

Protein Genetic Studies Among the Tupi-Mondé Indians of the Brazilian Amazonia

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ABSTRACT A sample of 417 individuals belonging to three Tupi-Mondé-speaking tribes (Gavião, Surui, Zoró) were variously studied in relation to 26 genetic protein systems. Previous investigations performed among the Surui in relation to some of these systems were confirmed. The three groups do not depart markedly from the genetic pattern already established for South American Indians and show low inter-ethnic admixture. When these results are combined with those from 10 other Tupi tribes, two clear geographic groupings (southeastern and northwestern) can be discerned. Using different methods to evaluate the same genetic distance matrices, different patterns of association between the Tupi-Mondé populations were obtained. The populations are probably too similar among themselves, blurring finer relationships. *Am. J. Hum. Biol.* 10:711-722, 1998. © 1998 Wiley-Liss, Inc.

In Brazil, the region comprising the northwest in the state of Mato Grosso along its border with the northeast of the state of Rondonia has been occupied by native populations for a long time. Immigration to the area by non-Indians began to increase by the turn of the century, when rubber tapping became economically attractive. The process was accelerated in the 1960s with colonization projects that involved farming, timber cutting, and mining. The groups considered in this study are a set of three culturally related Tupi-Mondé-speaking societies (Rodrigues, 1986). Despite their geographic proximity, the groups differ greatly in their experiences with the neo-Brazilian society. The Gavião were contacted in the early 1940s and became involved in the collection of natural rubber. The Surui, however, were approached in the 1960s, and starting in the early 1980s, their subsistence system shifted from slash-and-burn agriculture combined with hunting and gathering to coffee farming, cattle ranching,

and timber cutting. Finally, contact of the Zoró took place in the mid 1970s. By the time of fieldwork in 1990, the Zoró were still more isolated than the two other groups and continued to rely on traditional subsistence activities, although they obtained some cash through the selling of natural rubber and Brazil nuts (Santos, 1991).

Two of us (C.E.A.C. and R.V.S.) have been working with these Indians since the beginning of the 1980s, in studies that can be broadly defined as ecologically oriented. As a result, 29 contributions have been made to the scientific literature in the period 1981-

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TABLE 1. Phenotype distribution in 26 genetic systems on three Amazonian Indian tribes

System	Phenotype	Number of individuals in each class		
		Gavião	Surui	Zoró
ABO	O	184	141	80
	A1	2	0	0
MNSs	MS	9	—	1
	MSs	6	—	2
	Ms	13	—	7
	MNS	6	—	2
	MNSs	3	—	6
	MNs	8	—	11
	NS	1	—	0
	NSs	0	—	1
	Ns	4	—	0
P	P1	23	—	25
	P2	26	—	5
Rh ¹	CDE	1	—	0
	CDEe	1	—	0
	CDe	20	—	12
	CcDE	7	—	2
	CcDEe	3	—	3
	CcDe	3	—	1
	cDE	9	—	6
	cDEe	1	—	1
	cDe	4	—	5
Kell	K-	49	—	12
Duffy	a+	37	—	21
	a-	12	—	9
Hemoglobin	A	182	—	78
	A2	182	—	78
Glucose-6-phosphate dehydrogenase	B Males	89	68	40
	Females	93	57	35
Phosphogluconate dehydrogenase	A	176	100	30
	AC	6	0	0
Phosphoglucomutase 1	1A	21	16	—
	1B	39	16	—
	1A1B	71	30	—
	1A2A	1	0	—
	1A2B	19	28	—
	1B2A	2	7	—
	1B2B	25	28	—
	2B	4	11	—
Phosphoglycolate phosphatase	1-1	30	—	—
	2-1	41	—	—
	2-2	4	—	—
	3-1	1	—	—
	3-2	2	—	—
Adenylate kinase	1-1	162	139	79
	1-4	19	0	0
	4-4	1	0	0
Acid phosphatase	A	3	2	1
	AB	40	16	16
	B	139	119	62
Esterase A	1-1	172	—	78
	1-K	10	—	0
Esterase D	1-1	68	—	14
	2-1	96	—	40
	2-2	17	—	20
Glyoxalase 1	1-1	37	0	8
	2-1	79	10	15
	2-2	67	52	15
Carbonic anhydrase 2	1-1	182	—	75
Peptidase A	1-1	137	—	4
Peptidase B	1-1	182	—	78

TABLE 1. (Continued.)

System	Phenotype	Number of individuals in each class		
		Gavião	Surui	Zoró
Peptidase C	1-1	180	–	–
Haptoglobin	1-1	85	14	29
	2-1	81	61	29
	2-2	16	60	18
Transferrin	C	182	134	76
Ceruloplasmin	B	182	133	76
Albumin	A	182	133	76
Serum cholinesterase 1 ²	U	178	102	36
Serum cholinesterase 2 ²	C5+	14	4	1
	C5–	162	93	70

¹Tests with anti-D only have been performed in 137 additional Gavião, 151 Surui, and 50 additional Zoró bloods, with just one negative result among the Surui.

²Results reported in Alcântara et al. (1995).

1997, which included nutrition, epidemiology, other medical studies, physical growth, body morphology, and dermatoglyphics (list available on request). Concomitantly, the Surui were the subject of investigations involving HLA (Black, 1991; Black et al., 1991; Bhatia et al., 1995) and other protein blood genetic markers (Callegari-Jacques et al., 1994), as well as research at the DNA level (Kidd et al., 1991; Armour et al., 1996; Chang et al., 1996; Nei and Takezaki, 1996; Tishkoff et al., 1996).

The present genetic studies were derived from material obtained in fieldwork performed in July and August 1990, among these three Tupi-Mondé groups. Previous investigations on this material were reported in Heidrich et al. (1995), Bevilaqua et al. (1995), Santos et al. (1995), Ward et al. (1996), Hutz et al. (1996, 1997), Bonatto and Salzano (1997a,b), Bortolini et al. (1997), and Bogdawa (1997).

MATERIALS AND METHODS

The Gavião, Surui, and Zoró are three Tupi-Mondé-speaking populations that are closely related both culturally and biologically. They live in the southwestern portion of the Brazilian Amazonia, an area that became the focus of government-sponsored colonization schemes in the 1970s. Intensive migration has broken the isolation of these Amerindian groups (Coimbra, 1989; Santos, 1991). Each group is described separately, despite the fact that some intertribal marriages occur among them.

Gavião

This Tupi-Mondé group should not be confused with Ge-speaking persons of the same name, living in southeast Pará (Gavião-

Parkatejê), or Maranhão (Gavião-Pukobiê). The population studied lives in the Indian Area Igarapé Lourdes, State of Rondônia, Brazil. In 1990, they were distributed in two villages, but many of them had houses in both. Samples were obtained from people of the two communities (geographical coordinates: 61°8'W; 10°10'S). At the time of the visit, the total population was estimated at 288 individuals (Santos, 1991). As indicated previously, the Gavião were contacted by neo-Brazilians in the early 1940s and are more acculturated than the two other tribes. Studies about their physical growth (Santos and Coimbra, 1991) and health (Coimbra et al., 1994, 1996a,b) have recently been published.

Surui

The Surui live in the Indian Area Sete de Setembro (61°10'W, 10°50'S), located partly in Rondônia and partly in Mato Grosso. In 1990, they had a population of ~500 individuals distributed in 10 villages. The samples were collected at random among the villages. This tribe lives in a contiguous area with that occupied by the Zoró, situated at the east where the Gavião live. The Surui were contacted in 1969 by members of the National Indian Foundation (FUNAI). There are estimates that this population experienced a reduction in size of ~45% in 1972–1973 due to epidemics of infectious diseases. Their lives have undergone profound changes in the last few decades due to the adoption of cash income practices. They are the best studied of the three groups considered. A general review of these investigations can be found in Coimbra (1989), the

references given above for the Gavião, and the reports by Fleming-Moran et al. (1991) and Santos and Coimbra (1996).

Zoró

The Zoró live in a single village located 20 km from the Rio Branco river (60°20'W; 10°20'S). More extensive contacts with non-Indians began in 1977, at which time they had an estimated population size of 350. By this time they had already been affected by epidemics of infectious diseases, as it was estimated that they numbered 1,000–1,500 in the 1960s. By July–August, 1990, the Zoró numbered 215. Shortly after contact, they went to live with the Gavião, abandoning many of their traditional ways of living. They stayed with the Gavião until the end of 1977, when they moved to their present surroundings. They have been facing land problems in recent years due to invasions of their reservation by neo-Brazilians. Further information about them can be found in Santos (1991) and the references given for the Gavião and Surui.

Laboratory and statistical procedures

Blood samples were collected with anticoagulant, refrigerated shortly after collection, and sent by air to Porto Alegre. There they were processed and an aliquot was sent to Ribeirão Preto for further determinations. Most of the laboratory methods employed are described or referenced in Salzano et al. (1988), or Callegari-Jacques et al. (1996). The exception is the typing procedures for the determination of the phosphoglycolate phosphatase types, which were done as described in Barker and Hopkinson (1978).

The statistical analyses involved: (1) maximum likelihood estimation of allele frequencies, either by gene counting or using the MAXLIK program (Reed and Schull, 1968), (2) determination of Nei's (1972) standard genetic distances and of Nei et al.'s (1983) D_A genetic distances, as well as of the corresponding dendrograms using the neighbor-joining method, with the DISPAN program (Ota, 1993); the reliability of the trees was tested with 5,000 replications (Hedges, 1992), and (3) establishment of three-dimensional plots based on principal coordinate analyses of the same distance matrices (e.g., Sneath and Sokal, 1973), using the NTSYS program (Rohlf, 1993).

RESULTS

Table 1 presents the phenotype distributions in the 26 genetic systems investigated. Bad sample preservation and/or lack of reagents prevented the uniform typing of the three groups. For the Surui, however, data concerning some systems were available from a previous study (Callegari-Jacques et al., 1994). They were, therefore, incorporated in the comparisons.

The corresponding allele frequencies are shown in Table 2. Since the inheritance of the C5 variant of serum cholinesterase 2 is still not completely understood, allele frequencies were not computed for this system. Low or very little variability was found for ABO, Kell, HbA, HbA2, G6PD, PGD, AK, ESA, CA2, PEPA, PEPB, PEPC, TF, CP, ALB, and CHE1. The presence of **ABO*A1** and **PGD*C** among the Gavião is probably due to interethnic admixture. **ESA*KAR** is probably autochthonous, since it was previously found among the Kararaô (Callegari-Jacques et al., 1994), a Gê-speaking group that, however, lives far away from the Gavião. The occurrence of **AK*4** is more difficult to interpret. A variant with about the same electrophoretic mobility was observed in very low prevalences in the United Kingdom and Africa (Rapley et al., 1967; Hiernaux, 1976), but also in North American Indians (Athabaskans) and Eskimos (Scott and Wright, 1978). The finding of one Rh negative among the Surui (see footnote, Table 1) also could be due to admixture. No Rh-negatives have been detected in a previous sample of this tribe (N = 54; Callegari-Jacques et al., 1994). However, **CP*ACAY**, observed in this previous sample, was not detected in the present survey. In general, similarities between the two samples have been observed for the ABO, G6PD, PGD, PGM1 (classical types), AK, ACP, TF, ALB and CHE. Differences below 10% were found for **GLO*1** and C5+, whereas that for haptoglobin (**HP*1**) was of the order of 15%.

Comparing the three sets of allele frequencies with those obtained for Amazonian Indians in general (Table 2), few significant differences (above or below two standard deviations from the mean) were observed. They are restricted to a high **RH*R0** prevalence (0.200) among the Zoró, high frequency of **PGM1*2B** (0.287) among the Su-

TABLE 2. Allele or haplotype frequencies in 25 genetic systems on three Amazonian Indian tribes compared with Amazonian Indians in general

System and allele or haplotype	Gavião (n = 182) ¹	Surui (n = 135) ¹	Zoró (n = 78) ¹	Amazonian Indians	
				Average ± SD	No. of tribes
ABO					
ABO*0	0.995	1.000	1.000	0.993 ± 0.017	140
ABO*A1	0.005	0.000	0.000	0.002 ± 0.008	121 ²
MNSs					
L*MS	0.316	–	0.150	0.244 ± 0.154	80
L*Ms	0.418	–	0.500	0.510 ± 0.178	80
L*NS	0.092	–	0.100	0.073 ± 0.089	80
L*Ns	0.174	–	0.250	0.173 ± 0.125	80
P					
P*1	0.272	–	0.592	0.478 ± 0.201	92
Rh					
RH*RZ	0.102	–	0.033	0.056 ± 0.059	91
RH*R1	0.480	–	0.467	0.542 ± 0.166	91
RH*R2	0.296	–	0.300	0.341 ± 0.158	91
RH*R0	0.122	–	0.200	0.052 ± 0.061	91
Kell					
KELL*K-	1.000	–	1.000	0.999 ± 0.007	89
Duffy					
FY*A	0.505	–	0.452	0.669 ± 0.180	108
Hemoglobin					
HB*A	1.000	–	1.000	0.998 ± 0.009	99
HB*A2	1.000	–	1.000	0.991 ± 0.020	31
Glucose-6-phosphate dehydrogenase					
G6PD*B	1.000	1.000	1.000	0.999 ± 0.006	30
Phosphogluconate dehydrogenase					
PGD*A	0.984	1.000	1.000	0.993 ± 0.035	46
PGD*C	0.016	0.000	0.000	0.007 ± 0.035	46
Phosphoglucomutase 1					
PGM1*1A	0.365	0.331	–	0.327 ± 0.166	4
PGM1*1B	0.484	0.356	–	0.465 ± 0.198	4
PGM1*2A	0.008	0.026	–	0.051 ± 0.061	4
PGM1*2B	0.143	0.287	–	0.157 ± 0.029	4
Phosphoglycolate phosphatase					
PGP*1	0.654	–	–	0.837	2
PGP*2	0.327	–	–	0.163	2
PGP*3	0.019	–	–	0	2
Adenylate kinase					
AK*1	0.942	1.000	1.000	0.999 ± 0.004	43
AK*4	0.058	0.000	0.000	0	43
Acid phosphatase					
ACP*A	0.126	0.073	0.114	0.117 ± 0.083	45
Esterase A					
ESA*1	0.973	–	1.000	0.995 ± 0.012	33
ESA*KAR	0.027	–	0.000	0.002 ± 0.007	33
Esterase D					
ESD*1	0.641	–	0.459	0.695 ± 0.184	43
Glyoxalase 1					
GLO*1	0.418	0.081	0.408	0.292 ± 0.151	30
Carbonic anhydrase 2					
CA2*1	1.000	–	1.000	0.997 ± 0.010	33
Peptidases A,B, and C					
PEPA*1	1.000	–	1.000	0.998 ± 0.006	33
PEPB*1	1.000	–	1.000	0.999 ± 0.004	36
PEPC*1	1.000	–	–	1.000	31
Haptoglobin					
HP*1	0.690	0.330	0.572	0.596 ± 0.131	77
Transferrin					
TF*C	1.000	1.000	1.000	0.982 ± 0.055	80
Ceruloplasmin					
CP*B	1.000	1.000	1.000	0.968 ± 0.097	36
Albumin					
ALB*A	1.000	1.000	1.000	0.995 ± 0.015	44
Serum cholinesterase 1					
CHE1*U	1.000	1.000	1.000	0.996 ± 0.014	30

¹Modal number of individuals tested.

²In 19 samples the A antigen was not subtyped.

ruí, and low prevalence of **HP*1** (0.330) in this same tribe. The **PGP*1** frequency (0.654) found in the Gavião is also significantly lower than the average prevalence of this allele in two other Amazonian Indian communities (0.837).

Using Szathmary's and Reed's (1978) approach to the evaluation of ethnic admixture (data on 13 genetic systems that provide markers for such process) yields an overall mean admixture of 4% among the Gavião, <1% for the Surui, and zero for the Zoró.

What pattern of relationship is obtained when the three tribes of the present study are compared with those of other South American Indians? Information on 24 genetic systems for 31 other tribes, which could be compared with the present study, was available. This set of common data was used to generate Nei's (1972) standard distances and Nei et al.'s (1983) D_A distances. Neighbor-joining trees were then constructed. The resulting dendrograms, however, showed very low bootstrap values, and the inferred relationships obtained with the two distances were much different (data not shown).

An alternative procedure was then tried, with concentration in the Tupi groups only. Ten other tribes of this linguistic stock could be ascertained, with a similar amount of information (24 genetic systems). Their names and their geographic location are given in Figure 1, whereas the allele frequencies and appropriate bibliographic references are given in Appendices 1 and 2. The same type of analysis was performed for this data set (calculation of the two genetic distances, construction of the neighbor-joining trees, bootstrap runs). This time the bootstrap values were higher, and the two comparisons yielded essentially the same results. Figure 2 displays the information obtained with the D_A distance. Three clusters are clearly discernible. The one in the upper part of the figure includes two of the three groups considered here (Surui and Zoró) with four other tribes, whereas the Gavião cluster with the Waiampi, Araweté, and Urubu-Kaapor. At the bottom, three other tribes constitute the third cluster.

The clusters of Figure 2 show a clear association with the geographic location of the groups considered. Cluster 1 combines the

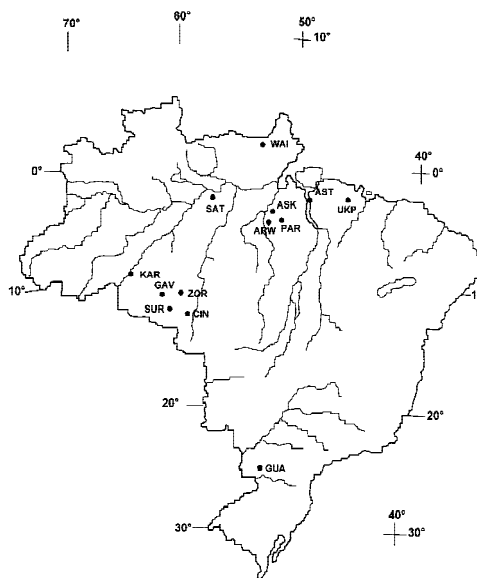


Fig. 1. Map of Brazil, showing the places where the 13 Tupi populations included in the genetic distances analysis live. ARW: Araweté; ASK: Asurini-Koatinemo; AST: Asurini-Trocará; CIN: Cinta Larga; GAV: Gavião; GUA: Guarani; KAR: Karitiana; PAR: Parakanan; SAT: Sateré-Mawé; SUR: Surui; UKP: Urubu-Kaapor; WAI: Waiampi; ZOR: Zoró.

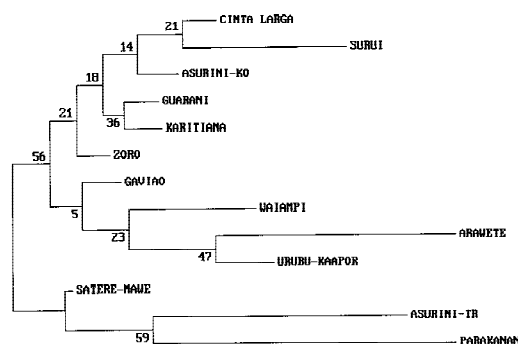


Fig. 2. Genetic relationships among 13 Tupi tribes, based on 24 systems: ABO, ACP, AK, ALB, CA2, CP, CHE1, DUFFY, ESA, ESD, G6PD, GLO, HBA, HBA2, HP, KELL, MNSs, P, PEPA, PEPB, PGD, PGM1, RH and TF. The dendrogram was obtained by the neighbor-joining method using D_A distances. Numbers indicate bootstrap values. Asurini-KO: Asurini from Koatinemo; Asurini-TR: Asurini from Trocará.

southwestern populations, with one exception (the Asurini of Koatinemo). Clusters 2 and 3 join the northeastern tribes, also with just one exception (the Gavião).

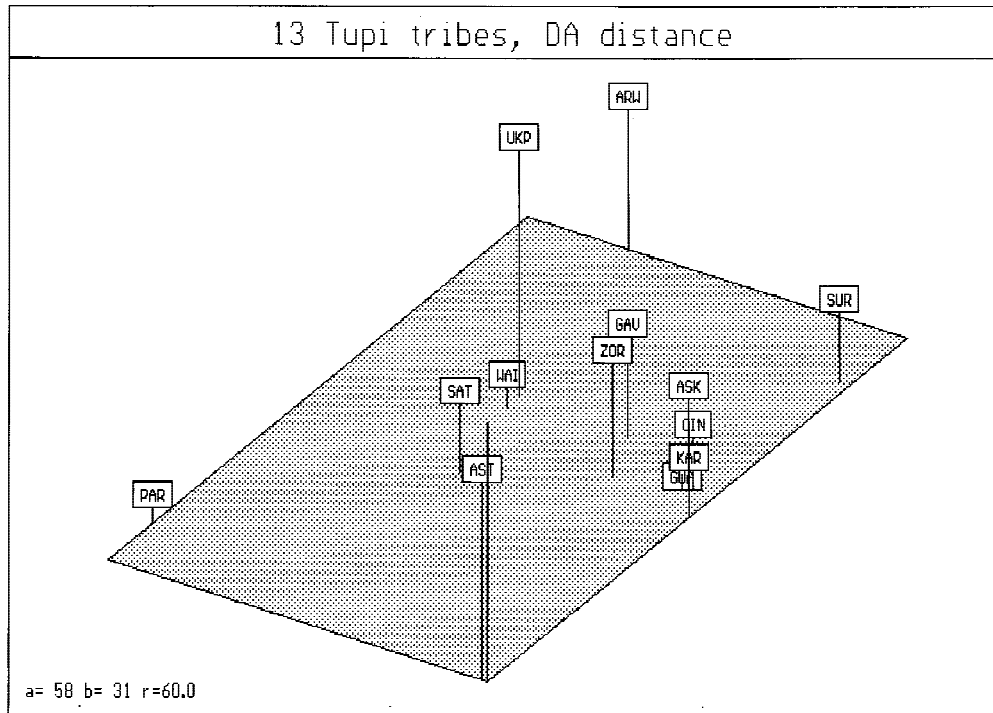


Fig. 3. Genetic relationships among the same 13 Tupi tribes considered in Figure 2, but now using principal coordinate analyses, based on the same distance matrix. The amount of the variation explained using these coordinates is 90%.

The same distance matrices can be examined using an alternative display method (principal coordinate analyses), and the results obtained are presented in Figure 3. The geographic dichotomy suggested by the dendrogram of Figure 2 is clearly shown in this new analysis, the southwestern populations clustering together at the right of the figure, and the northeastern ones scattered on the left side. Interestingly, however, and differently from the dendrogram, the Zoró show a closer association to the Gavião, rather than to the Surui.

DISCUSSION

The main results of this investigation can be listed as follows: (1) repeated sampling of the Surui population, with a time interval of 3 years, yielded essentially the same genetic results, (2) the Gavião, Surui, and Zoró allele frequencies showed little differences from previous studies performed in South American Indians, (3) low interethnic admixture rates were estimated, (4) the 13

Tupi populations considered in the genetic distance analyses can be clearly divided in two geographical sets, and (5) a decision about which of the three Tupi-Mondé groups are genetically closer to each other could not be reached, due to the diverse results obtained with different analytical methods.

In relation to the last point, the findings can be compared with previous studies of subjects of these three tribes at the mtDNA and nDNA levels. A summary of the previous results is given in Table 3. Clearly, none of the three arrangements given in the table is the preferred one. Probably, the three populations are too similar among themselves for the establishment of a given pattern.

Previous studies on the genetic relationships of Tupi groups have also been made by Black et al. (1988), Callegari-Jacques and Salzano (1989), Black (1991), Callegari-Jacques et al. (1994), and Bhatia et al. (1995). The resulting dendrograms varied in

TABLE 3. Comparison of results obtained with different genetic systems on the relationships among three Brazilian Indian tribes

Markers	Relationship observed ¹	References
mtDNA	Gavião/Surui, Zoró	Ward et al. (1996); Bonatto and Salzano (1997a,b); Bortolini et al. (1997); unpublished
D1S80	Gavião/Zoró, Surui	Heidrich et al. (1995); Hutz et al. (1997)
Beta-globin	Surui/Zoró, Gavião	Bevilaqua et al. (1995)
DYS19/ah	Surui/Zoró, Gavião	Santos et al. (1995)
Apo E	Gavião/Zoró, Surui	Hutz et al. (1996); unpublished
CD4, F13A1	Gavião/Surui, Zoró	Bogdawa (1997)
24 protein systems	Surui/Zoró, Gavião, or Gavião/Zoró, Surui	Present report

¹Closer similarity is indicated by a / sign.

a marked way, depending on the type of genetic distance and the markers used. Using alternative ways of representations of the same distance matrices, as done here, also may lead to conclusions different from those derived from the dendrograms. It seems, therefore, that any relationship observed in a given study should be considered with caution, unless a very large number of genetic markers, representing the genomes of the individuals studied in an unbiased way, is employed. Different ways of analysis should also be tried.

Several reasons for the above-indicated conflicting results may be suggested. First, the present gene pools of the groups studied could have been significantly and differentially altered in relatively recent times due to epidemics of infectious diseases and other consequences of contact with non-Indians. Second, many of the statistical methods employed presuppose conditions that are difficult to meet in nature. Third, the amount of interpopulation differences may be too small, at least with the studied markers, to differentiate them sharply. It is hoped that with the accumulation of information for many genetic systems, both at the protein and DNA levels, as well as with the refinement of statistical tools, a good approximation to the true biological history of South American Indians can be attained.

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APPENDIX A. Allele frequencies for 24 genetic systems studied in 11 Tupi tribes and respective references¹

Tribe (abbreviation)		N ABO	ABO*O	ABO*A	N ACP	ACP*A	ACP*B	ACP*C
ARAWETE	(ARW)	110	1.000	0.000	108	0.023	0.977	0.000
ASURINI-KOATINEMO	(ASK)	48	1.000	0.000	48	0.219	0.781	0.000
ASURINI-TROCARA	(AST)	125	0.992	0.008	103	0.078	0.922	0.000
CINTA LARGA	(CIN)	106	0.995	0.005	107	0.112	0.888	0.000
GUARANI	(GUA)	175	1.000	0.000	99	0.121	0.879	0.000
KARITIANA	(KAR)	89	1.000	0.000	87	0.103	0.897	0.000
PARAKANAN	(PAR)	217	1.000	0.000	205	0.124	0.876	0.000
SATERE-MAWE	(SAT)	170	1.000	0.000	170	0.141	0.859	0.000
SURUI (2 SAMPLES) ²	(SUR)	201	1.000	0.000	191	0.073	0.924	0.003
URUBU-KAAPOR	(UKP)	188	0.997	0.003	188	0.112	0.888	0.000
WAIAMPI	(WAI)	473	0.999	0.001	367	0.090	0.910	0.000

Tribe	N AK	AK*1	AK*3WAI	AK*4	N ALB	N CA2	CA2*1	N CP	CP*B
ARW	108	1.000	0.000	0.000	112	108	1.000	113	1.000
ASK	48	1.000	0.000	0.000	51	48	1.000	51	0.873
AST	104	1.000	0.000	0.000	107	101	1.000	107	0.435
CIN	105	1.000	0.000	0.000	92	107	1.000	89	0.904
GUA	99	1.000	0.000	0.000	80	99	0.980	99	1.000
KAR	87	1.000	0.000	0.000	90	87	1.000	103	0.980
PAR	203	1.000	0.000	0.000	252	117	1.000	248	0.964
SAT	170	1.000	0.000	0.000	170	169	1.000	170	1.000
SUR	194	1.000	0.000	0.000	200	54	0.991	159	0.984
UKP	188	1.000	0.000	0.000	205	191	1.000	204	0.980
WAI	373	0.981	0.019	0.000	361	– ³	–	185	1.000

Tribe	N CHE1	CHE1*U	N DUFFY	FY*A	N ESA	ESA*1	N ESD	ESD*1	N G6PD
ARW	113	1.000	110	0.766	101	1.000	104	0.769	44
ASK	52	1.000	48	0.323	48	1.000	48	0.531	19
AST	107	1.000	104	0.573	102	1.000	101	0.376	36
CIN	91	1.000	106	0.356	108	1.000	106	0.571	62
GUA	170	1.000	33	0.450	–	–	99	0.490	112
KAR	97	1.000	88	0.352	87	1.000	86	0.494	44
PAR	123	1.000	217	1.000	253	1.000	152	0.592	117
SAT	191	0.995	160	0.674	118	1.000	169	0.618	79
SUR	157	1.000	54	0.252	54	1.000	54	0.755	94
UKP	201	1.000	193	0.619	190	1.000	186	0.941	101
WAI	62	1.000	374	0.758	–	–	238	0.884	68

Tribe	N GLO	GLO*1	N HBA	N HBA2	HBA*2	N HP	HP*1	N KELL	KELL*K-
ARW	92	0.293	109	109	1.000	111	0.725	157	1.000
ASK	48	0.354	48	48	1.000	52	0.538	18	1.000
AST	99	0.652	119	104	1.000	99	0.692	124	1.000
CIN	106	0.231	103	103	1.000	89	0.612	106	1.000
GUA	99	0.182	134	100	1.000	131	0.569	34	1.000
KAR	81	0.167	88	88	1.000	94	0.644	89	1.000
PAR	112	0.429	211	114	1.000	231	0.452	217	1.000
SAT	119	0.358	170	170	1.000	245	0.706	170	0.994
SUR	113	0.120	54	54	1.000	197	0.376	50	1.000
UKP	185	0.543	189	189	1.000	204	0.730	193	1.000
WAI	–	–	630	117	0.970	230	0.500	474	1.000

Tribe	N MNSs	L*MS	L*Ms	L*NS	L*Ns	N P	P*1	N PEPA	N PEPB
ARW	89	0.000	0.759	0.000	0.241	89	0.094	46	108
ASK	46	0.309	0.506	0.071	0.114	48	0.441	48	48
AST	102	0.270	0.598	0.078	0.054	104	0.830	102	102
CIN	106	0.246	0.665	0.009	0.080	106	0.223	80	109
GUA	34	0.167	0.377	0.140	0.316	34	0.458	–	–
KAR	88	0.214	0.507	0.129	0.150	89	0.563	72	87
PAR	217	0.233	0.765	0.000	0.002	217	0.743	116	116
SAT	105	0.146	0.768	0.063	0.023	170	0.553	168	168
SUR	54	0.167	0.753	0.003	0.077	54	0.163	54	54
UKP	190	0.269	0.599	0.021	0.111	194	0.395	189	191
WAI	375	0.302	0.342	0.186	0.170	374	0.300	214	215

APPENDIX A. Allele frequencies for 24 genetic systems studied in 11 Tupi tribes and respective references¹

Tribe	N PGD	PGD*A	N PGM1	PGM1*1	PGM1*2	PGM1*4/10	N TF	TF*B	TF*C	TF*D
ARW	108	1.000	108	0.630	0.370	0.000	112	0.000	1.000	0.000
ASK	48	1.000	48	0.677	0.323	0.000	51	0.000	1.000	0.000
AST	98	1.000	103	0.966	0.034	0.000	128	0.000	0.991	0.009
CIN	107	1.000	105	0.762	0.238	0.000	91	0.000	1.000	0.000
GUA	99	1.000	99	0.828	0.172	0.000	129	0.000	1.000	0.000
KAR	87	1.000	87	0.701	0.299	0.000	98	0.000	1.000	0.000
PAR	212	0.995	207	0.978	0.022	0.000	252	0.000	0.998	0.002
SAT	170	1.000	170	0.959	0.041	0.000	170	0.000	1.000	0.000
SUR	153	1.000	190	0.692	0.308	0.000	199	0.000	1.000	0.000
UKP	188	1.000	188	0.779	0.221	0.000	205	0.000	1.000	0.000
WAI	372	1.000	372	0.885	0.111	0.004	441	0.006	0.948	0.046

Tribe	N RH	RH*RZ	RH*R1	RH*R2	RH*R0	RH*RY	RH*R	References (see Appendix 2)
ARW	110	0.005	0.177	0.731	0.087	0.000	0.000	8, 18, 20
ASK	48	0.155	0.584	0.199	0.062	0.000	0.000	4
AST	124	0.013	0.572	0.313	0.102	0.000	0.000	4, 10
CIN	106	0.061	0.788	0.057	0.094	0.000	0.000	7
GUA	31	0.071	0.719	0.123	0.087	0.000	0.000	1, 13, 14, 15, 16, 19
KAR	89	0.006	0.825	0.135	0.034	0.000	0.000	7, 8
PAR	217	0.027	0.599	0.157	0.053	0.088	0.076	3, 4, 11, 23
SAT	185	0.115	0.615	0.247	0.023	0.000	0.000	1, 12, 17
SUR	54	0.031	0.309	0.299	0.361	0.000	0.000	1, 7, 8, present study
UKP	193	0.055	0.225	0.707	0.013	0.000	0.000	1, 4
WAI	374	0.099	0.579	0.319	0.003	0.000	0.000	3, 5, 6, 8, 9, 21, 22, 23

¹N is the number of individuals studied for the indicated system. All observed alleles are presented except in systems where just two of them were considered. In these cases, the alternative alleles were as follows: CA2*2, CP*ACAY1, CHE1*A, FY*B, ESA*KARARAO, ESD*2, GLO*2, HB*HIGHA2, HP*2, KELL*K+, P*2, and PGD*C. For monomorphic systems (ALB, G6PD, HBA, CP, PEPA, and PEPB) only the number of individuals tested are given (G6PD: males only).
²The Surui are also listed here to show the combined allele frequencies we used for the genetic distance analysis.
³Missing values were replaced by the Tupi mean.

APPENDIX B. List of papers reporting primary data from which the allele frequencies listed in Appendix A were obtained

- Alcântara VM, Lourenço MAC de, Salzano FM, Petzl-Erler ML, Coimbra CEA, Santos RV, Chautard-Freire-Maia EA (1995) Butyrylcholinesterase polymorphisms (BCHE and CHE2 loci) in Brazilian Indians and admixed populations. *Hum. Biol.* 67:717–726.
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17. Salzano FM, Weimer TA, Franco MHL, Hutz MH, Mestriner MA, Simões AL, Freitas MJM (1985) Demography and genetics of the Sateré-Mawé and their bearing on the differentiation of the Tupi tribes of South America. *J. Hum. Evol.* 14:647–655.
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