Gm and Inv Allotypes of Brazilian Cayapo Indians

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INTRODUCTION

The inherited antigenic determinants (allotypes) of the Gm and Inv systems, located on molecules of the immunoglobulins, have proven to be very useful polymorphisms for the study of human variation [1]. The allotypes are transmitted in sets, each of which may be controlled by two or more closely linked genes; for convenience, the latter are referred to as phenogroups. A striking feature of the Gm phenogroups is that some of them occur in only one of the several races that have been tested so far; moreover, no two racial groups seem to have the same array of phenogroups. Such a distinctive distribution is not known to occur in any other human genetic system [1].

The Gm system has been studied in about 5,000 South American Indians. The number of Gm antigens studied, however, varied from investigation to investigation, and the distribution of some antigens among the populations is completely unknown. Fewer than 1,000 individuals have been tested for the Inv allotypes. The incompleteness in both systems led to the decision to include the study of the Gm and Inv markers in a multidisciplinary investigation whose objective is the understanding of the factors which influence the genetic variability of Brazilian Cayapo Indians [2–9].

MATERIALS AND METHODS

The Ge-speaking Cayapo Indians live, at present, in eight still quite isolated, semi-independent villages in the Brazilian states of Pará and Mato Grosso. Information about their recent history, exact location, and demographic characteristics is given in Salzano [3]. Twenty years ago, they were still hostile to non-Indians. The four subgroups of this tribe studied in relation to the Gm and Inv systems were visited during the years 1965–1970 and can be briefly characterized as follows: (1) Kuben-Kran-Kegn, lat 8°10'S, long 52°8'W, population = 310; (2) Txukahamae, lat 10°20'S, long 53°5'W, population

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= 190; (3) Mekranoti, lat 8°40′S, long 54°W, population = 240; (4) Xikrin, lat 5°55′S, long 51°11′W, population = 150. The degree of acculturation of these subgroups varies. The most acculturated are probably the Xikrin followed by the Kuben-Kran-Kegn; the Txukahamae and Mekranoti are the least affected by neo-Brazilian influences.

Blood was collected in 10 or 15 ml Becton-Dickinson vacutainers with EDTA or ACD; all persons, with the exception of the very young (less than 2 years of age), present in the villages at the time of our visit were included in the study. Specimens were refrigerated shortly after collection and carried by air to Pôrto Alegre. There, the plasma was separated from the red cells and stored at -20° C. The plasma was subsequently converted to serum by treatment with a solution of M/40 CaCl₂ and sent, frozen, to Cleveland for Gm and Inv testing. These determinations were done as previously described [10] using the reagents listed in table 1. The table presents the numerical system suggested by

 $\begin{tabular}{ll} TABLE & 1 \\ \hline REAGENTS & USED & TO & DETECT & Gm & AND & Inv & Antigens \\ \hline \end{tabular}$

WНО		Anti- γ -gl	OBULIN	Anti-D		
	Original	Antibody	Dilution	Ident.	Dilution	
Gm antigen:			4		,	
1	a	Mor	1/64	Bra	1/3	
2	x	Tyl	1/32	Ham	1/3	
3	b^2	Aus	1/4	Ham	1/3	
		How	1/8	Mil	1/3	
5	b1	Pay	1/4	Cam	9/10	
		Pay	1/4	107	1/3	
6	c	Cur	1/8	Cons	9/10	
13	$\mathbf{p_3}$	Ing	1/4	Cam	9/10	
		Ing	1/4	107	1/3	
14	b^4	Bur	1/8	Cam	1/3	
		Bur	1/16	107	1/3	
21	g	Monkey E	1/16	Ham	1/3	
Inv antigen:						
1	1	Mas	1/4	Roe	1/3	

the World Health Organization as well as the alphabetic system used by some investigators. The former is used in this paper.

The Gm phenogroup frequencies were estimated by means of the computer program MAXIM [11].

RESULTS

Table 2 presents the phenotypes and their frequencies observed in the four populations sampled. About 99% of the individuals are Gm (1, 21) or Gm (1, 2, 21). Among the Txukahamae, we observed one individual who is Gm (1, 2, 13, 21). This suggests the presence of the $Gm^{1, 13}$ phenogroup which is common among some Mongoloids [1]. The Xavante and Trio are the only other South American Indian tribes whose serum has been tested for Gm (13). This antigen was not detected among the former [12], but occurs in polymorphic frequencies among the Trio [17]. The occurrence of the Gm (1, 3, 5, 13, 14, 21) and Gm (1, 2, 3, 5, 13, 14, 21)

 ${\bf TABLE~2}$ Gm and Inv Phenotypes in Four Populations of Brazilian Cayapo Indians

	Population									
	Тхиканамае		Mekr	ANOTI	Kuben-Kran-Kegn		Xikrin		T	OTAL
	N	%	N	%	N	%	N	%	N	%
Gm phenotype:										
1,21	78	50	48	52	100	75	47	80	273	62.0
1,2,21	75	49	42	45	32	24	12	20	161	36.6
1,2,13,21	1	1							1	0.2
1,5,13,14,21					2	1			2	0.5
1,3,5,13,14,21			2*	2					2	0.5
1,2,3,5,13,14,21			1*	1			• • •		1	0.2
Total	154	100	93	100	134	100	59	100	440	100
Inv phenotype:										
1	115	75	55	59	82	61	38	64	290	65.9
Total	154	100	93	100	134	100	59	100	440	100

Note.— χ^2 for heterogeneity among localities for Gm (1,21) and Gm (1,2,21), $\chi^2_{(3)} = 29.6$, P < .001; for Inv (1), $\chi^2_{(3)} = 8.6$, P < .05.

phenotypes among the Mekranoti is due to a white man $(Gm^{3, 5, 13, 14}/Gm^{1, 21})$ captured in his infancy. He has adopted the Indians' way of life and has married an Indian woman; one of his children has the same phenotype that he has, while the phenotype of his other child is Gm (1, 2, 3, 5, 13, 14, 21) (probable genotype $Gm^{3, 5, 13, 14}/Gm^{1, 2, 21}$). More difficult to explain is the presence of phenotype Gm (1, 5, 13, 14, 21) in a woman and her son among the Kuben-Kran-Kegn. This suggests Negro admixture. The relative isolation of this group, however, makes the suggestion unlikely; nevertheless, an event like the one described above could have occurred in a previous generation. Individuals with the Gm (5) specificity appeared with variable frequency in samples of Indians from Surinam, French Guiana, Bolivia, and Brazil; but only the Xavante and Trio were tested for Gm (13) and Gm (14) which may be transmitted with Gm (5). Gm (14) was not observed in samples from either of these tribes [12, 13].

The frequency of sera with Inv (1) varied from 59% to 75% in the Cayapo populations reported in this study. This range of values appears to be characteristic of South American Indians (see below).

The Gm phenogroup and Inv allele frequencies are given in table 3. The four populations can be clearly separated into two groups (Txukahamae/Mekranoti; Kuben-Kran-Kegn/Xikrin) on the basis of the frequencies of the phenogroups $Gm^{1, 21}$ and $Gm^{1, 2, 21}$. Such a distinction is not apparent, however, in the frequencies of Inv^1 . The Mekranoti, Kuben-Kran-Kegn, and Xikrin show similar values for

^{*} These phenotypes were observed in the sera of a white man $(Gm^{3,5,12,14}/Gm^{1,21})$ captured by the Indians in his infancy and in the sera of two of his children by an Indian woman.

TABLE 3

Gm Phenogroup and Inv Allele Frequencies in Four Populations of Brazilian Cayapo Indians

				Pop	ULATION					
	Txu	Канамае	Ме	KRANOTI	Kuben	-Kra	n-Kegn	2	KIKRIN	4
PHENOGROUP OR ALLELE	p	± σ	Þ	± σ	p	±	σ	p	±	σ
$Gm^{1,21}$.709	.028	.717	.036	.865		.022	.893		.029
$Gm^{1,2,21}$.288	.028	.267	.035	.128		.021	.107		.029
$Gm^{1,13}$.003	.003								
$Gm^{3,5,13,14*}$.016	.009						
$Gm^{1,5,13,14}$.007		.005			
Inv1	.497	.022	.361	.040	.377		.043	.403		.052

^{*} See footnote of table 2.

this marker (.36-.40); the Txukahamae, however, have a somewhat higher frequency (.50).

Table 4 summarizes the Gm studies performed to date on samples from a total of 5,351 South American Indians. The number of Gm antigens surveyed in each of the 25 studies varied from two to 15. The only phenogroup that shows variation and which was detectable in all the studies is $Gm^{1,2}$. The frequencies vary from 0 to .54. The three highest values, observed among the Makiritare, Palikour, and Mocétène, are separated by a somewhat large interval from the remainder. The latter occur in an almost continuous distribution which cannot be clearly correlated with the geographic location of these populations. The Cayapo present the same frequency as the Xavante (.21) while the frequencies for three other Brazilian tribes vary from .22 to .32.

Similar data for the Inv^1 gene frequencies are shown in table 5. Nine surveys (including ours) have been conducted testing a total of 1,300 persons. Six of the nine studies reported frequencies of Inv^1 varying from .33 to .45. The Cayapo value (.42) is included in this most common interval.

A surprisingly large number of the samples studied by us showed antibody activity against the sensitized red blood cells. These findings are summarized in table 6. The overall frequency of agglutinators is 26%. The great majority of the individuals tested were adults, but there is an indication of a decreased prevalence in young children ($\sim 1/14$ in those < 10 years versus $\sim 1/3$ in those ≥ 10 years). This is contrary to the finding among white and black populations in Cleveland [23] and suggests that the agglutinating activity in the Indian serum samples may be from a different cause than that responsible for the agglutinating activity in the serum samples from whites and blacks. The frequency of agglutination is independent of the sex of the donor ($\chi^2_{(1)} = 2.3$; P > .10). There exists however, heterogeneity among the four populations sampled, the Mekranoti showing higher (42%) and the Kuben-Kran-Kegn lower (17%) prevalences ($\chi^2_{(3)} = 16.9$;

TABLE 4
Gm Studies Performed to Date on South American Indians

Population	Reference	No. Studied	Gm Antigens Studied	$Gm^{1,2}$
Venezuela:				
Paraujano	[14] [14] [14]	114 122 137	1,2,5 1,2 1,2	.17 .50 .17
Guyana:				
Wapishana	[15] [15] [15]	116 116 84	1,2 1,2 1,2	.22 .32 .12
Surinam:				
OyanaCaribTrio	[16] [16] [17]	15 19 252	1,2,5,6 1,2,5,6 *	.14 .31 .33
French Guiana:				
Galibi Oayana Palikour Emerillon Oyampi	[17] [17] [17] [17] [17]	191 97 75 40 98	1,2,5,6 1,2,5,6 1,2,5,6 1,2,5,6 1,2,5,6	.30 .21 .54 .21
Bolivia:				
Aymara† Aymara‡ Uru/Aymara Quechua Mocétène Chipaya	[18] [19] [19] [18] [18] [20]	358 1,855 311 131 76 96	1,2,5 1,2,5,6 1,2,5,6 1,2,5 1,2,5 1,2,5	.11 .06 .06 .10 .48 .00
Brazil:				
Aweikoma Caingang Guarani Xavante Cayapo	[21] [21] [21] [12] Present study	58 - 52 - 34 - 464 - 440	1,2,5,6 1,2,5,6 1,2,5,6 1,2,3,5,6,13,14 1,2,3,5,6,13,14,21	.32 .26 .22 .21 .21

^{*} Anti-Gm (1,2,4,6,11,13,14,15,16,17,21,22,24,am,Ad).

P < .001). The reasons for the large numbers of agglutinators, as well as for the population differences, are unknown. Systematic medical examinations were performed among the Txukahamae only [8], but neither they nor individuals from the other groups showed any signs of being affected by rheumatoid arthritis, a frequent cause of agglutination of sensitized red blood cells (RBC). It is true that the blood collection among the Mekranoti was made after what seemed to be a very serious malaria epidemic; the tribal life during this crisis was seriously disturbed, and the prevailing health and nutritional situation was certainly not representative of the group's best condition. Their immune system may therefore have been much challenged during this period. Further studies in groups at this

[†] May have been included in the larger sample reported in [19].

[‡] Quilici et al. [20] present results on 1,466 Aymara who are probably included in this sample. Their estimate of the frequency of $Gm^{1,2}$ was .04.

TABLE 5

Inv Gene Frequencies in South American Indians

Population	Reference	No. Studied	Inv ¹ Frequency
Venezuela:			
Waica	[22]	102	.41
Paraujano	[22]	112	.35
Piaroa	[22]	68	.76
Bolivia:			
Chipaya	[20]	77	.59
Brazil:			
Aweikoma	[21]	27	.33
Caingang	[21]	52	.44
Guarani	[21]	31	.19
Xavante	[12]	391	.45
Cayapo	Present study	440	.42

cultural level might indicate whether this high prevalence of anti-human globulins is a reflection of the particular set of environmental conditions prevailing among hunters and gatherers or if this is an isolated finding confined to the Cayapo only.

All the serum samples (except one from the Txukahamae) that agglutinated the sensitized RBC were tested at a 1/20 dilution in saline for the rheumatoid factor (RF) by means of the latex test and at the same dilution for cold agglutinins against uncoated group O cells. The latter test will be referred to as the saline test. This test was done on the basis of the findings by Layrisse and Layrisse [24] that a high proportion of the serum samples from Yanomama Indians in Venezuela have cold agglutinin activity. All were run at room temperature (approximately 20° C). The data are presented in table 7 in the form of 2 × 2 contingency tables. It is immediately apparent that the agglutination of the sensitized RBC is not dependent upon a positive reaction in either the latex or the saline test, since 57/115 (about 50%) of the samples tested were negative for both tests. Positive reactions in the saline and latex tests occur independently among the Mekranoti and the Txukahamae, but seem to be correlated among the Kuben-Kran-Kegn. Since only one Xikrin sample was positive in the saline test, no evaluation can be made for independence in this population.

The frequencies of positive reactions in the latex test varied from 28% to 47% (table 7), but the variation among the four populations is not significantly different $(\chi^2_{(3)} = 2.054; .70 > P > .50)$. The frequencies of the positive reactions in the saline test varied from 6% to 46% (table 7); this variation is significant $(\chi^2_{(3)} = 11.673; .01 > P > .001)$. The biological significance of these observations remains to be established.

The saline agglutinating activity was absorbed from 15 samples that were also positive in the latex test to see if the antibodies against the latex particles would

TABLE 6

Prevalence of Carriers of Anti-Human Globulins in Four Populations of Brazilian Cayapo Indians

			AGE A	ND PRESEN	CE OF AN	II-HUMAN	GLOBULINS		
			,				I	ALL AGES	
	<	5 Yr	5-	-9 Yr	≥1	0 Yr	-	Ag	GL.
Population and Sex of Individuals Studied	N	Aggl.	N	Aggl.	N	Aggl.	Total	N	%
Txukahamae:									
M	7	0	13	0	60	15	80	15	19
F	8	1	17	2	49	19	74	22	30
Total	15	1	30	2	109	34	154	37	24
Mekranoti:									
M	3	1	3	0	30	13	36	14	39
F	1	0	12	2	44	23	57	25	44
Total	4	1	15	2	74	36	93	39	42
Kuben-Kran-Kegn:									
M	0	0	2	0	63	13	65	13	20
F	0	0	1	0	68	10	69	10	14
Total	0	0	3	0	131	23	134	23	17
Xikrin:									
M	2	0	5	0	24	7	31	7	23
F	1	0	3	0	24	10	28	10	36
Total	3	0	8	0	48	17	59	17	29
All localities:									
M	12	1	23	0	177	48	212	49	23
F	10	1	33	4	185	62	228	67	29
Total	22	2	56	4	362	110	440	116	26

Note.—Aggl. = agglutinators, persons whose sera showed activity against red cells coated with at least one of the anti-D sera used (see table 1).

be affected. The reaction against the latex particles remained unchanged in all 15 samples, hence the antibody molecules active in the two tests are different. Dialysis against cold distilled water removed all agglutinating activity from the supernatant fluid for both tests and for the action against the sensitized RBC. The activity was recovered when the precipitate was redissolved in saline. The active molecules are, therefore, probably IgM as are the anti-Gm and anti-Inv molecules, with but rare exceptions. Forty of the samples (10 from each population) that caused sensitized RBC to agglutinate were investigated to see if they were directed against a specific Gm antigen. None of them were.

Shortage of serum prevented us from pursuing the problem further.

 2×2 Contingency Table Comparisons of Reactions of Serum Samples in Latex and Saline Tests TABLE 7

		%	o 4	:	÷	:	:
	XIKRIN	Total N	1 16	17	:	:	:
	X	1	1 8	6	53		
		+	0 8	8	47	:	:
		%	30 70	:	:	:	:
	AN-KEGN	Total N	7 16	23	:	:	:
	KUBEN-KRAN-KEGN	1	2 13	15	99		10: \
EST	H	+	ນຕ	8	34	5.957	.02 > P > .01
LATEX TEST		%	46 54		:	:	:
	OTI	Total N	18	39	:	:	:
	Mekranoti	I	12	28	72		
		+	9 10	11	28	0.4341	>.50
		%	19	:	:	:	:
	MAE	Total N	7 29	36	:	:	:
	Тхиканамае	1	5 20	25	69		
		+	2 6	11	31	0.0161	08:<
		Saline Test	+ 1	Total	%	$\binom{2}{(1)}$	
		174	4		٠,	~	۱ ۳

Note.—See text for further details.

DISCUSSION

The discovery of new polymorphisms and the accumulation of knowledge about them in different racial groups will no doubt enable us, in a not very distant future, to obtain a much more meaningful picture of the pattern of human biological variability. The Gm and Inv polymorphisms, especially the former because of the number of allotypes already identified, will play an important role in this genetic taxonomy. Unfortunately at present the number of populations tested simultaneously for all known gene markers is still small, and appropriate methods have not been devised to allow the combination of these data with those provided by the study of morphological variation or with those related to the natural and socioeconomic environment of these groups. Perhaps it is because of this that the study of genetic markers has until now failed to establish coherent patterns of variation in South American Indians. For instance, the data reviewed here concerning the distribution of $Gm^{1,2}$ cannot be clearly correlated with factors of geographic distribution or of linguistic differentiation, and the picture obtained using this marker is not similar to that provided by Inv^1 .

Similar difficulties are encountered when we try to correlate our findings on these polymorphisms with the demographic and morphological information, as well as with the findings provided by other genetic systems [3-7] at the Cayapo intratribal level. The available information about the recent history and demography of these groups indicate that the Txukahamae and Mekranoti should show the lowest degree of genetic differentiation; dissimilarities between them and the Kuben-Kran-Kegn should be more marked, while the Xikrin, who separated earlier from the others, should present the highest degree of differentiation. The Gm findings are to some extent in accordance with this, the Txukahamae and Mekranoti showing exactly the same value for $Gm^{1, 21}$, but they are clearly different in relation to the Inv^1 gene marker. On the other hand, if we consider the anthropometric [4] and dermatoglyphic [6] data, we will see that the relationships implied by them do not parallel those obtained with the Gm and Inv systems. It should also be mentioned that the computation of genetic distances taking into consideration six loci (those related to blood groups Rh, MNSs, Duffy, Kidd, and Diego, as well as the haptoglobins) for these four populations [7] did not yield any clear picture, the differences being of about the same order of magnitude in all comparisons. This pattern of intratribal variability, however, is to some extent expected with gene markers that are not subjected to strong selective pressures, under the fission-fusion model of genetic structure [25, 26]. As was indicated elsewhere [25-27], this type of structure (fissions and fusions of groups of individuals separated along kinship lines in moderate-size nomadic groups) is such that new combinations of gene frequencies can be explored, but after a sufficient interval of time the entire tribe should be viewed as the ultimate breeding unit.

The high frequency of carriers of anti-human globulins observed by us poses a series of questions that should be answered. Since the number of agglutinators is high in all four populations, localized disease agents can be excluded as a tentative explanation. On the other hand, the high prevalences could be related to

unknown racial characteristics or more likely to the ecological conditions of these groups. As was stressed by Neel and Salzano [26], the factors which condition the acquisition of antibodies at this cultural level may differ in important respects from those prevalent in civilized populations.

SUMMARY

Data from 440 individuals belonging to four populations of Brazilian Cayapo Indians are reported. About 99% of them are Gm (1, 21) or Gm (1, 2, 21), while the frequency of sera with Inv (1) varies from 59% to 75%. These values are generally in accordance with those previously obtained among other South American Indians. The four populations can be separated into two groups if the distribution of $Gm^{1, 21}$ and $Gm^{1, 2, 21}$ is considered, but this distinction is not apparent in the frequencies of Inv^1 . A surprisingly high number of samples showed antibody activity against the sensitized red cells, the total frequency of agglutinators being as high as 26%. It is suggested that the prevalence of anti-human globulins should be studied in other populations living at this stage of cultural development.

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