

## Gene Flow Across Tribal Barriers and Its Effect Among the Amazonian Içana River Indians

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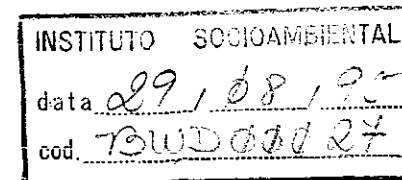
**KEY WORDS** Brazilian Indians, Gene flow, Demography of Amerindians, Genetic distances

**ABSTRACT** Demographic information was obtained from 622 individuals of five communities of primarily Baniwa Amerindians living near the Içana river in Brazil. Four of these populations, plus another from the same area, were also studied genetically. The latter investigation included the blood and, in some cases, saliva of 531 subjects, variously tested in relation to 40 genetic systems. Demographically these groups are characterized by young age, high intertribal admixture, low non-Indian admixture, high exogamy but low marital distance and high inbreeding, high fertility but low variance in offspring number, and relatively low mortality. Their gene pool shows a peptidase B variant ( $PEPB^{2BAN1}$ ) and "private" polymorphism of carbonic anhydrase<sub>2</sub> ( $CA_2^{BAN1}$ ) until now observed only among them. Other distinctive characteristics are the low frequencies of  $L^{NS}$  (0.08),  $L^{Ns}$  (0.09),  $R^Z$  (0.01),  $R^O$  or  $r$  (0.02),  $ACP^A$  (0.08),  $GALT^D$  (0.01), and the relatively high prevalences of  $Gm^{1:11,13,16}$  (0.05) and  $Gc^1$  (0.82).  $Tf^{Dchi}$  occurs with a low prevalence (0.01). Genetic distance analysis reveals that the one Baniwa sample by history comprised of minimally admixed individuals is quite similar genetically to the Wapishana, another Aráwak-speaking tribe some 900 km to the east, and that the genetic distances between the Baniwa communities reflect the amount of historical admixture in a way that indicates which should be excluded from considerations of intertribal genetic distances. Finally, the genetic relation of the Baniwa to the nearby tribes is examined.

The region of the confluence of the Içana and Negro rivers, in the northwestern tip of Brazil (Fig. 1) is interesting from many points of view. Still covered by forest, it is cut by many streams that provide the routes for human access. Within this network of rivers live Amerindians of diverse linguistic families, who have experienced in different degrees contact with non-Indians. Sporadic missionary work took place there during the

seventeenth and eighteenth centuries, but became firmly established only in the nineteenth century. Other contact with neo-Brazilians occurred through rubber gathering and agricultural activities, mainly in this century. The acculturation process experienced by members of these tribes was has-

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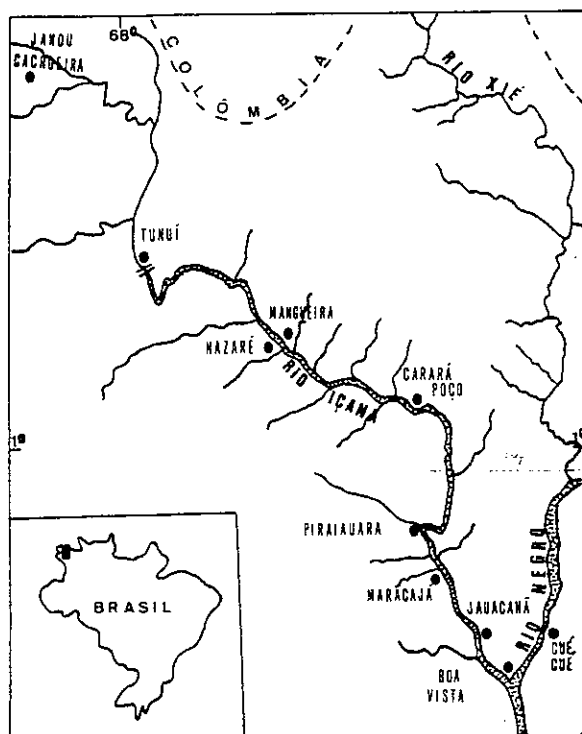


Fig. 1. Map showing the location of the communities studied plus three others for reference. The insert at lower left furnishes the area's position in Brazil's map.

tened by the introduction in the area, by the missionaries, of the *nheengatu* (*nyengatu*) or *lingua geral*, an artificial language of Tupi origin. Its purpose was to facilitate the communication between catechists and Indians, who spoke different languages. As a result of this and other influences a large portion of the populations of the area has lost its tribal affiliations, but the inhabitants of some regions remain tribal and unadmixed. Goldman (1948) indicated as distinctive cultural features of the Indians of this area the following: primary emphasis upon bitter manioc cultivation and fishing, with hunting of secondary importance; the use of large multi-family houses, each constituting a local kinship group, rather than villages; a complex of men's rites associated with an ancestor cult, inadequately referred to in the

literature as *yurupary*; the existence of patrilineal sibs; painted bark-cloth masks; frequent and prolonged *chicha* drinking; chewing of powdered coca mixed with leaf ash and use of hallucinogenic plants; shamanism associated with the jaguar; and striking emphasis upon sorcery. Tribal organization was either weak or absent (which favored the missionaries' work). In this communication we report upon genetic studies of a group in transition, predominantly Baniwa, its communities being in various stages of acculturation. We propose also to consider the genetic relationship of this tribe with the surrounding tribes of the region.

#### MATERIALS AND METHODS

Our studies were performed in six communities, distributed from the junction of the

Negro and Içana rivers up to the Içana headwaters and the neighboring region, near Colombia (Fig. 1). Boa Vista is adjacent to the New Tribes Mission of Foz do Içana; Cué Cué, Jauacanã, Maracajá, and Nazaré/Mangueira are independent Indian populations located along the rivers; Jandu Cachoeira is another station of the New Tribes Mission. The sample from this last community was obtained from representatives of six villages who had gathered there, attracted by a measles vaccination program.

The individuals from the groups considered here could be classified as follows: a) subjects who have lost their tribal affiliations and who speak only the *nyengatu* besides Portuguese; b) those who identify themselves as, or had ancestors from, Tucanoan tribes (the Tucano proper and the Cubeo); and c) those who identify themselves as, or had ancestors from the Arawak-speaking Baniwa, Arekena (Uarekena, Warekena), and Tariana. Baniwa communities, which have maintained their tribal autonomy, are mostly found at the Içana headwaters and on the frontier with Colombia (Oliveira, 1975), examples being those located around Jandu Cachoeira.

In terms of acculturation all these tribes would be classified either as in "permanent contact" with or "integrated" into the neo-Brazilian society (Ribeiro, 1957). Their population numbers have been estimated as follows: a) Tucano: 2,500 (E. Arnaud, personal communication); b) Cubeo: 1,000 (Reichel-Dolmatoff, 1967); c) Baniwa: 1,500 (Figueiredo and Folha, 1975; Mohrenweiser et al., 1979); d) Arekena: considered extinct as an independent tribe by Ribeiro (1957) (Malcher, 1964, believed that a few remaining Arekena were to be found at the time along the Guaiania river in Venezuela); e) Tariana: 1,000 (Ribeiro, 1957; E. Arnaud, personal communication).

Baniwa cultural change in the last 20 years (Oliveira and Galvão, 1973) and Baniwa kinship terminology (Oliveira, 1975) have been described using information obtained with the data to be described below, collected in Nazaré/Mangueira during 1971 by one of us. Field work in the other populations was conducted in 1976 (Jandu Cachoeira) and 1980 (Cué Cué, Boa Vista, Jauacanã, and Maracajá).

The demographic information was obtained as follows: after appropriate contacts with the leaders of the communities, the subjects would be assembled in a given place

and the members of the nuclear families (father, mother, and children) interviewed. Careful reproductive histories were then obtained, and the ages of the individuals estimated by visual inspection. The names of all first-degree relatives of the persons seen were also annotated, but no attempt was made to evaluate the ages of those not examined. Subsequently, we tried to collect blood and saliva samples from all individuals present who were above 7 years of age; for several reasons, however, not all such persons listed in the censuses (Table 1) could be included in the genetic studies (Table 6).

After collection the blood and saliva samples were permanently kept under refrigeration until they reached the different testing laboratories. The typing procedures have been described or referenced in Neel et al. (1977a,b), Gershowitz and Neel (1978), Salzano et al. (1980), and Constans and Salzano (1980). Differences in the number studied by system were due to shortage of material and/or of reagents for some tests.

#### RESULTS

Table 1 shows the age and sex distribution observed in five communities (no census was performed in Jandu Cachoeira). As can be seen, these are young populations, the estimated average age being about 21 years. The sex ratio generally shows the male excess expected in groups with this age composition.

As is summarized in Table 2, the relative contribution of five different tribes to the composition of the groups studied (as assessed by the ancestry of spouses) was variable; but the Baniwa were generally the main single contributors (Cué Cué being an exception). About one-third of the spouses living in the five localities listed in Table 2 could not trace their tribal origin and were classified as *nyengatu*. The acknowledged non-Indian contribution is small, but these individuals were not included in the genetic studies. Also excluded were samples showing markers in the ABO and ADA systems that were indicative of admixture.

The groups considered generally showed a high degree of exogamy, but the average marital distance was low (13-63 km; Table 3). The mobility pattern observed was therefore one of exchange among the many small scattered localities situated along the rivers, but within a limited geographical range.

For Nazaré/Mangueira it was possible to draw genealogical relationships involving

TABLE 1. Age and sex distribution in five Içana Indian communities

Population and sex	Age interval			Unknown	Total	Estimated average age (X ± SD)
	0-14	15-30	≥31			
<b>Cué-Cué</b>						
Males	15	8	5	16	44	18 ± 15
Females	4	6	4	14	28	25 ± 18
Total	19	14	9	30	72	20 ± 16
Percentage	45	33	22	—	—	—
Sex ratio	375	133	125	114	157	—
<b>Boa Vista</b>						
Males	27	27	15	45	114	22 ± 17
Females	27	27	14	39	107	20 ± 17
Total	54	54	29	84	221	21 ± 17
Percentage	40	39	21	—	—	—
Sex ratio	100	100	107	115	106	—
<b>Jauacanã</b>						
Males	16	9	14	27	66	26 ± 21
Females	15	17	11	29	72	24 ± 19
Total	31	26	25	56	138	25 ± 20
Percentage	38	32	30	—	—	—
Sex ratio	107	53	127	93	92	—
<b>Maracajá</b>						
Males	13	6	6	22	47	22 ± 23
Females	10	11	6	22	49	21 ± 19
Total	23	17	12	44	96	22 ± 21
Percentage	44	33	23	—	—	—
Sex ratio	130	54	100	100	96	—
<b>Nazaré/Mangueira</b>						
Males	26	10	11	—	47	18 ± 17
Females	23	11	14	—	48	21 ± 17
Total	49	21	25	—	95	20 ± 17
Percentage	52	22	26	—	—	—
Sex ratio	113	91	79	—	98	—
<b>Total</b>						
Males	97	60	51	110	318	21 ± 18
Females	79	72	49	104	304	22 ± 18
Total	176	132	100	214	622	21 ± 18
Percentage	43	32	25	—	—	—
Sex ratio	123	83	104	106	105	—

TABLE 2. Relative contribution of different tribes and of non-Indians to the composition of five Içana Indian communities (%), as assessed by the ancestry of spouses

Tribe or ethnic group	Localities					Total (N = 146)
	Cué-Cué (N = 14)	Boa Vista (N = 40)	Jauacanã (N = 24)	Maracajá (N = 20)	Nazaré/Mangueira (N = 48)	
"Nyengatu"	50	56	37	68	6	36
Baniwa	11	34	46	32	92	52
Tucano	14	0	7	0	0	3
Arekena	7	5	2	0	0	3
Cubeo	0	0	6	0	0	1
Tariana	0	0	2	0	0	1
Non-Indian	18	5	0	—	2	4

N = Number of spouses considered.

seven generations, and from it to calculate the mean coefficient of inbreeding of this population (Table 4). The efficiency of the estimate depends, of course, on the completeness with which we can trace the people's ancestors. In the nine marriages from which all four grandparents could be ascertained with

certainty, the F value reached the high value of 0.035, equivalent to the situation when all spouses are as closely related as first cousins once removed.

Table 5 indicates that these populations are characterized by a high fertility (about seven children born per woman who com-

TABLE 3. Types of marriages observed in five Içana Indian communities

Type of marriage	Localities				
	Cué-Cué	Boa Vista	Jauacanã	Maracajá	Nazaré/Mangueira
Both partners locally born	0	1	0	0	0
One partner from another population	4	9	10	2	3
Both partners from outside	3	10	2	8	19
Total number of marriages	7	20	12	10	22
Number of populations involved	10	19	11	14	14
Average marital distance (km)	13	48	50	33	63

<sup>1</sup>Marital distance: distance by river between the birthplaces of spouses.

TABLE 4. Frequency of consanguineous marriages in Nazaré/Mangueira<sup>1</sup>

Degree of relationship	Degree of information <sup>2</sup>			Total
	GPK	PK	I	
Double first cousins	1	0	0	1
First cousins	2	0	0	2
Second cousins	4	3	0	7
Unrelated	2	10	3	15
Total	9	13	3	25
Inbreeding coefficient	0.035	0.004	0.000	0.014

<sup>1</sup>Only marriages in which at least one spouse was alive were included.

<sup>2</sup>GPK: all four grandparents known; PK: parents known, incomplete information on grandparents; I: incomplete information about the spouses parents.

TABLE 5. Fertility, mortality, and opportunity for selection in the populations studied

Population	All families			Completed families			Death before age 15
	No. females	No. live births	Mean ± SD	No. females	No. live births	Mean ± SD	
Cué-Cué	7	35	5.0 ± 2.2	3	20	6.7 ± 2.5	14
Boa Vista	20	107	5.3 ± 3.3	7	51	7.3 ± 3.1	10
Jauacanã	12	58	4.9 ± 2.2	5	31	6.2 ± 2.2	17
Maracajá	10	56	5.6 ± 4.3	4	35	8.7 ± 4.9	14
Nazaré/Mangueira	21	100	4.8 ± 2.9	8	48	6.0 ± 3.0	15
Total	70	356	5.1 ± 3.0	27	185	6.8 ± 3.1	14
Index of opportunity for selection <sup>1</sup>		Im		If		If/ps	
Total population		0.16		0.20		0.23	0

<sup>1</sup>Im = pd/ps, where pd = proportion of premature deaths and ps = proportion surviving or 1 - pd; If = Vf/x<sup>2</sup>, where Vf = variance offspring number in completed sibships and x = mean number of live births per woman who completed her reproduction. I = Im + If; Index of opportunity for selection (Crow, 1958).

pleted reproduction), but by relatively low prereproductive mortality for people living at this stage of sociocultural development (14%). The variance in offspring number per woman who completed her reproduction is also not high, resulting in a low index of opportunity for selection (0.39).

The genetic data available are listed in Table 6. Forty systems have been studied, but 20 of these [namely, ABO, Kell, ceruloplasmin, albumin, hemoglobin, (beta and delta loci), phosphoglucomutase<sub>2</sub> (PGM<sub>2</sub>), esterase A (ESA<sub>1,3</sub>), carbonic anhydrase<sub>1</sub> (CA<sub>1</sub>),

nucleoside phosphorylase (NP), peptidase A (PEPA), peptidase C (PEPC), phosphoglucose isomerase (PHI), isocitrate dehydrogenase (ICD), triosephosphate isomerase (TPD), lactate dehydrogenase (LDH), malate dehydrogenase (MDH), Adenosine deaminase (ADA), adenylate kinase (AK), phosphogluconate dehydrogenase (PGD) and glucose-6-phosphate dehydrogenase (G6PD)] showed no variation. Gene frequencies for the remaining 20 are presented in Table 7.

The main features in the systems that showed variation can be summarized as fol-

TABLE 6. Phenotype frequencies for 40 genetic systems in the populations studied

System and phenotype	Localities					Total
	Cué-Cué	Boa Vista	Jauacaitá	Maracajá	Jandu Cachoeira	
<b>ABO</b>						
O	13	65	39	34	363	514
<b>MNS<sub>2</sub></b>						
MS	1	6	0	0	11	18
MS <sub>e</sub>	2	20	5	13	96	136
Ms	3	29	15	11	144	202
MNS	3	2	3	1	14	23
MNS <sub>e</sub>	3	3	1	3	47	57
MNs	1	5	10	2	42	60
NS	0	0	0	1	3	4
NS <sub>s</sub>	0	0	1	1	3	5
Ns	0	0	0	0	3	3
<b>P</b>						
P <sub>1</sub>	4	22	12	9	262	309
P <sub>2</sub>	9	43	16	22	101	191
<b>Rh<sup>2</sup></b>						
CDE	0	1	0	1	0	2
CDE <sub>e</sub>	0	1	1	0	8	10
CDe	3	2	9	10	127	151
CcDE	1	4	2	2	0	9
CcDE <sub>e</sub>	3	17	10	13	156	199
CcDe	0	6	3	1	11	21
cDE	5	33	3	4	57	102
cDE <sub>e</sub>	1	1	2	1	4	9
<b>Kell</b>						
K(-)	13	65	39	34	363	514
<b>Lewis</b>						
Le(a-b+)	-	-	-	-	272	272
Le(a-b-)	-	-	-	-	91	91
<b>Duffy</b>						
Fy(a+)	11	52	25	27	190	272
Fy(a-)	2	13	14	7	36	91
Fy(a+b-)	-	-	-	-	190	190
Fy(a+b+)	-	-	-	-	156	156
Fy(a-b+)	-	-	-	-	17	17
<b>Kidd</b>						
Jk(a+)	-	-	-	-	290	290
Jk(a-)	-	-	-	-	73	73
<b>Diego</b>						
Di(a+)	2	1	14	7	156	180
Di(a-)	11	64	25	27	207	334
<b>ABH secretion</b>						
Sec.	1	62	39	32	-	134
Non-sec.	0	0	0	2	-	2
<b>Haptoglobin<sup>3</sup></b>						
1-1	0	15	5	8	99	127
2-1	7	27	22	15	177	248
2-2	6	21	10	11	87	135
0	0	1	0	0	0	1
<b>Transferrin<sup>3</sup></b>						
C	13	64	37	34	365	513
C-D <sub>Chi</sub>	0	0	0	12	12	12
<b>Ceruloplasmin<sup>3</sup></b>						
B	13	64	37	34	377	525
<b>Albumin<sup>3</sup></b>						
A	13	64	37	34	377	525
<b>Gm<sup>1</sup></b>						
1:21	5	25	9	18	170	227
1.2:21	7	33	24	17	157	238
1:11,13,16,21	0	0	0	0	22	22
1.2:11,13,16,21	0	0	0	0	14	14

TABLE 6. Phenotype frequencies for 40 genetic systems in the populations studied (continued)

System and phenotype	Localities					Total
	Cué-Cué	Boa Vista	Jauacaná	Maracajá	Jandu Cachoeira	
<b>Km<sup>1</sup></b>						
1+3-	-	-	-	-	51	51
1+3+	-	-	-	-	190	190
1-3+	-	-	-	-	122	122
<b>GeIEI<sup>5</sup></b>						
1-1	-	-	-	-	252	252
2-1	-	-	-	-	117	117
2-2	-	-	-	-	8	8
<b>GePA GFI<sup>6</sup></b>						
1F	2	10	3	0	-	15
1F-1S	0	27	7	13	-	47
1S	2	9	6	10	-	27
2-1F	3	7	3	3	-	16
2-1S	4	6	17	8	-	35
2	2	4	2	0	-	8
<b>Hemoglobin<sup>3</sup></b>						
A	13	65	39	32	377	514
A <sub>2</sub>	-	-	-	-	377	377
<b>PGM<sup>1</sup></b>						
1-1	6	44	33	20	248	272
2-1	6	20	8	13	104	141
2-2	1	1	1	1	11	14
<b>PGM<sup>2</sup></b>						
1-1	13	65	42	34	363	514
<b>ESA<sup>1-3</sup></b>						
A	13	65	41	34	363	514
<b>ESD<sup>7</sup></b>						
1-1	12	43	16	24	224	272
2-1	1	19	22	10	122	164
2-2	0	3	4	0	12	16
<b>GLO</b>						
1-1	0	5	1	1	-	7
2-1	7	29	5	10	-	51
2-2	6	31	35	21	-	93
<b>CA<sup>1</sup></b>						
1-1	-	-	-	-	363	363
<b>CA<sup>2</sup></b>						
1-1	13	58	42	34	338	445
1-BAN 1	0	7	0	0	37	44
BAN 1	0	0	0	0	2	2
<b>NP<sup>3</sup></b>						
1-1	-	-	-	-	363	363
<b>PEPA<sup>3</sup></b>						
1-1	13	65	40	34	363	455
<b>PEPB<sup>3</sup></b>						
1-1	11	64	40	29	362	446
1-BAN 1	0	0	0	0	1	1
<b>PEPC</b>						
1-1	13	65	41	34	-	443
<b>PHF<sup>8</sup></b>						
1-1	-	-	-	-	363	363
<b>ICD<sup>9</sup></b>						
1-1	-	-	-	-	363	363
<b>TPP<sup>10</sup></b>						
1-1	-	-	-	-	363	363
<b>Acid phosphatase<sup>3</sup></b>						
A	1	0	2	0	6	9
AB	7	3	10	10	43	63
B	5	60	22	24	314	405
<b>LDH<sup>3</sup></b>						
1-1	-	-	-	-	363	363

(continues)

TABLE 6. Phenotype frequencies for 40 genetic systems in the populations studied (continued)

System and phenotype	Localities					Total
	Cué-Cué	Boa Vista	Jauacanã	Maracajá	Jandu Cachoeira	
MDH <sup>2</sup>						
1-1	—	—	—	—	363	363
GALT <sup>3</sup>						
1-1	—	—	—	—	359	359
1-D	—	—	—	—	3	3
D	—	—	—	—	1	1
ADA <sup>3</sup>						
1-1	13	65	42	34	363	517
AK <sup>3</sup>						
1-1	13	65	42	34	363	517
PGD <sup>3</sup>						
A	13	65	42	34	363	517
G6PD						
B (Males)	7	34	18	19	—	78
(Females)	6	31	22	15	—	74

<sup>1</sup>Forty-seven of these were tested with anti-T<sub>2</sub>. All were T<sub>2</sub>(a).  
<sup>2</sup>In the Jandu Cachoeira sample the C<sub>1</sub>(+) bloods were tested with anti-C<sub>1</sub>. All were C<sub>1</sub>(+). All the CeDe cells in this same sample were tested with anti-f, giving negative reactions with it.  
<sup>3</sup>Results for Jandu Cachoeira were already reported by Mohrenweiser et al. (1979).  
<sup>4</sup>The data for Jandu Cachoeira have been published by Gershowitz and Neel (1978); those for the four other localities are from Hamel et al. (1984).  
<sup>5</sup>IE: Immunoelectrophoresis.  
<sup>6</sup>PAGIF: Polyacrylamide isoelectric focusing.  
<sup>7</sup>Results for Jandu Cachoeira were already reported by Mestriner et al. (1980).

lows: a) There is a marked amount of inter-village variability (much higher, for instance, than that observed among the Macushi living in the neighboring Territory of Roraima, who were studied with about the same degree of completeness; see Salzano et al. 1984), but sample sizes are small. b) No clear geographical trends are observed. c) Especially noteworthy are the variant of peptidase B (PEPB<sup>2BAN1</sup>), the "private" polymorphism of carbonic anhydrase<sub>2</sub> (CA<sub>2</sub><sup>BAN1</sup>), both described in detail by Mohrenweiser et al. (1979), and the relatively high frequency (2%) of transferrin D<sub>Chi</sub> (Tf<sup>DChi</sup>) in Jandu Cachoeira; seven carriers of CA<sub>2</sub><sup>BAN1</sup> have now been found in Boa Vista also. All of them are biologically related, and the allele is traceable to one Arawak source only (either an Arekena man or a Baniwa woman, both already deceased). d) Considering the range of frequencies found among South American Indians, and taking the population of Jandu Cachoeira as the best representative of the Baniwa, it will be seen that 9 of the alleles listed in Table 7 show values in the lower third of the range, 12 in the medium third, and only 5 in the upper third. Two of the latter refer to the PEPB and CA<sub>2</sub> variants discovered among the Baniwa (item c).

#### DISCUSSION

The Içana river Indian populations studied are characterized demographically by a) young age; b) high intertribal admixture; c) low non-Indian admixture; d) high exogamy, but low marital distance; e) high fertility, but low variance in offspring number; f) relatively low mortality. These features are not much different from those observed in other Amerindian groups, the similarities with the already mentioned Macushi Indians of the Roraima Territory being particularly noteworthy. As was described by Salzano et al. (1984), the latter present a mean age of 19 years and have a large percentage of locally born couples (34%) but a low average marital distance (33 km), high fertility (mean of 8 children per woman who completed her reproduction) with low variance in offspring number, relatively low prereproductive mortality (18%), and a low index of opportunity for selection (0.33). But the Içana river and Macushi Indians differ on the history of intertribal crosses, which were restricted among the Macushi and almost confined to another tribe only (the Wapishana).

In the present study we were able to collect a detailed genealogy linking the members of

TABLE 7. Allele frequencies for systems that showed variation in five Içana Indian populations, compared with the range of frequencies found in South American Indians

System and allele	Localities					Range of frequencies, South American Indians
	Cué-Cué	Boa Vista	Jauacanã	Maracajá	Jandu Cachoeira	
MNSs						
L <sup>M</sup> S and M <sup>M</sup> S	0.38	0.28	0.11	0.24	0.20	0.00 - 0.72
L <sup>M</sup> S anomalous	0.42	0.65	0.66	0.61	0.63	0.19 - 0.84
L <sup>N</sup> S subdivisions	0.19	0.02	0.07	0.09	0.08	0.00 - 0.37
L <sup>N</sup> S subdivisions	0.08	0.05	0.16	0.06	0.09	0.00 - 0.41
P <sup>1</sup>	0.17	0.19	0.24	0.16	0.53	0.09 - 1.00
Rh						
R <sup>1</sup>	0.35	0.21	0.51	0.53	0.59	0.09 - 0.96
R <sup>2</sup>	0.57	0.67	0.32	0.38	0.38	0.03 - 0.73
R <sup>Z</sup>	0.04	0.06	0.07	0.06	0.01	0.00 - 0.33
R <sup>O</sup> or r	0.04	0.06	0.10	0.03	0.02	0.00 - 0.23
Lewis						
Le <sup>a</sup>	—	—	—	—	0.50	0.33 - 0.87
Duffy						
Fy <sup>a</sup>	0.61	0.55	0.40	0.55	0.74	0.24 - 1.00
Kidd						
Jk <sup>a</sup>	—	—	—	—	0.55	0.11 - 1.00
Diego						
D <sup>i</sup>	0.08	0.01	0.20	0.11	0.24	0.00 - 0.44
ABH secretion						
Se	1.00	1.00	1.00	0.76	—	0.36 - 1.00
Haptoglobin						
Hp <sup>1</sup>	0.27	0.45	0.43	0.46	0.52	0.20 - 0.83
Transferrin						
Tf <sup>DChi</sup>	0.00	0.00	0.00	0.00	0.02	0.00 - 0.37
Gm						
1;21	0.65	0.66	0.52	0.72	0.68	0.44 - 1.00
1;2;21	0.35	0.34	0.48	0.28	0.27	0.01 - 0.54
1;11,13,16	0.00	0.00	0.00	0.00	0.05	0.00 - 0.05
Km <sup>1</sup>	—	—	—	—	0.40	0.14 - 0.91
Gc						
Gc <sup>1F</sup>	0.27	0.43	0.21	0.24	0.82 <sup>1</sup>	0.31 <sup>1</sup> - 0.93 <sup>1</sup>
Gc <sup>1S</sup>	0.31	0.40	0.47	0.60	—	—
PGM <sub>1</sub>						
PGM <sub>1</sub>	0.69	0.83	0.88	0.78	0.83	0.55 - 1.00
ESD						
ESD <sup>1</sup>	0.96	0.81	0.64	0.85	0.80	0.43 - 1.00
GLO						
GLO <sup>1</sup>	0.27	0.30	0.09	0.19	—	0.17 - 0.30
CA <sub>2</sub>						
CA <sub>2</sub> <sup>BAN1</sup>	0.00	0.05	0.00	0.00	0.05	0.00 - 0.05
PEPB						
PEPB <sup>2BAN1</sup>	0.00	0.00	0.00	0.00	0.001	0.000 - 0.001
Acid Phosphatase						
ACP <sup>A</sup>	0.35	0.02	0.21	0.15	0.08	0.01 - 0.37
GALT						
GALT <sup>3</sup>	—	—	—	—	0.01	0.00 - 0.13

<sup>1</sup>Combined frequency for (Gc<sup>1F</sup> + Gc<sup>1S</sup>).

one of the communities investigated (Nazaré/Mangueira). This is no easy task in societies without a written tradition like this one, with classificatory systems and taboos different from those of our own. Previous inbreeding estimates have been made for three other Brazilian Indian tribes, the Caingang (F = 0.005; Salzano, 1961, 1964), Xavante (F = 0.004; Salzano et al., 1967) and Juruna (F = 0.022; Oliveira and Salzano, 1969). Neel et al. (1964) and Salzano et al. (1967) discussed the difficulty of arriving at precise estimates, owing to the lack of knowledge of remote consanguinity. The number here obtained for couples from who we knew all four grandparents (0.035) is of the same order of magnitude

as the one considered to be the true value for the Kavante (0.02 - 0.03; Salzano et al., 1967) and is similar to the coefficient of kinship for pairs of South American Indians living in the same place (0.025; Roisenberg and Morton, 1970).

With the increase in the number of genetic markers available, detected through different techniques, we are reaching a much better picture of the nature and the level of variability present in human populations than that which was possible even a few years ago. The gene pool of the Baniwa Indians (as estimated from the Jandu Cachoeira population) presents a peptidase B variant (PEPB<sup>2BANI</sup>) and a "private" polymorphism of carbonic anhydrase<sub>2</sub> (CA<sub>2</sub><sup>BANI</sup>) until now observed only among members of this tribe. Other distinctive characteristics are the low frequencies of L<sup>NS</sup> (0.08), L<sup>NS</sup> (0.09), R<sup>0</sup> (0.01), R<sup>0</sup> or r (0.02), ACP<sup>A</sup> (0.08), and GALT<sup>D</sup> (0.01) and the relatively high frequencies of Gm<sup>1:11,13,16</sup> (0.05) and Gc<sup>1</sup> (0.82). Tf<sup>D</sup>Chi occurs, though with a low prevalence (0.02). This allele has a distribution that seems to be restricted to the northern areas of the continent only. The tribes or groups of northern South America that manifest it are the Quechua of Peru, the Paez of Colombia, the Yupa (with the highest frequency reported thus far), Piaroa, and Warao of Venezuela (Arends and Gallango, 1965), and the Ticuna, Waiápi and Baniwa of Brazil (Mohrenweiser et al., 1979; Neel et al., 1980; Black et al., 1983).

Information concerning the Gc isoelectrofocusing subtypes in Amerindians and related groups is increasing (Constans and Salzano, 1980; Matsumoto et al., 1980; Dykes et al., 1983; Szathmary et al., 1983; Salzano et al., 1984, 1985; present communication) and some first generalizations are now possible. In one Siberian population (Tuvintsi) the frequency of Gc<sup>1S</sup> (0.28) is lower than that of Gc<sup>1F</sup> (0.52), but in two Eskimo and in

15 of 18 American Indian samples the opposite is true (frequency of Gc<sup>1S</sup> > frequency of Gc<sup>1F</sup>); the exceptions are the Pima of the United States and the Kraho and Pacaás Novos of Brazil. The most common interval of allele frequencies (present in half of the samples, including the Içana river Indians) is 0.37 - 0.48 for Gc<sup>1S</sup> and 0.34 - 0.39 for Gc<sup>1F</sup>.

We have computed genetic distances among these populations using the metric described in Smouse (1982) and the allele and haplotype frequencies from the MNSs, Rh, P, Fy, Di, Hp, Gm, Gc, PGM<sub>1</sub>, and AP systems. These measures are presented in the upper diagonal portion of Table 8. The amount of intercommunity divergence is extreme, but there is no apparent geographic pattern to these differences, such as might be expected from the essentially linear positioning of the populations along the Içana river. The pattern that is evident in the distance matrix is imposed by admixture with non-Arawak peoples. From Table 2, we first extracted the frequency of known Arawak ancestry as the sum of the percentages attributed to Baniwa, Arekena, and Tariana. We have assumed that the Jandu Cachoeira population is approximately 96% Arawak (no direct evidence for non-Arawak admixture is available, but we will allow for a small amount). The difference between the Arawak percentages for two populations is taken as the difference in admixture rates between them, and these "admixture distances" are presented as the lower triangular portion of Table 8. As a general consequence of admixture, we should anticipate that two populations having similar admixture rates should be most similar genetically, and that the Jandu Cachoeira collection, being almost (or completely) unadmixed, should be most typical of the precontact Baniwa.

The correlation of genetic admixture with distance values, apparent by visual inspection, can be formally assessed by a Mantel

TABLE 8. Genetic distance values among pairs of Içana Indian populations above the diagonal, and admixture distances below the diagonal

	CC	MA	BV	JA	JC
CC	—	.41	.51	.48	.61
MA	.14	—	.32	.35	.40
BV	.21	.07	—	.48	.52
JA	.32	.18	.11	—	.49
JC	.78	.64	.57	.46	—

CC, Cúe Cúe; MA, Maracajá; BV, Boa Vista; JA, Jauarajá; JC, Jandu Cachoeira; —, no admixture.

TABLE 9. Genetic distances among tribes within four language families: Arawaks (BA, Baniwa, WA, Wapishana), Caribs (MK, Makiritare, MC, Macushi), Yanomama (SA, Sanema, YA, Yanomam, YE, Yanomame, NI, Ninam), Ticuna (TI, Ticuna; averages below the diagonal

	BA	WA	MC	MK	SA	YA	YE	NI	TI
BA	—	.28	.29	.15	.56	.57	.52	.30	TI
WA		—	.21	.33	.67	.66	.64	.12	BA
MC			—	.31	.66	.61	.62	.38	WA
MK				—	.55	.52	.52	.38	MC
SA					—	.79	.74	.76	MK
YA						—	.21	.33	SA
YE							—	.43	YA
NI								—	YE
TI									—

(1967) test of matrix correlation. The estimated correlation is  $r = 0.63$ , a value exceeded by chance only 2.5% of the time when there is no true correlation. Thus, we have a strong, statistically significant correlation. Evidently, the large degree of internal divergence within the Baniwa is caused by diverse admixture levels of the respective communities. Only the Jandu Cachoeira collection, essentially unadmixed, should be viewed as typical of the precontact Baniwa.

It is also useful to place the Baniwa into a larger context, comparing them with several groups of northern and western Brazil. To that end, we have used the same procedures and the same loci to compare the Baniwa (only Jandu Cachoeira) with the Ticuna, the Makiritare and Macushi (both Carib speakers), the Yanomama (represented by four dialectical subdivisions, alternatively viewed as protolanguages of the same family), and the Wapishana (an Arawak group of Roraima Territory, about 900 km to the east). These distances are presented in the upper triangular portion of Table 9, and it is immediately apparent that the Baniwa and Wapishana are among the most similar of the pairs, in spite of being separated by a large distance. Only the Sanema and Yanomama, two contiguous Yanomama dialect groups, are as similar. In the lower triangular portion of Table 9 we have indicated average within- and among-language family distances. As a general rule, tribes within a language family are more similar than those in different families, a fact we have alluded to before (e.g., Spielman et al., 1974; Smouse, 1982). For the Arawaks, as well as for other groups, historical (primarily phyletic) considerations outweigh geographical proximity as an indicator of genetic similarity.

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# A Population Study of the Jugular Foramen Bridging of the Human Cranium

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**KEY WORDS** Human skull, Jugular foramen bridging, Frequency, Asiatic and North American populations

**ABSTRACT** The author previously proposed a simple standard for diagnosing the jugular foramen bridging in man. The incidence of this bridging was investigated according to that standard in nine cranial series of Indians, Micronesians, Japanese, Ainu, Mongols, Aleuts, Alaskan Eskimos, Canadian Eskimos, and Ontario Iroquois. No sex difference in incidence of trait was recognized. Side difference in trait incidence was also slight but statistically significant in the combined series of all the population samples examined. The bridging trait occurred more frequently on the right side than on the left side. Occurrences of the bridging trait were definitely associated between sides. Incidence of the trait was less in East Indians, Ontario Iroquois and Micronesians, but greater in Alaskan Eskimos and Canadian Eskimos. The incidences in Japanese, Ainu, Aleuts, and Mongols being intermediate. The differences in trait incidence among the nine population samples are considered to reflect the differences in genetic compositions of these populations.

Little attention has been devoted to the bony bridging of the jugular foramen by non-metricians of the human skull engaged in population studies. Oetkeking (1930) described the division of the jugular foramen and gave incidences of this trait in American Indians of the Pacific Northwest. Shima (1941) reported the incidence of the jugular foramen bridging in Mongols, and Morita (1950) and Mitsuhashi (1958) the incidence of this trait in Japanese. Recently a number of anthropologists have listed jugular foramen bridging as one of the minor nonmetric cranial variants for population studies (Corrucini, 1974; Kaul et al., 1979; Milne et al., 1983; Pardoe, 1984). However, except for Pardoe (1984), the above-mentioned researchers never gave a definition of the bony bridging of the jugular foramen.

Using 64 fetal crania aged 9 months to term and 222 adult crania of Japanese, the present author made precise observations on the region of the jugular foramen and offered a simple standard for diagnosing the jugular foramen bridging (Dodo, 1985a). Furthermore, the incidences of this trait between the Japanese fetal and adult cranial series (10.9% and 12.2%, respectively) were statistically significant.

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