The Brazilian Xavante Indians Revisited: New Protein Genetic Studies

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ABSTRACT A total of 94 individuals from the Xavante village of Rio das Mortes were variously studied in relation to 28 protein genetic systems. No variation was observed for 15 of them, in accordance with previous studies. Of the remaining 13, four (Rh, Duffy, acid phosphatase, and GC) showed significant departures from the averages obtained in 32 other South American Indian populations. If studies performed in the 1960s are considered, there is indication that no significant changes in this village's gene pool has occurred in the last 30 years. Comparison with two other Xavante populations included nine systems with variation, and for three of them (MNSs, Rh, and Duffy) significant differences were found. Genetically the Rio das Mortes are closer to the São Marcos than to the Simões Lopes Xavantes. A dendrogram considering 25 genetic systems and 33 South American Indian populations was constructed. There the Xavante were grouped together, in two neighboring clusters, with three other tribes who speak Ge languages. But these clusters also present populations who speak other languages, and the reproducibility of the tree is low. South American Indians, at least with this set of markers, do not seem to be clearly classified into defined subgroups. Am J Phys Anthropol 104:23–34, 1997. © 1997 Wiley-Liss, Inc.

The Xavante Indians of the Brazilian Mato Grosso are one of the best studied human populations in terms of human biology. After a thorough social anthropological investigation (reported in detail by Maybury-Lewis, 1967), they were studied from a genetic, demographic, and medical point of view in the 1960s (cf. Neel et al., 1964; Neel and Salzano, 1967). Afterwards, they were chosen as one of the tribes to be investigated in a comparative project aimed at studying the human ecology of Central Brazilian Indian populations (Gross et al., 1979). In the 1990s a series of studies on their health, demography, ecology, and genetics was initiated. Specifically, one Xavante population, which was located in a village called São Domingos

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in the 1960s and which nowadays is known as the Rio das Mortes or Etenhiritipá Xavante, has been followed for nearly 50 years. The results of these investigations have been widely disseminated in the scientific literature. The earlier papers were reviewed in Salzano and Callegari-Jacques (1988) and the most recent ones in Santos et al. (1996).

The present report furnishes information for 28 protein genetic systems studied among the Rio das Mortes Xavante and addressed the following questions: 1) Can we identify significant genetic changes in this community between the 1960s studies and the present one? 2) How different, genetically, are the Rio das Mortes Xavante from other Xavante communities? And 3) how do the Xavante compare with the other South American Indians from whom genetic data are available?

MATERIALS AND METHODS

The Xavante speak a Ge language and at present number around 10,000 persons, distributed along several dozen villages on six reservations (Areões, Marechal Rondon, Parabubure, Pimentel Barbosa, Sangradouro, and São Marcos). In 1946 a Xavante group headed by a chief called Apowe was the first to establish permanent contact with members of the Brazilian Indian Service (Serviço de Proteção aos Índios) (Maybury Lewis, 1967; Flowers, 1983a,b). Members of this group and their descendants are now settled in villages located at the Pimentel Barbosa reservation (51°40′W, 13°20′S). When fieldwork was carried out in 1990, the majority of the population was living in a single village (Rio das Mortes). This village was identified as São Domingos by Neel et al. (1964) and in the set of papers published in 1967 (e.g., Salzano et al., 1967). The social and economic changes which affected them in the period 1947–1995 were described in Santos et al. (1996), who also considered their demographic dynamics, subsistence system, and nutritional ecology. Briefly, since they have guaranteed their land rights, they have also maintained their cultural traditions, and their health is less compromised than that of many other Brazilian Indians. Compared to the 1970s, they spend less time on agricultural work and more on hunting, fishing, and gathering; market participation has not increased, and the population almost doubled in the past 18 years.

Blood samples were collected with anticoagulant, refrigerated shortly afterwards, and flown in this condition to Porto Alegre, where they were processed and aliquots sent to Ribeirão Preto and Curitiba for further determinations (the Curitiba results have been published by Alcântara et al., 1995). The methods employed for the studies reported here have been described or referenced in Callegari-Jacques et al. (1996).

Allele frequencies were obtained by maximum likelihood methods (Reed and Schull, 1968), and the heterogeneity chi-square test was employed for comparisons among Xavante samples. The genetic dissimilarities between the Xavante populations and between this tribe and other South American Indian groups were evaluated using both Nei's (1972) standard genetic distance (D) and D_A, a modified Cavalli-Sforza distance proposed by Nei et al. (1983). The modification aims to remove a deficiency of Cavalli-Sforza's (1969) distance, namely, a heavy dependency on the number of low frequencies alleles in the sample. Nei et al. (1983) have shown that D_A has a better performance than D in reconstructing trees for closely related populations, such as those in humans.

The genetic relationships among the studied populations were represented either by trees, constructed with the UPGMA (Sneath and Sokal, 1973) and neighbor-joining, NJ (Saitou and Nei, 1987) methods, or by three-dimensional plots based on principal coordinate analyses of the same distance matrices (e.g., Sneath and Sokal, 1973). The reliability of the trees was tested by bootstrap replications, following the suggestions of Hedges (1992).

For the genetic-distances analyses, the DISPAN (Ota, 1993), the BIOSYS (Swofford and Selander, 1981), or the NTSYS (Rohlf, 1993) programs were used.

RESULTS AND DISCUSSION

Table 1 presents the phenotype and allele frequencies for the 28 genetic systems included in the present study. As expected, the Xavante are monomorphic for the ABO, Kell,

TABLE 1. Phenotype and allele frequencies for 28 genetic systems studied in the Xavante Indians

System	Number tested	Phenotypes found	Number found	Allele or haplotype	Allele or haplotype frequency
ABO	85	0	85	**ABO*O**	1.000
MNSs	59	MS	6	**L*MS**	0.286
		MSs	11	**L*Ms**	0.426
		Ms	14	**L*NS**	0.163
		MNS	8	**L*Ns**	0.125
		MNSs	8		
		MNs	6		
		NS	3		
		Ns	3		
P	85	P1	65	**P*1**	0.515
		P2	20		
Rh	34	CDe	15	**RH*R1**	0.559
		CcDEe	2	**RH*R2**	0.162
		CcDe	6	**RH*R0** or **RH*r**	0.279
		cDE	2		
		cDEe	5		
		cDe	4		
Kell	85	K−	85	**KELL*K−**	1.000
Duffy	85	a+	59	**FY*A**	0.447
		a−	26		
Diego	78	a+	27	**DI*A**	0.191
		a−	51		
Hemoglobin A	83	A	83	**HB*A**	1.000
Hemoglobin A2	83	A2	83	**HB*A2**	1.000
Phosphogluconate dehydrogenase	83	A	83	**PGD*A**	1.000
Phosphoglucomutase 1	82	1A	6	**PGM1*1A**	0.207
		1A1B	18	**PGM1*1B**	0.646
		1A2B	4	**PGM1*2A**	0.049
		1B	37	**PGM1*2B**	0.098
		1B2A	6		
		1B2B	8		
		2A2B	2		
		2B	1		
Glucose-6-phosphate dehydrogenase	Males: 33	B	33	**G6PD*B**	1.000
	Females: 50	B	50		
Adenylate kinase	83	1-1	83	**AK*1**	1.000
Acid phosphatase	83	A	1	**ACP*A**	0.217
		AB	34		
		B	48		
Esterase A	82	1-1	82	**ESA*1**	1.000
Esterase D	82	1-1	30	**ESD*1**	0.634
		2-1	44		
		2-2	8		
Glyoxalase I	83	1-1	1	**GLO*1**	0.223
		2-1	35		
		2-2	47		
Carbonic anhydrase 2	82	1-1	82	**CA2*1**	1.000
Peptidase A	76	1-1	76	**PEPA*1**	1.000
Peptidase B	82	1-1	82	**PEPB*1**	1.000
Peptidase C	82	1-1	82	**PEPC*1**	1.000
Haptoglobin	83	1–1	22	**HP*1**	0.549
		2–1	46		
		2–2	14		
		0	1		
Transferrin	54	C1	39	**TF*C1**	0.852
		C1C2	12	**TF*C2**	0.130
		C2	1	**TF*C3**	0.009
		C1C3	1	**TF*C4**	0.009
		C1C4	1		
Ceruloplasmin	83	B	83	**CP*B**	1.000
Albumin	83	A	83	**ALB*A**	1.000
GC	80	1F-1S	2	**GC*1F**	0.113
		1S	2	**GC*1S**	0.144
		2-1F	16	**GC*2**	0.737
		2-1S	17	**GC*VAR**	0.006
		2	42		
		2-VAR	1		
Serum cholinesterase 1[1]	90	A	0	**CHE1*A**	0
		F	0	**CHE1*F**	0
Serum cholinesterase 2[1]	94	C5+	19		
		C5−	75		

[1] Results reported in Alcântara et al. (1995).

Hemoglobin A and A2, phosphogluconate dehydrogenase, glucose-6-phosphate dehydrogenase, adenylate kinase, esterase A, carbonic anhydrase 2, peptidases A, B, and C, ceruloplasmin, albumin, and serum cholinesterase 1 systems. These systems generally do not show variation in unadmixed South American Indians. As for the remaining 13 systems, the results also do not depart markedly from other investigations for nine of them, but they are significantly different (as assessed by the standard errors of the averages obtained for 32 other South American Indian populations with which they were compared) in the Rh, Duffy, acid phosphatase, and GC systems (in relation to GC, the comparison was made with 22 other South American Indian populations only, due to lack of information). The data base for the 32 South American Indian populations (see Appendix) was obtained from a large list of references (too large to be reproduced here but available on request), while the GC comparison was largely based in the results compiled by Corvello et al. (1989), with additions, however, from our data base.

The peculiar presence of two Rh-negative individuals among the Simões Lopes Xavante, observed in previous studies (Gershowitz et al., 1967), was not confirmed in the present investigation (although 34 individuals only had been examined for the full set of five Rh antisera, 85 had been tested with anti-D, with uniformly negative results). Differently from the previous investigations, we also now observed in Rio das Mortes four cDe individuals, while none was found in the 1960s. This led to a high estimate of **RH*RO** (or **RH*r**) (0.28, while the combined average of these two alleles in the 32 other South American Indian populations is only 0.07).

On the other hand, the high prevalence of **GC*2**, already found by Shreffler and Steinberg (1967), was fully confirmed here (0.74, while the average in the 22 other populations was 0.19). In relation to this system, it is also notable that we found a rare variant in association with the **GC*2** allele. The double bands showed a lower electrophoretic mobility than those determined by **GC*1S** and can therefore be classified to the GC1C group of variants (Cleve and Constans, 1988). Further characterization was prevented by the lack of comparative material.

Alleles **FY*A** had a lower (0.45 vs. 0.62) and **ACP*A** a higher (0.22 vs. 0.12) prevalence in relation to the set of South American Indian tribes compared.

Using chi-square analyses, we contrasted the results obtained in the 1960s in Rio das Mortes with the present ones for six systems (MNSs, P, Rh, Duffy, haptoglobin, and GC). For four of them, no significant differences were found (P values ranging from 0.07–0.60). The difference found for Rh ($P < 0.001$) was already mentioned, as well the similarity in the GC prevalences. One additional system (P) presented different frequencies in the two studies ($P < 0.01$), but this may be due to the use of a particularly strong reagent in the earlier determinations. As expected, the admittedly limited amount of information obtained indicates that the considerable changes which occurred in Rio das Mortes in the last 30 years (Santos et al., 1996) were not sufficient to significantly alter its gene pool.

Similar analyses were done comparing the combined results of the two Rio das Mortes surveys with those obtained in two other Xavante communities, São Marcos and Simões Lopes (Gershowitz et al., 1967; Shreffler and Steinberg, 1967; Tashian et al., 1967). Comparisons had to be restricted to the genetic markers available in the 1960s; these included nine systems with variation (MNSs, P, Rh, Duffy, Diego, acid phosphatase, haptoglobin, albumin, and GC). For three of them (MNSs, Rh, and Duffy), significant differences were found. The Rio das Mortes Xavante present low prevalences of **L*MS, RH*RZ, RH*R1,** and **FY*A** and high prevalences of **L*Ns** and **RH*RO** or **RH*r,** as compared to the other two groups. The application of the D_A distances and the UPGMA method to 16 systems studied in the three populations furnished a dendrogram with a clear separation of Simões Lopes from the two other communities (São Marcos and Rio das Mortes or São Domingos). This dendrogram was reproducible in 100% of the 10,000 bootstrap replications performed. Exactly the same results were obtained when Nei's (1972) standard dis-

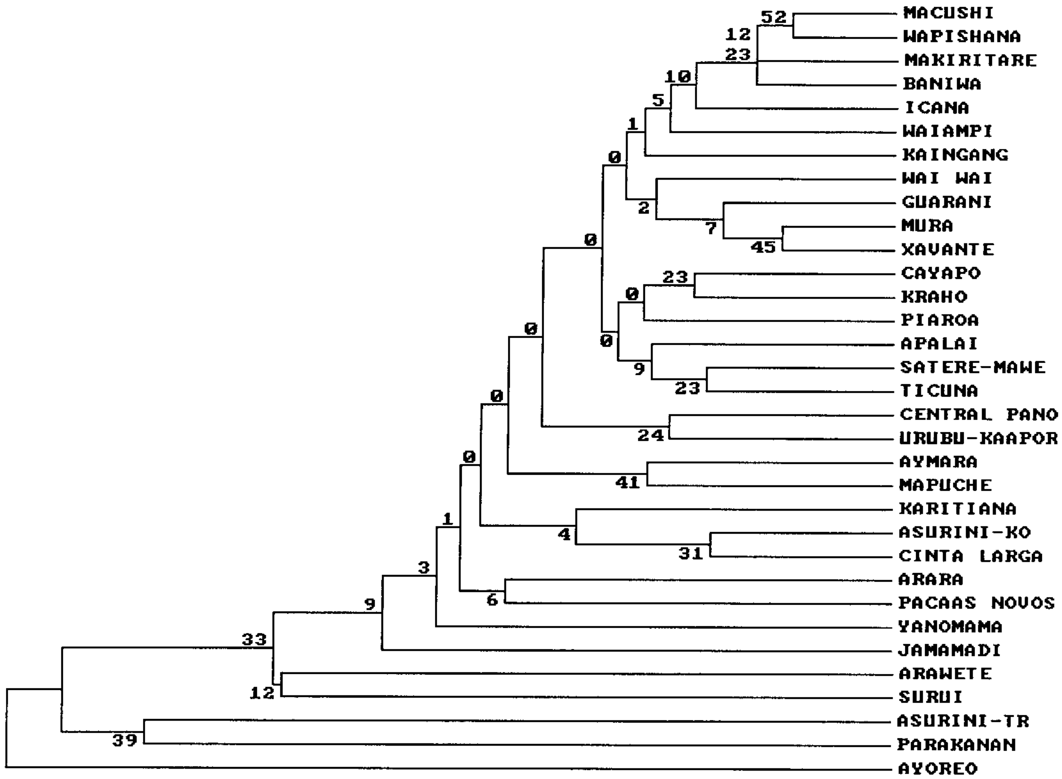

Fig. 1. Genetic relationships (Nei et al.'s (1983) D_A distance, UPGMA method) among 33 South American Indian populations, considering 25 genetic systems (ABO, ACP, AK, ALB, CA2, CP, DIEGO, DUFFY, ESA, ESD, G6PD, GLO, GM, HBA, HP, KELL, MNSs, P, PEPA, PEPB, PGD, PGM1, PGM2, RH, and TF). The numbers indicate bootstrap values based on 10,000 replications. Asurini-KO, Asurini from Koatinemo; Asurini-TR, Asurini from Trocará.

tances and the neighbor-joining methods were used (data not shown).

Genetically, how can the Xavante as a whole be positioned in relation to the South American Indians in general? We had already made a comparison between them and three other Ge tribes (Cayapo, Kraho, and Kaingang) (Salzano et al., in press) using Nei's (1972) standard genetic distances and the neighbor-joining method. In this case, Cayapo and Kraho associated among themselves, while the Kaingang and Xavante were set apart. The dendrogram obtained for the Xavante plus 32 other South American Indian populations, considering 25 genetic systems, Nei et al.'s (1983) D_A distances, and the UPGMA method is presented in Figure 1. There the four Ge groups appear in two neighboring clusters, which, however, also present populations who speak other languages. Moreover, the reproducibility of the tree is very low, as shown by the bootstrap values. Similarly low reproducible trees were obtained using the D_A distances and the neighbor-joining method as well as Nei's (1972) standard genetic distance with either the UPGMA or neighbor-joining procedures. Reducing the number of populations (for instance, including the Ge and Tupi groups only) does not significantly improve this result. We also examined the dendrograms obtained using each system separately with these alternative distances and methods to verify if a given set was responsible for this low reproducibility. No particularly aberrant set was detected. We conclude that these 25 systems do not clearly distinguish any cluster of populations from the others, indicating a low degree of interpopulation diversity. Similar results were obtained by

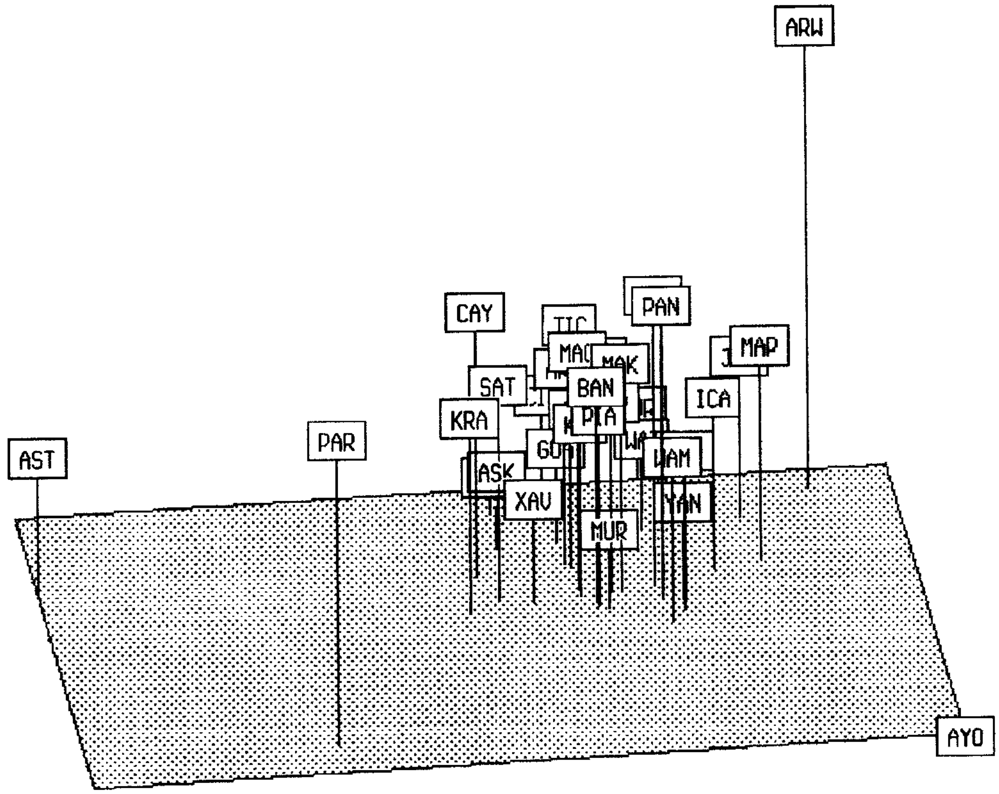

Fig. 2. Principal coordinates representation of the genetic relationships (D_A distance) among 33 South American Indian populations, considering 25 genetic systems. Keys for the tribes' names: APA, Apalai; ARA, Arara; ARW, Araweté; ASK, Asurini from Koatinemo; AST, Asurini from Trocará; AYM, Aymara; AYO, Ayoreo; BAN, Baniwa; CAY, Cayapo; CIN, Cinta Larga; GUA, Guarani; ICA, Içana Indians; JAM, Jamamadi; KAI, Kaingang; KAR, Karitiana; KRA, Kraho; MAC, Macushi; MAK, Makiritare; MAP, Mapuche; MUR, Mura; PAC, Pacaás Novos; PAN, Central Pano; PAR, Parakanã; PIA, Piaroa; SAT, Sateré-Mawé; SUR, Surui; TIC, Ticuna; URU, Urubu-Kaapor; WAI, Wai Wai; WAM, Waiãpi; WAP, Wapishana; XAV, Xavante; YAN, Yanomama.

Bhatia et al. (1995) using markers from the HLA system and 20 South American Indian populations.

The principal coordinates analysis provides a different tool in representing the genetic dissimilarities obtained for the 33 Indian populations considered (Fig. 2). The three-dimensional plot shows a tight cluster of tribes, with four discrepant groups. The Xavante are included in the central set, with the also Ge-speaking Cayapo and Kraho occupying close positions. This result is in agreement with the dendrogram display. Considering now the 15 Ge and Tupi populations only (Fig. 3), a higher diversity is apparent within the last linguistic group, with the four Ge (Xavante, Cayapo, Kraho, and Kaingang) clustering together in a more central position.

The Xavante have also been studied genetically at the DNA level. The markers investigated are located in mitochondrial DNA (Ward et al., 1996), nuclear autosomal DNA, namely HLA class II alleles (Cerna et al., 1993), beta globin haplotypes (Bevilaqua et al., 1995), and D1S80 (Heidrich et al., 1995; Hutz et al., 1997), and Y-chromosome DNA (Santos et al., 1995). Comparison with the present studies is difficult, however, because the DNA variability has been much less extensively studied than the protein variation in South America (and elsewhere). Briefly, there is a discrepancy between the mtDNA and nDNA results, the Xavante

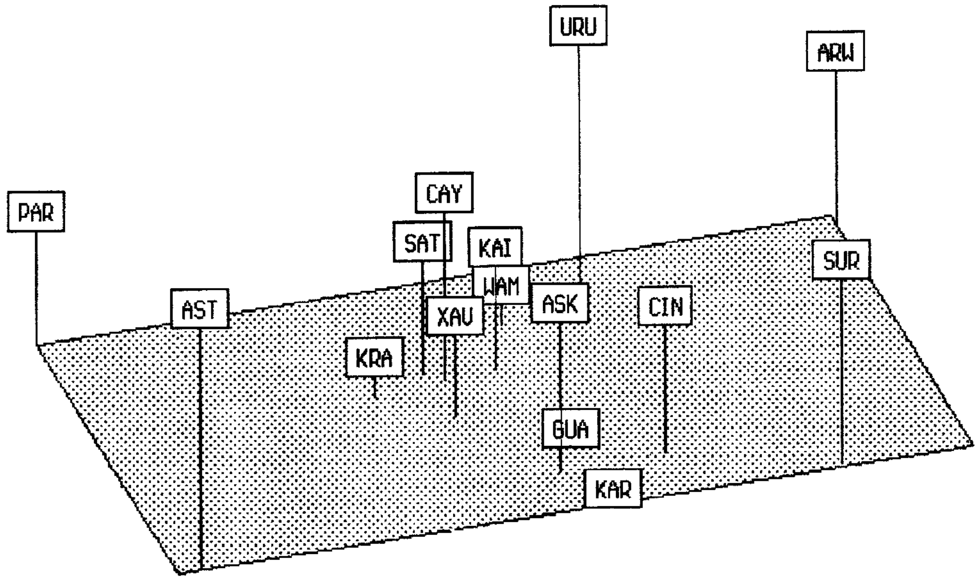

Fig. 3. Principal coordinates representation of the genetic relationships (D_A distance) among 15 Ge and Tupi Indian populations, considering 25 genetic systems. Keys for the tribes' names are given in the legend of Fig. 2.

showing low variability at the mtDNA control region but high diversity (compared to five other South American Indian populations) at the beta-globin nDNA region. They could not be set apart from other tribes in relation to Y-chromosome haplotypes, but the D1S80 system clearly discriminated them from other South American Indian groups. There is a remarkable degree of restriction of the HLA class II polymorphism among the Xavante, who curiously showed more similarity in this genetic region to a sample of North American Indians than to three other Argentinian tribes.

Interpretation of all the genetic data, both at the protein and DNA levels, demands the collation of them with other kinds of biological, sociocultural, and environmental information. Our research group has obtained data about population movements, fertility, mortality, epidemiology, nutritional state, and daily life of the Xavante which might be much useful for such analysis, and we are now conducting some of these cross-comparisons. Unfortunately, few other human groups have been subjected to these investigations in such detail.

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APPENDIX. Number of individuals (N) and most frequent allele frequencies, per system, used in the present analysis[1]

Tribe	N-ABO	ABO*O	ABO*A	N-ACP	ACP*A	ACP*B	N-AK	AK*1
Apalai-Wayana	133	1.000	.000	125	.188	.812	125	1.000
Arara	60	1.000	.000	58	.103	.897	59	1.000
Arawete	110	1.000	.000	108	.023	.977	108	1.000
Asurini-Koatinemo	48	1.000	.000	48	.219	.781	48	1.000
Asurini-Trocara	125	.992	.008	103	.078	.922	104	1.000
Aymara	4,380	.972	.020	1,524	.240	.760	1,379	.997
Ayoreo	455	1.000	.000	121	.302	.698	182	1.000
Baniwa	368	1.000	.000	363	.076	.924	363	1.000
Central Pano	113	1.000	.000	335	.061	.939	335	1.000
Cayapo	772	1.000	.000	466	.237	.763	238	1.000
Cinta Larga	106	.995	.005	107	.112	.888	105	1.000
Guarani	175	1.000	.000	99	.121	.879	99	1.000
Icana Indians	151	1.000	.000	144	.125	.875	154	1.000
Jamamadi	38	1.000	.000	37	.027	.973	36	1.000
Kaingang	305	.997	.000	234	.017	.977	449	1.000
Karitiana	89	1.000	.000	87	.103	.897	87	1.000
Kraho	190	1.000	.000	191	.291	.709	191	1.000
Macushi	1,254	.999	.001	684	.028	.971	683	1.000
Makiritare	810	1.000	.000	717	.054	.946	662	1.000
Mapuche	1,146	.911	.056	103	.189	.811	—	—
Mura	104	1.000	.000	103	.136	.864	103	1.000
Pacaas Novos	222	1.000	.000	221	.032	.968	222	1.000
Parakana	217	1.000	.000	205	.124	.876	203	1.000
Piaroa	281	1.000	.000	267	.146	.854	267	1.000
Satere-Mawe	170	1.000	.000	170	.141	.859	170	1.000
Surui	54	1.000	.000	54	.074	.917	55	1.000
Ticuna	1,877	.989	.006	1,763	.062	.827	1,762	1.000
Urubu-Kaapor	188	.997	.003	188	.112	.888	188	1.000
Wai Wai	166	1.000	.000	166	.229	.771	165	1.000
Waiapi	473	.999	.001	367	.090	.910	373	.981
Wapishana	763	.994	.006	569	.059	.941	569	1.000
Xavante	622	1.000	.000	459	.197	.803	83	1.000
Yanomama	3,806	1.000	.000	3,301	.013	.987	2,606	1.000

Tribe	N-ALB	ALB*A	N-CA2	CA2*1	N-CP	CP*B	N-DIEGO	DI*A
Apalai-Wayana	129	1.000	136	1.000	129	.950	—	—
Arara	61	1.000	58	1.000	60	1.000	60	.096
Arawete	112	1.000	108	1.000	113	1.000	—	—
Asurini-Koatinemo	51	1.000	48	1.000	51	.873	—	—
Asurini-Trocara	107	1.000	101	1.000	107	.435	76	.269
Aymara	1,379	1.000	1,318	1.000	1,694	1.000	920	.050
Ayoreo	358	1.000	141	1.000	281	1.000	450	.000
Baniwa	377	1.000	377	.946	377	1.000	363	.245
Central Pano	463	1.000	335	.999	335	1.000	113	.190
Cayapo	740	1.000	524	1.000	216	.963	689	.228
Cinta Larga	92	1.000	107	1.000	89	.904	106	.187
Guarani	80	1.000	99	.980	99	1.000	89	.155
Icana Indians	148	1.000	154	.977	148	1.000	151	.083
Jamamadi	37	1.000	37	1.000	37	1.000	—	—
Kaingang	449	1.000	452	1.000	449	1.000	519	.197
Karitiana	90	1.000	87	1.000	103	.980	—	—
Kraho	193	1.000	190	1.000	192	1.000	167	.114
Macushi	694	1.000	742	1.000	694	.997	1,150	.121
Makiritare	720	.990	390	1.000	646	1.000	810	.199
Mapuche	71	1.000	—	—	71	1.000	858	.023
Mura	104	.995	103	1.000	104	.990	104	.065
Pacaas Novos	222	1.000	221	1.000	222	1.000	—	—
Parakana	252	1.000	117	1.000	248	.964	159	.216
Piaroa	146	1.000	—	—	145	1.000	281	.107
Satere-Mawe	170	1.000	169	1.000	170	1.000	170	.143
Surui	65	1.000	54	.991	24	.896	50	.175
Ticuna	761	1.000	1,293	1.000	758	1.000	1,869	.162
Urubu-Kaapor	205	1.000	191	1.000	204	.980	77	.202
Wai Wai	166	1.000	164	1.000	166	1.000	166	.220
Waiapi	361	1.000	—	—	185	1.000	226	.229
Wapishana	576	.980	568	.998	575	.997	762	.165
Xavante	829	.998	82	1.000	540	.993	616	.169
Yanomama	3,504	.925	356	1.000	2,432	1.000	3,805	.006

APPENDIX. (continued)

Tribe	N-DUFFY	FY*A	N-ESA	ESA*1	N-ESD	ESD*1	N-G6PD	G6PD*B
Apalai-Wayana	133	.712	136	1.000	136	.724	32	1.000
Arara	60	.553	58	1.000	58	.784	11	1.000
Arawete	110	.766	101	1.000	104	.769	22	1.000
Asurini-Koatinemo	48	.323	48	1.000	48	.531	10	1.000
Asurini-Trocara	104	.573	102	1.000	101	.376	18	1.000
Aymara	1,650	.659	—	—	1,399	.764	467	.993
Ayoreo	310	.746	253	1.000	141	1.000	18	1.000
Baniwa	363	.738	371	1.000	358	.796	12	1.000
Central Pano	113	.748	329	1.000	341	.833	10	1.000
Cayapo	740	.743	435	.998	688	.482	49	1.000
Cinta Larga	106	.356	108	1.000	106	.571	31	1.000
Guarani	33	.450	—	—	99	.490	56	1.000
Icana Indians	151	.512	153	1.000	154	.786	39	1.000
Jamamadi	38	.719	37	1.000	37	.784	10	1.000
Kaingang	323	.646	213	1.000	456	.683	229	1.000
Karitiana	88	.352	87	1.000	86	.494	22	1.000
Kraho	149	.778	190	1.000	190	.434	—	—
Macushi	1,254	.656	742	.963	999	.680	17	1.000
Makiritare	810	.735	451	1.000	459	.793	31	1.000
Mapuche	747	.689	—	—	51	.824	78	1.000
Mura	104	.573	103	1.000	103	.801	21	1.000
Pacaas Novos	213	.717	221	1.000	221	.783	55	1.000
Parakana	217	1.000	253	1.000	152	.592	59	1.000
Piaroa	227	.575	146	1.000	267	.770	5	1.000
Satere-Mawe	160	.674	118	1.000	169	.618	40	1.000
Surui	50	.252	54	1.000	53	.755	13	1.000
Ticuna	1,873	.639	1,263	1.000	1,293	.662	26	1.000
Urubu-Kaapor	193	.619	190	1.000	186	.941	51	1.000
Wai Wai	150	.362	159	.978	146	.818	74	1.000
Waiapi	374	.758	—	—	238	.884	34	1.000
Wapishana	762	.701	568	.977	567	.794	9	1.000
Xavante	624	.528	267	1.000	81	.630	121	1.000
Yanomama	3,753	.571	651	1.000	419	.857	197	1.000

Tribe	N-GLO	GLO*1	N-GM	GM*AG	GM*AXG	N-HBA	HB*A
Apalai-Wayana	136	.224	93	.722	.171	119	1.000
Arara	53	.632	64	.612	.388	59	1.000
Arawete	92	.293	96	.549	.441	109	1.000
Asurini-Koatinemo	48	.354	47	.684	.316	48	1.000
Asurini-Trocara	99	.652	106	.875	.115	119	1.000
Aymara	—	—	580	.910	.044	2,051	1.000
Ayoreo	—	—	328	.997	.001	451	1.000
Baniwa	13	.269	363	.679	.272	363	1.000
Central Pano	37	.444	335	.790	.208	335	1.000
Cayapo	26	.462	960	.598	.399	559	1.000
Cinta Larga	106	.231	106	.407	.556	103	1.000
Guarani	99	.182	34	.740	.215	134	1.000
Icana Indians	151	.215	138	.643	.357	149	1.000
Jamamadi	37	.027	44	.426	.574	38	1.000
Kaingang	235	.392	52	.708	.244	833	1.000
Karitiana	81	.167	87	.528	.223	88	1.000
Kraho	—	—	192	.865	.116	191	1.000
Macushi	496	.215	692	.591	.376	849	1.000
Makiritare	77	.299	718	.561	.436	570	1.000
Mapuche	105	.376	—	—	—	981	1.000
Mura	102	.133	86	.809	.179	102	1.000
Pacaas Novos	221	.213	212	.412	.588	267	1.000
Parakana	112	.429	134	.914	.086	211	1.000
Piaroa	137	.343	146	.785	.215	266	1.000
Satere-Mawe	119	.358	80	.651	.312	170	1.000
Surui	51	.167	54	.641	.144	55	1.000
Ticuna	1,762	.168	1,763	.642	.349	1,887	1.000
Urubu-Kaapor	185	.543	159	.550	.384	189	1.000
Wai Wai	166	.322	—	—	—	165	1.000
Waiapi	—	—	526	.768	.207	630	1.000
Wapishana	47	.319	573	.583	.351	699	1.000
Xavante	86	.227	453	.761	.238	573	1.000
Yanomama	420	.238	3,447	.853	.147	3,294	1.000

APPENDIX. (continued)

Tribe	N-HP	HP*1	N-KELL	KELL*K	N-PEPA	PEPA*1	N-PEPB	PEPB*1
Apalai-Wayana	134	.724	133	1.000	136	1.000	136	1.000
Arara	63	.897	30	1.000	58	1.000	58	1.000
Arawete	111	.725	157	1.000	46	1.000	108	1.000
Asurini-Koatinemo	52	.538	18	1.000	48	1.000	48	1.000
Asurini-Trocara	99	.692	124	1.000	102	1.000	102	1.000
Aymara	3,446	.675	2,951	1.000	1,379	.999	1,379	.999
Ayoreo	468	.433	448	1.000	138	1.000	186	1.000
Baniwa	363	.517	363	1.000	363	1.000	363	.999
Central Pano	315	.683	113	1.000	335	1.000	335	.976
Cayapo	749	.577	772	1.000	521	1.000	558	1.000
Cinta Larga	89	.612	106	1.000	80	1.000	109	1.000
Guarani	131	.569	34	1.000	—	—	—	—
Icana Indians	147	.432	151	1.000	152	1.000	144	1.000
Jamamadi	37	.527	38	1.000	37	1.000	37	1.000
Kaingang	832	.721	316	.995	—	—	—	—
Karitiana	94	.644	89	1.000	72	1.000	87	1.000
Kraho	192	.698	190	1.000	191	.979	191	1.000
Macushi	1,001	.552	1,067	1.000	741	1.000	743	1.000
Makiritare	847	.440	624	1.000	407	1.000	409	1.000
Mapuche	393	.776	453	1.000	—	—	—	—
Mura	104	.486	104	1.000	103	1.000	103	1.000
Pacaas Novos	208	.817	215	1.000	221	1.000	221	1.000
Parakana	231	.452	217	1.000	116	1.000	116	1.000
Piaroa	362	.765	109	1.000	146	1.000	146	1.000
Satere-Mawe	245	.706	170	.994	168	1.000	168	1.000
Surui	62	.476	50	1.000	53	1.000	54	1.000
Ticuna	1,887	.663	1,777	1.000	1,765	1.000	1,765	1.000
Urubu-Kaapor	204	.730	193	1.000	189	1.000	191	1.000
Wai Wai	166	.609	166	1.000	154	1.000	159	1.000
Waiapi	230	.500	474	1.000	214	1.000	215	1.000
Wapishana	676	.496	700	.998	568	.981	569	1.000
Xavante	604	.485	722	1.000	75	1.000	81	1.000
Yanomama	3,426	.824	3,806	1.000	1,949	1.000	2,005	1.000

Tribe	N-MNSs	L*MS	L*Ms	L*NS	L*Ns	N-P	P*1
Apalai-Wayana	133	.250	.664	.039	.047	133	.406
Arara	—	—	—	—	—	60	.635
Arawete	89	.000	.759	.000	.241	89	.094
Asurini-Koatinemo	46	.309	.506	.071	.114	48	.441
Asurini-Trocara	102	.270	.598	.078	.054	104	.830
Aymara	740	.197	.468	.041	.294	2,573	.323
Ayoreo	454	.709	.256	.000	.035	359	.152
Baniwa	363	.198	.635	.080	.087	363	.473
Central Pano	113	.084	.646	.000	.270	108	.326
Cayapo	718	.216	.526	.042	.216	694	.571
Cinta Larga	106	.246	.665	.009	.080	106	.223
Guarani	34	.167	.377	.140	.316	34	.458
Icana Indians	145	.227	.625	.069	.079	137	.189
Jamamadi	38	.210	.329	.000	.461	38	.513
Kaingang	286	.462	.277	.123	.138	266	.363
Karitiana	88	.214	.507	.129	.150	89	.563
Kraho	189	.159	.555	.116	.170	190	.749
Macushi	1,252	.153	.548	.051	.248	1,254	.549
Makiritare	809	.314	.406	.139	.141	809	.433
Mapuche	806	.124	.509	.078	.289	554	.275
Mura	99	.270	.493	.064	.173	104	.573
Pacaas Novos	117	.517	.427	.056	.000	79	.497
Parakana	217	.233	.765	.000	.002	217	.743
Piaroa	255	.367	.539	.010	.084	257	.582
Satere-Mawe	105	.146	.768	.063	.023	170	.553
Surui	50	.167	.753	.003	.077	50	.163
Ticuna	1,869	.088	.802	.018	.092	1,876	.507
Urubu-Kaapor	190	.269	.599	.021	.111	194	.395
Wai Wai	166	.096	.446	.187	.271	166	.355
Waiapi	375	.302	.342	.186	.170	374	.300
Wapishana	762	.332	.473	.042	.153	644	.486
Xavante	596	.373	.395	.089	.143	623	.623
Yanomama	3,416	.168	.546	.028	.258	3,694	.394

APPENDIX. (continued)

Tribe	N-PGD	PGD*A	N-PGM1	PGM1*1	PGM1*2	N-PGM2	PGM2*1
Apalai-Wayana	125	.984	125	.696	.304	125	1.000
Arara	49	1.000	58	.543	.457	58	.914
Arawete	108	1.000	108	.630	.370	108	1.000
Asurini-Koatinemo	48	1.000	48	.677	.323	48	1.000
Asurini-Trocara	98	1.000	103	.966	.034	104	1.000
Aymara	1,379	.994	1,605	.784	.215	1,457	1.000
Ayoreo	175	1.000	185	.816	.184	183	1.000
Baniwa	363	1.000	363	.826	.174	363	1.000
Central Pano	335	1.000	335	.881	.119	335	1.000
Cayapo	238	1.000	653	.763	.237	632	1.000
Cinta Larga	107	1.000	105	.762	.238	105	1.000
Guarani	99	1.000	99	.828	.172	91	1.000
Icana Indians	154	1.000	154	.821	.179	154	1.000
Jamamadi	37	1.000	37	.595	.405	37	1.000
Kaingang	442	.992	444	.916	.082	211	1.000
Karitiana	87	1.000	87	.701	.299	87	1.000
Kraho	191	1.000	196	.775	.225	191	1.000
Macushi	696	.998	696	.816	.174	697	1.000
Makiritare	717	.992	721	.837	.163	185	1.000
Mapuche	—	—	101	.589	.411	93	.849
Mura	103	.990	103	.898	.102	103	1.000
Pacaas Novos	222	1.000	222	.669	.331	222	1.000
Parakana	212	.995	207	.978	.022	207	.998
Piaroa	267	1.000	267	.740	.260	146	1.000
Satere-Mawe	170	1.000	170	.959	.041	170	1.000
Surui	53	1.000	54	.704	.296	54	1.000
Ticuna	1,764	1.000	1,775	.829	.171	1,765	1.000
Urubu-Kaapor	188	1.000	188	.779	.221	188	.989
Wai Wai	166	1.000	165	.806	.194	—	—
Waiapi	372	1.000	372	.885	.111	373	.965
Wapishana	569	.989	569	.766	.234	569	1.000
Xavante	264	1.000	82	.853	.147	—	—
Yanomama	3,208	1.000	3,342	.954	.046	1,351	1.000

Tribe	N-RH	RH*RZ	RH*R1	RH*R2	RH*R0	N-TF	TF*C	TF*D
Apalai-Wayana	133	.119	.460	.317	.104	129	1.000	.000
Arara	60	.017	.766	.191	.026	68	1.000	.000
Arawete	110	.005	.177	.731	.087	112	1.000	.000
Asurini-Koatinemo	48	.155	.584	.199	.062	51	1.000	.000
Asurini-Trocara	124	.013	.572	.313	.102	128	.991	.009
Aymara	3,231	.048	.414	.468	.033	3,432	1.000	.000
Ayoreo	455	.006	.713	.279	.002	294	1.000	.000
Baniwa	363	.011	.591	.377	.021	377	.984	.016
Central Pano	113	.191	.331	.472	.006	128	1.000	.000
Cayapo	772	.044	.455	.453	.034	583	1.000	.000
Cinta Larga	106	.061	.788	.057	.094	91	1.000	.000
Guarani	31	.071	.719	.123	.087	129	1.000	.000
Icana Indians	140	.056	.365	.523	.056	148	1.000	.000
Jamamadi	38	.053	.815	.066	.066	37	1.000	.000
Kaingang	342	.078	.509	.327	.070	593	.999	.000
Karitiana	89	.006	.825	.135	.034	98	1.000	.000
Kraho	190	.000	.598	.355	.047	192	1.000	.000
Macushi	1,251	.028	.616	.345	.011	1,067	1.000	.000
Makiritare	810	.018	.390	.553	.039	776	1.000	.000
Mapuche	1,004	.025	.531	.304	.053	368	.993	.000
Mura	104	.026	.690	.180	.104	104	1.000	.000
Pacaas Novos	210	.049	.506	.232	.154	222	1.000	.000
Parakana	217	.027	.599	.157	.053	252	.998	.002
Piaroa	254	.006	.403	.559	.032	344	.941	.059
Satere-Mawe	185	.115	.615	.247	.023	170	1.000	.000
Surui	50	.031	.309	.299	.361	64	1.000	.000
Ticuna	1,876	.022	.651	.316	.011	1,887	.989	.011
Urubu-Kaapor	193	.055	.225	.707	.013	205	1.000	.000
Wai Wai	166	.124	.644	.132	.100	166	.949	.000
Waiapi	374	.099	.579	.319	.003	441	.948	.046
Wapishana	763	.043	.544	.368	.045	696	1.000	.000
Xavante	573	.044	.584	.316	.040	575	1.000	.000
Yanomama	3,806	.088	.808	.084	.020	3,680	1.000	.000

[1] The letter N before the system indicates the number of individuals studied.