZELLWEGER & al. (1990). 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 overestimate)[1]. Geographically speaking the term Chaco will continue as the denomination of the whole of the region, but from a phytogeographical point of view the name must have a more restricted usage.

[1]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 & al., 1975).

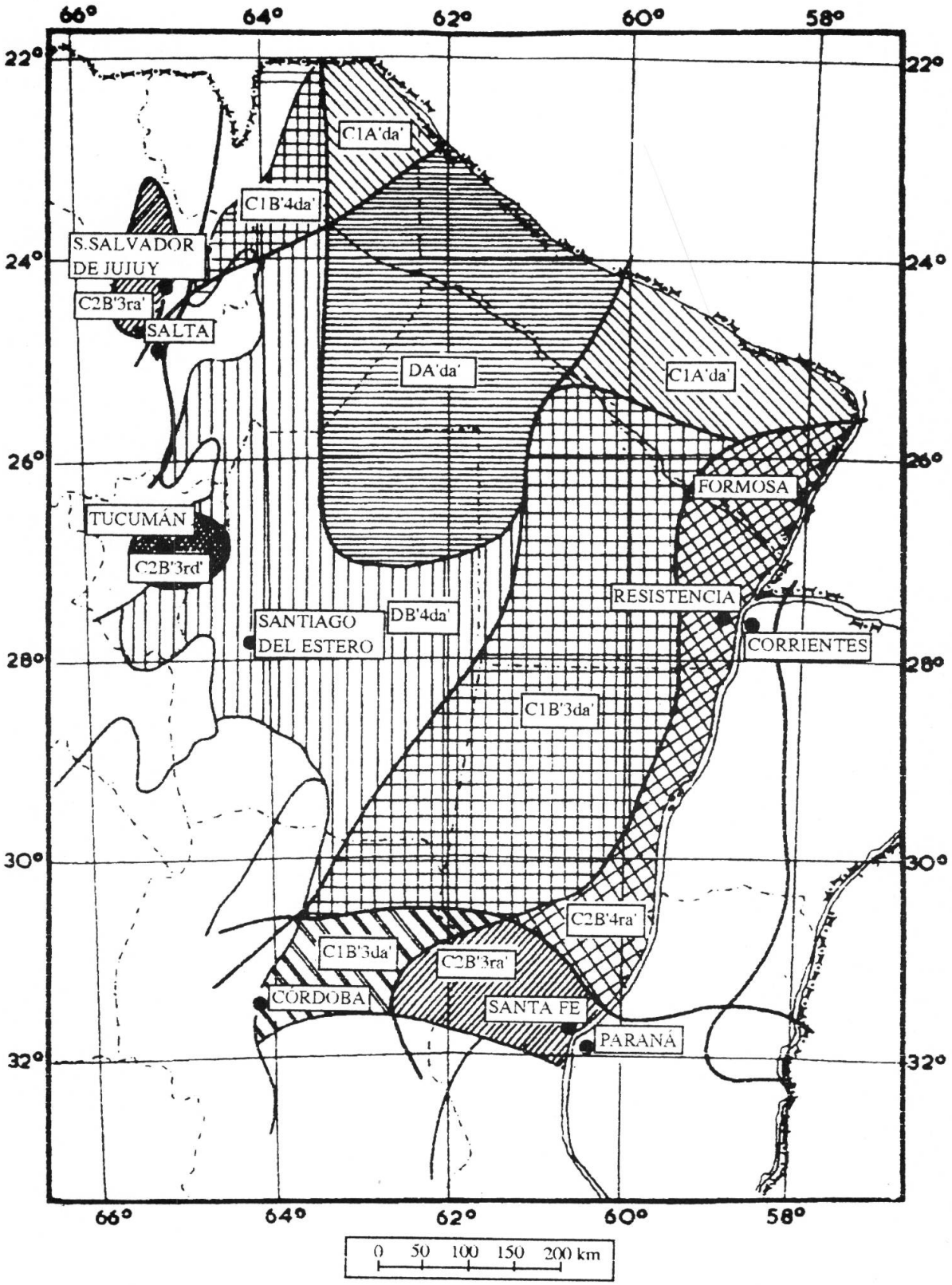

Fig. 3. — Climate types for the Argentine Chaco, according to the Second System of Thornthwaite. Modified from GALMARINI & R. DEL CAMPO, 1964.

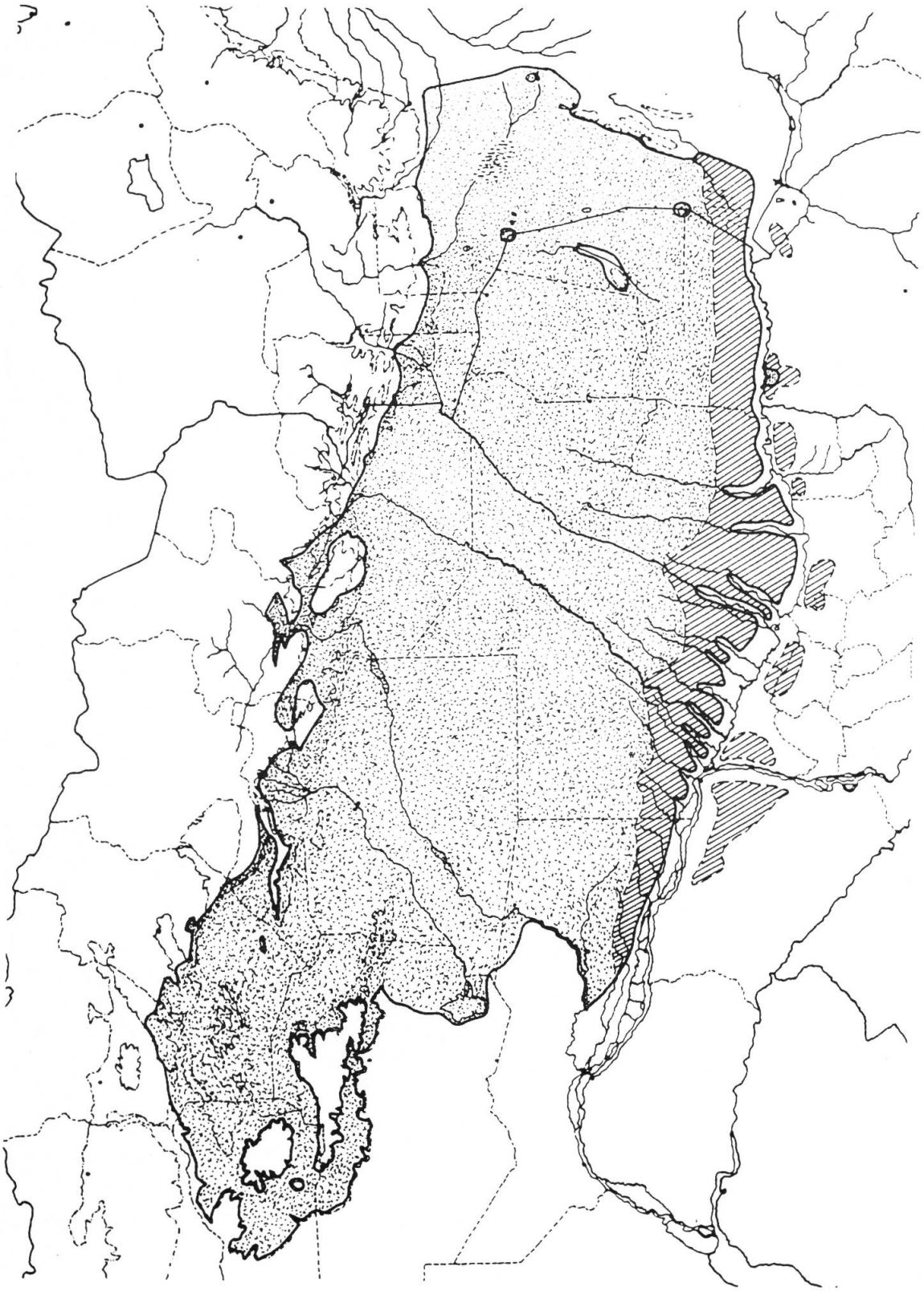

Fig. 4. — A new proposal for the geographical limits of the Chaco sensu stricto. The transitional belt is indicated by oblique hatching.

d) The Chaco sensu stricto

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 (PRADO, 1991), phytosociological study of the more relevant plant communities in the region both in classical and numerical analyses, and putting the vegetation of this area against the background of similar formations in South America (PRADO, 1991), a map of what is here regarded as Chaco *sensu stricto* is presented (Fig. 4). It must be noted that the Sierra Chaco, although taken as a separate entity throughout the analysis, is accepted as part of the Chaco s.s.; however, the *Polylepis australis* woodlands are not to be regarded as chaquenian, as in CABRERA (1976). 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, VERVOORST (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 & al. (1979) for the Córdoba province, and D'ANGELO & al. (1987) together with 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 (Fig. 4) 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 & al. (1989 & 1992), together with the present author's field experience and the plant distribution maps presented elsewhere (PRADO, 1991; PRADO & GIBBS, in press). Other differences with previous concepts of the Chaco shown in this new map consist in the exclusion of the vegetation of some of the "cerros" of Paraguay, such as the Cerros León, Cabrera and Chovoreca, clearly linked to the Subandean Piedmont Forests (RAMELLA & SPICHIGER, 1989) and also to the arboreal forms of Caatingas of NE Brazil (PRADO, 1991). Also excluded are the gallery forests on the rivers crossing the Chaco, particularly in their lower courses close to the Paraguay and Paraná rivers, and the vegetation of the Río Timane in the Paraguayan Chaco. Of the alleged Chaco vegetation in SW Brazil only a reduced sector remains as such (Fig. 4), together with some limited neighbouring transitional areas. It is noteworthy as well that the expansion of the Chaco s.s. beyond the line Santa Cruz de la Sierra-Chiquitos is here dramatically limited with respect to previous maps.

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