

Failure of Linguistic Relationships to Predict Genetic Distances Between the Waiãpi and Other Tribes of Lower Amazonia

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ABSTRACT Data on blood group, serum protein, erythrocyte enzyme, and histocompatibility antigen (HLA) traits are presented for the Waiãpi, a Tupi-speaking tribe of the Brazilian and French Guianas. Intra- and intertribal comparisons have been made between these data, and previously published data from French Guiana, from another Tupi tribe and from other tribes of neighboring areas, and from the continent as a whole. For this purpose, we have modified the usual measure of genetic distance to obtain a value which is independent of the number of loci being considered. The intertribal genetic distances do not correlate with linguistic affinity. Social differences, which may have affected the rate of drift from the continental mean, correlate better with genetic distances.

The Indian populations of the tributaries of the lower Amazon speak languages which derive from at least four distinct roots—Tupi-Guarani, Carib, Arawak, and Ge (Loukotka, 1968). Languages belonging to the different linguistic groups are found geographically interspersed throughout the area. It has generally been assumed that the linguistic divisions correspond to patterns of origin and, hence, that they correlate with cultural and genetic relationships. Salzano et al. (1977) have shown that several Ge-speaking groups of Pará and Matto Grosso states of Brazil are separated by relatively short genetic distances. In this paper, we have put the theory of linguistic-genetic correlation to a rather rigorous test by focusing on the comparison of two widely separated Tupi tribes, the Waiãpi and the Parakanã, and on their neighbors (Fig. 1).

The Parakanã have been described previously (Black et al., 1980b). The Waiãpi are a linguistically defined tribe of Indians living on both sides of the Brazil-French Guiana border (Fig. 1). They represent one of the northernmost extensions of the Tupi-Guar-

ani linguistic family, which extends south to Argentina. The Waiãpi include three distinct social groupings: (1) the villages along the upper Oyapoque River, which forms the boundary between French Guiana and Brazil; (2) the villages of Amapari, Aramirã, and Nipuku (now Mariru) in the Brazilian territory of Amapá; and (3) the village of Molokopote on the Rio Jari in the Brazilian state of Pará. To distinguish the three groups, we will refer to them as the Waiãpi of Oyapoque, Amapá, and Molokopote. The three groups together we will refer to as a tribe. The name of the tribe has been spelled in various ways—Oyampi, Oiampi, Wajampi, Waiampi; we will use the anthropologically preferred orthography, "Waiãpi" (Campbell, 1976; Gallois, 1980).

This study utilizes new data on blood groups, serum proteins, and enzymes from the Amapá group and new HLA studies on the Amapá and Molokopote groups. These are compared to published data on: the Oyapoque group (Tchen et al., 1978a-c, 1981); the

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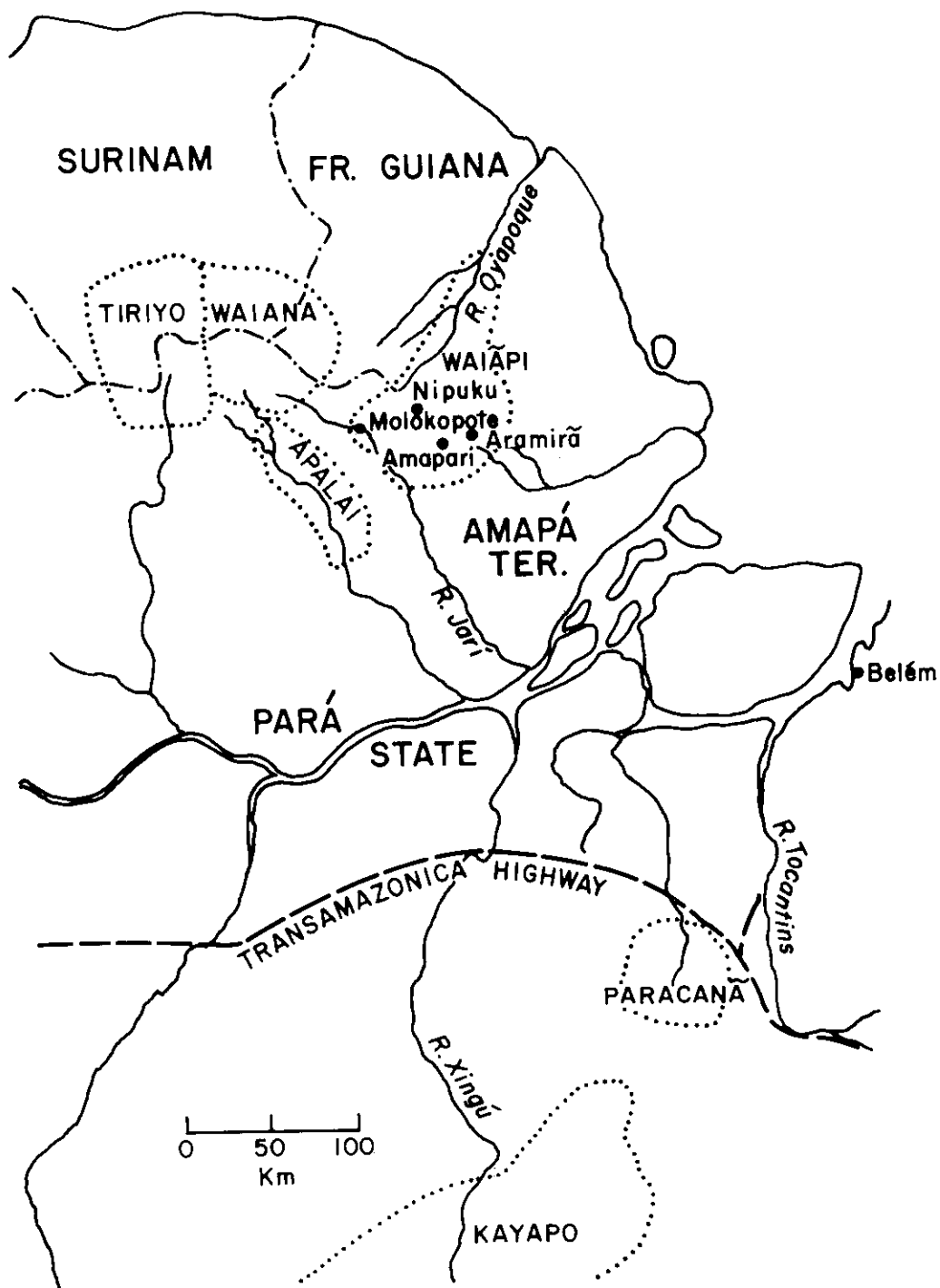


Fig. 1. Map of lower Amazonia and eastern Guianas showing the current territories of the tribes mentioned in this paper.

Parakanā, a tribe of about 200 members who live 800 km south of the Waiāpi (Black et al., 1980b); the Tiriyo (Salzano et al., 1974; Geerdink et al., 1974; Black et al., 1980a), a Carib group of about 1,000 persons living not far from the Waiāpi; and the Kayapo (Salzano et al., 1972a,b; Black et al., 1980a), members of a Ge-speaking cultural group of about 2,000 persons, who live adjacent to the Parakanā. Published HLA data on the Parakanā, Tiriyo, and Kayapo, have been supplemented with the results of recent tests to give some increase in number of observations and minor changes in gene frequencies. Comparisons are also made between the four tribes and the continental mean as given by an unweighted average of published data for 14 tribes: the Yupa (Layrisse and Wilbert, 1966), Bari (Layrisse et al., 1964), Warao (Wilbert and Layrisse, 1980), Makiritare (Gershowitz et al., 1970), and Yanomama (Gershowitz et al., 1972) of Venezuela, the Emerillon of French Guiana (Tchen et al., 1981), the Tiriyo (Salzano et al., 1974; Geerdink et al., 1974), Waiāpi (Tchen et al., 1981; present report), Parakanā (Black et al., 1980b), Kayapo (Salzano et al., 1972a; Salzano et al., 1977), and Ticuna (Neel et al., 1980) of Brazil, the Quechua of Peru (Matson et al., 1966; Tittor et al., 1973), and the Aymara (Ferrell et al., 1978), and Mapuche (Matson et al., 1967) of Chile.

Gallois (1980) has found references to what she believes were the progenitors of the Waiāpi in Jesuit records from the lower Xingu River area (south of the Amazon River) during the 17th century. Also, she located a reference to their presence on the Rio Jari during the 18th century. Tchen et al. (1978a) state that the Waiāpi have lived in French Guiana for more than two centuries. In attempting to trace the origins of the tribe, one must, however, recognize that although there may have been social continuity in this historic sequence, there may have been considerable genetic change through incorporation of persons from outside the original group. The patriarch of the Molokopote, who use the Waiāpi language, came, in fact, from the Apalai, a neighboring Carib-speaking group. Furthermore, one of his wives was from another Carib-speaking group. At the time of our study, 32% of the Molokopote genetic pool was derived, within two generations, from these Carib groups. There were 23 Molokopote when our specimens were collected

TABLE 1. Numbers of persons and test results included in the genetic comparisons

Tribe	Amapari	Amapá Nipuku	Waiāpi Aramirá	Oyapoque	Molokopote	Parakanā	Tiriyo	Kayapo	14 South American tribes
Social Village Population	112	84	17	312	23	200		2,000	
MNSs	90	33	12	240	—	100	632	686	8,611
Rh	90	33	12	239	—	100	632	740	8,664
P	90	33	12	239	—	100	632	694	8,618
Duffy	90	33	12	239	—	100	632	740	8,664
Diego	90	33	12	95	—	49	632	689	8,316
Transferrin	91	32	12	226	—	129	510	551	8,369
Haptogloblin	87	30	12	—	—	118	632	981	8,678
PGM ₁	90	33	12	237	—	93	411	583	8,277
PGM ₂	90	33	12	238	—	93	240	583	7,707
HLA-A	69	51	13	36	17	121	109	145	—
HLA-B	69	51	13	36	17	121	109	145	—
HLA-C	69	51	13	—	17	121	109	145	1,477

Tests:

in 1978, 213 in the Amapá group when specimens were collected from that group in 1980, and 312 along the Oyapoque when Tchen's samples were collected in 1976.

The Waiápi language has been cataloged by Olson (1974) and it is clearly Tupi derived, although the Waiápi and Parakanã languages are not mutually intelligible. Campbell (1976) has noted that differences in dialect exist between the Amapá and Oyapoque groups. Two women at Nipulku came from Oyapoque, but otherwise all inhabitants of Amapá were born there. Culturally, the Waiápi show more similarities to the neighboring Carib tribes than to the Parakanã. Cross-cousin marriages are preferred instead of the uncle-niece patterns of the Parakanã. Manioc-processing methods, weapons, housing, and dress all resemble the Tiriyo more than the Parakanã.

METHODS

Technical methods for determination of genetic characteristics were unchanged from those of previous studies (Black et al., 1980a,b). Because of the difficulties commonly encountered in distinguishing the related HLA types AW30, AW31, and AW32; BW38 and BW39; and BW51 and BW52, these antigen splits are not used in genetic distance comparisons, but their antigenic groups are referred to as A19, B16, and B5, respectively. The number of individual tests included in genetic distance analyses are given in Table 1. Immunoglobulin allotypes were determined by the method of Vyas et al. (1968) using antisera for Gm 1, 2, 3, 5, 6, 13, 17, and 21 and Km (1) (Pandey et al., 1982).

Genetic distance was determined by a modification of the chord measurement of Cavalli-Sforza and Edwards (C-S, E) (1967). In the original formula, the distance measured at individual loci, D_i , is calculated by:

$$D_i = 2 \frac{\sqrt{2}}{\pi} \sqrt{1 - \sum \sqrt{p'p''}}$$

where p' and p'' are the gene frequencies for each allele in the two populations being compared. Multiallelic loci can vary in multiple dimensions and distances between populations calculated by the C-S, E method are greater when multiallelic traits are used than when based on biallelic loci (da Rocha et al., 1974).

To calculate a combined distance based on several loci, D_c , the C-S, E procedure simply

utilizes the root of the sum of the squares of the D_i value for each locus. This procedure gives larger D_c values when the number of loci is increased. The combined distance calculated by the C-S, E formula will thus vary according to the type and number of loci included.

Each allele in the systems included in this study has the same potential range of gene frequency, 0 to 1; that is, there is no evidence of a mechanism which would prevent loss of any allele from a whole population. Where there are two alleles, the locus has only one degree of freedom, but when there are three alleles an extra dimension is added to the range of variation between two populations (Edwards, 1971). The total possible difference between these two populations is then equal to the hypotenuse of a triangle with the dimensions of the two sides equal to 1, i.e., the range is from 0 to $\sqrt{2}$. Similarly, when there are four alleles and three degrees of freedom, the range is the hypotenuse of a triangle with sides 1 and $\sqrt{2}$; it is thus equal to $\sqrt{3}$. With five alleles the range extends to $\sqrt{4}$, etc. To convert the C-S, E distances for individual loci to comparable units, we have divided each by $\sqrt{A-1}$ where A is the number of alleles expressed at that locus in the two populations being compared.

Having reduced distances for bi- and multi-allelic loci to a common unit, we now wanted to weight the multiallelic data in calculating combined distances. Accordingly, the square of the distance for each locus is multiplied by $A-1$, the total summed, and divided by the sum of all $A-1$ s, before the root is taken as in the C-S, E procedure:

$$D_c = \sqrt{\frac{\sum [D_i^2 (A_i - 1)]}{\sum (A_i - 1)}}$$

This procedure not only provides a measure of distance which weights the contributions of each degree of freedom equally, but it has the added advantage of restoring to the combined distance estimate a characteristic of single biallelic locus distances by which a value of 1.0 indicates no relationship, and all other values fall between 1.0 and zero.

Because comparison data for this study have been garnered from several sources, the loci on which we have information differ from one population to another. We have calculated distances based on common loci (MNSs, Rh, P, Duffy, and HLA-B), but to strengthen the basis of the comparisons at each popula-

tion level (intervillage, intertribe, etc.) we have also used expanded data sets with all information available for each level.

A special case arises in the systems with multiple linked loci. Crossovers within the MNSs and Rh system are sufficiently rare that it is most appropriate to treat each haplotype as an allele, and to take, as the total number of alleles, the number of haplotypes represented with substantial (>1%) frequency in any of the populations being compared. Crossovers in the HLA system are more frequent, but linkage disequilibrium is sufficiently strong that a role for selection in determining haplotype frequency cannot be excluded. We have used HLA haplotype data for comparisons within those population levels where this data is available, but used only the HLA-B frequencies for comparisons to the continental mean and for the common locus comparisons. It must be noted that analysis by HLA haplotype measures divergence during the few thousand years over which the founders' haplotypes would persist without crossover (Mourant, 1980), whereas analysis by HLA antigens measures divergence over the much longer period required for mutations to change genetic constitution. In spite of this difference, the mean D_i for the haplotypes, 0.118, is only slightly greater than that for the same data calculated by individual antigens, 0.101.

RESULTS

The results of genetic tests of the Amapá group and of HLA tests for each tribe are given in Tables 2 and 3. As is usual in South American Indian populations with little or no post-Columbian admixture, the genes I^c , k , AK^1 , $Gd(+)$ B, and ADA^1 all had frequencies of 1.00 in the Waiāpi of Amapá; neither did the Amapá nor the Molokopote groups have any HLA or Gm antigen not previously found in Indian tribes without non-Indian admixture.

The frequency of the P^1 gene in Amapá is one of the lowest recorded in any South American Indian population. The frequency of the Tfd^{Chi} gene (0.07) is the highest ever recorded in Brazil. It reflects well the frequency of 0.033 found by Tchen et al. (1978b) in the Oyapoque group, and echoes higher values previously found in northern South America (Arends and Gallango, 1964, 1965). The HLA antigens AW30 and CW1 occur in relatively high frequency in the Warao of eastern Venezuela (Layrresse et al., 1976); they have also been found, but only at very low

frequency, in a few other Brazilian tribes (Black et al., 1980b; Lawrence et al., 1980). The AW32 gene has previously been found in one Parakanā who had an Asurini mother (also Tupi) as well as in the Mapuche of Chile (Black et al., 1980a). Only two Gm haplotypes were found in the tribe, the same two as occur in high frequency in other South American tribes (Salzano et al., 1973). Similarly, at least two Km allotypes are represented and Km^1 comprises a major part of the total.

Estimated relative genetic distances are given in Table 4. The central comparison, that of the two Tupi-speaking tribes to each other and to their neighbors, is consistent in that most individual distance measurements, as well as the means, show greater proximity between geographic neighbors, Waiāpi-Tiriyo and Parakanā-Kayapo, than between the linguistic affines, Waiāpi-Parakanā. Because of the similar trends at individual loci, D_c values calculated for common loci and for all loci are generally parallel. It is notable that the distance between the Tiriyo and Kayapo, which share neither geographic nor linguistic proximity, is as short or shorter than that between any other pair of tribes.

The average pairwise distance between tribes, 0.134, is not appreciably greater than the average distance between the Amapá villages, 0.128, even though we know that many individuals in different villages have common parents or grandparents. Apparently, the effect of drift in the small village populations is sufficiently stronger than in the larger tribal populations to counterbalance the effects of common recent ancestry.

With respect to divergence from the continental mean gene frequencies, the Parakanā have moved a substantially greater distance than any of the other tribes.

DISCUSSION

The data available for this study did not regularly include information on the Kidd system and, therefore, we have been unable to utilize the widely employed "6-locus genetic distance" (Neel and Ward, 1970). Nevertheless, we did wish to be able to make comparisons to findings already in the literature. For this reason, we have developed a modification of the original Cavalli-Sforza and Edward (1967) genetic distance measurement which reduces estimates from multi-allelic loci to the same scale as biallelic data and permits different numbers of loci to be

TABLE 2. Blood group, serum proteins, immunoglobulin allotypes, and erythrocytic enzyme phenotypes and gene frequencies in the Waiãpi of Amapá, Brazil

System	No. tested	Phenotypes found	Number found	Gene	Frequency		
ABO	135	O	135	I ^O	1.00		
MNSs	135	MS	23	L ^{MS}	0.38		
		MSs	25	L ^{Ms}	0.31		
		Ms	18	L ^{NS}	0.02		
		NS	15	L ^{Ns}	0.29		
		MNS	3				
		MNSs	30				
P	135	MNs	21				
		P ₁	56	P ¹	0.24		
Rh	135	P ₂	79				
		CDe	30	R ¹	0.50		
		CcDEe	77	R ²	0.49		
		CcDE	1	R ^Z	0.01		
Kell	135	cDE	27				
		K-	135	k	1.00		
Duffy	135	a+	129	Fy ^a	0.79		
		a-	6				
Diego	33	a+	5	Di ^a	0.08		
		a-	28				
Hemoglobin	135	HbA	135	Hb ^A	1.00		
		G6PD	Males: 68 Females: 63	Gd(+)B	Gd ^b	1.00	
6PGD	135	Pd A	135	PGD ^A	1.00		
		Phosphoglucosmutase ₁	135	1-1	PGM ₁ ¹	0.91	
				2-1		22	
Phosphoglucosmutase ₂	135			2-2	1		
				1-1	135	PGM ₂ ¹	1.00
				1-1	135	AK ¹	1.00
Adenylate kinase	135			1-1	135	ADA ¹	1.00
				1-1	29	Hp ¹	0.51
Adenosine deaminase	135			2-1	73		
				2-2	27		
				0	6		
Haptoglobin	135			C	118	Tf ^D _{Chi}	0.07
				CD _{Chi}	16		
				D _{Chi}	1		
Transferrin	135	B	135	Cp ^B	1.00		
				A	135	Aj ^A	1.00
Ceruloplasmin	135			1,17;21	59	Gm ^{1,17,21}	0.67
				1,2,17;21	74	Gm ^{1,2,17,21}	0.33
Albumin	133			Km(1)+	88	Km ¹	0.41
				Km(1)-	46		
Gm	134						

TABLE 3. Gene Frequencies for HLA antigens in the tribes being compared

Antigens	133 Amapá	17 Molokopote	121 Parakanã	109 Tiriyó	145 Kayapo	All S. Am. Indians
HLA-A2	0.248	0.375	0.269	0.379	0.441	0.410
W24	0.372	0.375	0.049	0.237	0.090	0.237
28	0.290	0	0.234	0.089	0.069	0.111
W30	0.023	0	0	0	0	0.005
W31	0.068	0	0.443	0.291	0.410	0.209
W32	0	0.249	0.004	0	0	0.008
HLA-B5	0.169	0	0	0.089	0.041	0.157
15	0.120	0	0.020	0.093	0.276	0.161
W35	0.398	0.562	0.506	0.423	0.417	0.272
W39	0.124	0.218	0.218	0.217	0.156	0.208*
40	0.188	0.218	0.256	0.169	0.110	0.201
CW1	0.030	0.062	0	0	0	0.027
W3	0.402	0.375	0.314	0.272	0.386	0.331
W4	0.274	0.342	0.462	0.429	0.438	0.332
B1	0.293	0.218	0.220	0.299	0.176	0.296

*All B16 splits combined.

TABLE 4. Genetic distances between villages, social groups, tribes, and tribes relative to the continental mean¹

System	Intervillage				Social groups		Intertribal						Distance from continental mean					
	DF	Amapari -Nipuku	Amapari -Aramirã	Nipuku -Aramirã	DF	Amapã -Oyapoque	DF	Waiãpi -Tiriyó	Waiãpi -Parakanã	Waiãpi -Kayapo	Tiriyó -Kayapo	Tiriyó -Parakanã	Parakanã -Kayapo	DF	Waiãpi	Tiriyó	Parakanã	Kayapo
<i>D_i</i>																		
MNSs	3	0.138	0.075	0.238	3	0.125	3	0.106	0.254	0.092	0.033	0.212	0.197	3	0.075	0.044	0.214	0.044
Rh	2	0.045	0.067	0.003	2	0.189	5	0.072	0.155	0.069	0.080	0.146	0.158	5	0.052	0.058	0.124	0.049
P	1	0.032	0.044	0.011	1	0.072	1	0.077	0.247	0.178	0.102	0.171	0.069	1	0.001	0.018	0.153	0.084
Duffy	1	0.304	0.078	0.374	1	0.074	1	0.072	0.348	0.004	0.068	0.278	0.344	1	0.008	0.078	0.354	0.011
Transferrin	1	0.010	0.040	0.028	1	0.050												
Haptoglobin	1	0.075	0.136	0.211			1	0.118	0.100	0.038	0.080	0.216	0.136					
Diego					1	0.200	1	0.104	0.091	0.028	0.076	0.194	0.118	1	0.092	0.012	0.182	0.064
PGM ₁					1	0.041	1	0.065	0.138	0.106	0.041	0.202	0.234					
PGM ₂					1	0.150	1	0.083	0.075	0.120	0.202	0.157	0.045					
HLA haplotype	16	0.133	0.113	0.127	14	0.180	26	0.105	0.130	0.119	0.076	0.110	0.107					
HLA-B														4	0.115	0.128	0.156	0.145
<i>D_c</i>																		
All loci	25	0.133	0.102	0.157	25	0.161	40	0.099	0.156	0.109	0.080	0.142	0.137	15	0.078	0.079	0.181	0.087
Common loci	14	0.115	0.099	0.169	14	0.168	14	0.077	0.206	0.095	0.077	0.170	0.181	14	0.077	0.082	0.181	0.088

¹DF, degrees of freedom; *D_i*, distance by individual system; *D_c*, combined distance by multiple systems.

compared on a common scale. In as much as locus heterogeneity may still distort distances based on different comparisons (Robertson, 1975), we have standardized the loci used within each of our basic comparison groups: i.e., intervillage, intertribe, etc., and also calculated distances based on a set of characteristics common to all groups.

Locus heterogeneity is not a serious problem within the present data. The greatest distances, as for instance that between the Waiãpi and Parakanã, are manifest by relatively large distances measured by most individual loci, and the short distance between the Tiriyo and Kayapo is consistent for all except the PGM₂ system. If, then, we set this problem aside for the moment, we can adjust the six-locus data to a scale comparable to ours by dividing those values by $\sqrt{\sqrt{3} + \sqrt{4} + 4}$, or 2.781. On this basis, the mean pairwise distance between the three Amapá villages is similar to the mean distances between villages of the Yanomama and Makiritare (Neel and Ward, 1970), but substantially greater than the Kayapo (Salzano et al., 1977) or Ticuna (Neel et al., 1980) intervillage distances. The mean pairwise distance between the four tribes we have studied is, again, not very different from the distances between the 12 tribes studied by Neel and Ward, but substantially less than the distances between the four widely dispersed tribes studied by da Rocha et al. (1974). The average distance from the continental mean of the four tribes of lower Amazonia, 0.106, is also less than the mean distance of 23 more dispersed tribes considered by Neel et al. (1980).

Linguistic classification has been a convenient and widely used tool in the study of Amazonian tribes, although all serious students of the area have been aware of its limitations. The failure of a linguistic relationship to predict genetic distance in this study is surprising, therefore, not because it was found, but because of its totality. The linguistically related pair are less closely related genetically than any other pair. To explain this, one must look for factors which have increased the separation of the Tupi tribes.

Geographically, they are separated not only by a great distance, but also by the Amazon river and its marshy lowlands which, for several centuries, have been inhabited by cosmopolitan cultures. Nevertheless, the Tiriyo are separated from the Kayapo by the same geography and they remain genetically close.

A factor which correlates better is the distance and direction in which these tribes have drifted from the continental mean. The Parakanã are a rather retiring and nonbelligose tribe, which has rarely incorporated captives from other groups into its membership. This characteristic, coupled with the small size of the tribe, the high degree of polygamy, and their preferred uncle-niece marriages, has doubtless hastened the process of drift within the group. The Waiãpi too, at least in recent decades, have been less bellicose than the Tiriyo or Kayapo. Their proximity to the continental mean implies that they must have incorporated persons from diverse groups into their membership, if not by warfare, then, perhaps, as at Molokopote, by peaceful fusion. The fact that they carry traits more characteristic of the tribes of northern South America than of Brazil suggests that some of this admixture has come from this non-Tupi area. The Tiriyo and Kayapo have countered the effects of drift by taking women and children from other tribes and incorporating them into their membership.

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