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A Genetic Study of Two French Guiana Amerindian Populations

I. Serum Proteins and Red Cell Enzymes

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Summary. Phenotypes and gene frequencies are presented for 20 serum and erythrocyte proteins in two Amerindian populations of inner French Guiana. No genetic variability was detected in 12 of these systems. Heterozygosity was calculated for the others and the reasons for its variation are discussed.

The French Guiana Amerindian populations may be divided into two groups: those of the coastal and those of the interior. The Arawak and the Palikour, who speak an Arawakan language, and the Galibi, Carib speaking, live on the coast. The Wayana, who speak a Carib language, the Wayampi, and the Emerillon live in the interior. The latter two groups belong to the Tupi-Guarani linguistic family.

Whereas the coastal populations have acquired some non-Indian characteristics, those of the interior may be considered as pure Amerindians, particularly the Wayampi and the Emerillon. These populations have a culture and a mode of life adapted to their survival in the tropical forest. They practice slash and burn agriculture, hunting, fishing, and food gathering. It has been frequently emphasized that it is an urgent task to study such populations before their structure is greatly modified by the Western industrial mode of life. A better understanding of human evolution and of the interrelationship between man and the environment may emerge from a consideration of the past studies and from those yet to be undertaken.

During a genetic survey in August 1976, blood samples of nearly all the Wayampi and Emerillon of French Guiana were collected and studied for several genetic markers. Data on the HLA antigens have been published elsewhere (Tchen et al., 1978a). We report here the analysis of the serum proteins and red cell enzymes.

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Subjects and Methods

Populations

In August 1976, the Wayampi of French Guiana numbered 310, 180 living in the Trois-Sauts area, the others in the Camopi area (Fig. 1). Part of the Wayampi population, numbering about 100, live in Brazil on the river Kouk.

At the same time, the Emerillon population numbered 121, 96 of whom lived in the Camopi area, the others on the Tanpok, a tributary of the Maroni river. These two populations have lived in the same area for more than three centuries, with no non-Indian admixture and rare intertribal marriages (Grenand, 1972). Genealogies up to seven generations were ascertained from ethnologic studies. For the analysis of serum proteins and red cell enzymes, 238 blood samples of the Wayampi and 55 of the Emerillon were used.

Typings

Blood samples were drawn in vacuum tubes containing EDTA-Na_2 as anticoagulant. The samples were chilled immediately and sent by air to Paris where they arrived within 48 h of collection. Erythrocytes and plasma were then separated and kept respectively in liquid nitrogen and at −80° C.

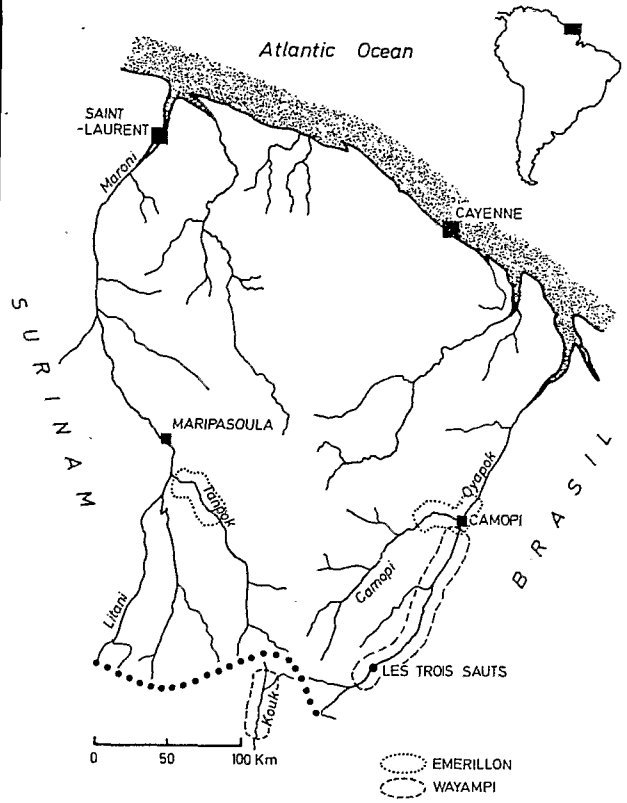

Fig. 1. French Guiana. Tribal distribution of the Emerillon and Wayampi

The following systems were studied:

1. Serum Proteins. Albumin (Alb), complement component (C3), group-specific component (Gc), and transferrin (Tf). Albumin was studied using high-voltage agarose gel electrophoresis at pH = 8.6, with a running time of 1 h. Transferrin was studied conjointly with C3 complement fraction according to Teisberg's technique (1970). Group-specific component typing was also carried out according to Teisberg's technique (1970). Subsequent immunofixation was carried out according to the method of Alper and Johnson (1969).

2. Erythrocyte Proteins. Acid phosphatase 1 (AcP 1), adenosine deaminase (ADA), adenylate kinase 1 (AK_1), esterase D (Est D), soluble glutamic-pyruvic transaminase (GPT), hemoglobin (Hb), isocitrate dehydrogenase (ICDH), lactate dehydrogenase A and B (LDH), malate dehydrogenase (MDH), peptidase A (Pep A), peptidase B (Pep B), phosphoglucomutase 1 (PGM_1), phosphoglucomutase 2 (PGM_2), 6-phosphogluconate dehydrogenase (6-PGD), phosphohexose isomerase (PHI), and superoxide dismutase (SOD, also called 'oxidase').

Packed red cells were lysed by freezing for GPT, by the addition of one volume of 2/1000 2-mercaptoethanol followed by freezing for AcP 1 and ADA, and by the addition of one volume of distilled water for the other enzymes.

All the proteins were studied by horizontal starch gel electrophoresis at 4° C. The techniques used have been described by Hopkinson et al. (1963) for AcP 1, Fildes and Harris (1966) for AK 1, Smithies (1955) for Hb, Chen et al. (1972a) for ICDH, Blake et al. (1969) for LDH, Sinha and Hopkinson (1969) for Pep A, Lewis and Harris (1967) for Pep B, and Fildes and Parr (1963) for 6-PGD. For ADA we used the techniques described by Spencer et al. (1968), but with the phosphate buffer system at pH = 6.5 and phosphate buffer at pH = 7.5 for staining. Est D was studied using the technique described by Hopkinson et al. (1973) with the Tris-maleate buffer at pH = 7.4 and 4-methyl-umbelliferyl acetate for staining. GPT was studied using the technique described by Gussman and Rames (1972), with a buffer identical to that of PGM, but with nondiluted packed cells applied on Whatman 17 and a running time of 22 h at 6 V/cm. MDH was visualized on the same gel as LDH by adding 20 mg of *L*-malic acid per gel as substrate. The phosphoglucomutase isoenzymes were studied by horizontal starch gel electrophoresis at 6 V/cm according to the techniques described by Spencer et al. (1964), but using a dilution of 1/20 for the gel, which gave a better resolution than the dilution of 1/10 initially described, with a running time of 20 h, and hemolysate on Whatman 17 for paper inserts.

For SOD, the achromatic zones described by Brewer (1967) on tetrazolium stained gels were clearly visible on all gels stained for ICDH or 6-PGD. No special reactant was used.

Phosphohexose isomerase was studied by the techniques described by Detter et al. (1968), using the Tris-citric acid buffer (bridge buffer: 0.25 M Tris and 0.057 M citric acid; gel buffer: 0.017 M Tris and 0.0032 M citric acid).

Gene Frequencies

The frequencies were calculated by gene counting without excluding relatives, since a rather large sample from each population was studied (superior to 36% in all cases except Gc protein in the Emerillon: 12%). Standard deviation was calculated, using the formula:

$$SD = \sqrt{\frac{pq}{n} \cdot \frac{N-n}{N-1}}$$

with p and q = frequencies observed,
n = size of the sample,
N = size of the population.

Heterozygosity

The heterozygosity at each locus was calculated using the formula:

$$H = 1 - \sum_{i=1}^{n} p_i^2$$

with p_i = gene frequency of allele i
n = number of alleles at the locus.

Results and Discussion

Monomorphic Systems

No polymorphism was found for the following 12 systems: Alb, C_3, Hb, ADA, ICDH, LDH, MDH, Pep A, Pep B, 6-PGD, PHI, SOD.

Table 1 gives the number of tests performed for each protein in the two populations. Among these proteins, C_3, Hb, ADA, and 6-PGD are known to be polymorphic in some populations (Giblett, 1969). The alleles found here are: C_3 2, Hb A, ADA 1, and 6-PGD A. The C_3 polymorphism, first described in 1965 (Ropartz et al.), has not, to our knowledge, been investigated in other Amerindians. Rare variants of Alb, LDH, and 6-PGD have been found in middle or South Amerindians by some authors (Bowman et al., 1966; Weitkamp et al., 1968, 1970, 1972a and b; Arends et al., 1969, 1970; Harvey et al., 1969; Tanis et al., 1973, 1974, 1977; Geerdink et al., 1974; Vergnes et al., 1976a; Neel et al., 1977). In the case of albumin one should point out that the possibility of finding a variant often depends upon the technique used. With our technique, which was used principally to detect analbuminemia, many of the variants already described could not be detected. Unfortunately we had no possibility of making further investigations.

Polymorphic Systems

Table 2 gives the frequencies of the various alleles for the proteins presenting a polymorphism, together with the number of phenotypes observed and expected in the case of the Hardy-Weinberg equilibrium. The frequencies found are similar to those already published for other Amerindian populations.

In four systems (AK_1, PGM_1, PGM_2, and Tf) rare variants have been identified; these variants are described in a following paper (Tchen et al., 1978b).

Table 1. Monomorphic systems in Emerillon and Wayampi

System	Allele	Total typed	
		Emerillon	Wayampi
Albumin	Normal	51	226
C3	2	47	226
Hemoglobin	A	48	213
ADA	1	55	237
ICDH	Normal	49	219
LDH A and B	Normal	49	219
MDH	Normal	49	219
Pep A	Normal	48	214
Pep B	Normal	48	215
6-PGD	A	55	237
PHI	Normal	49	219
SOD	Normal	49	219

Table 2. Polymorphic systems in Emerillon and Wayampi

System		Emerillon		Wayampi	
		Observed	Expected	Observed	Expected
AcP 1: Phenotypes:	A	—	0.6	—	4.6
	B-A	11	9.8	65	56.1
	B	39	39.6	168	172.3
Total		50	50	233	233
Gene frequencies (SD):	AcP 1 A	0.11 (0.03)		0.14 (0.02)	
	AcP 1 B	0.89 (0.03)		0.86 (0.02)	
AK_1: Phenotypes:	1	55	55	226	224.2
	3-1	—	—	10	13.6
	3	—	—	2	0.2
Total		55	55	238	238
Gene frequencies (SD):	AK_1 1	1		0.97 (0.01)	
	AK_1 2	—		0.03 (0.01)	
Est D: Phenotypes:	1	28	27.0	186	184.3
	2-1	21	23.0	49	52.3
	2	6	5.0	3	3.4
Total		55	55	238	238
Gene frequencies (SD):	Est D 1	0.70 (0.04)		0.88 (0.01)	
	Est D 2	0.30 (0.04)		0.12 (0.01)	
Gc: Phenotypes:	1	8	7.9	82	82.1
	2-1	5	5.2	28	26.7
	2	1	0.9	1	2.2
Total		14	14	111	111
Gene frequencies (SD):	Gc 1	0.75 (0.08)		0.86 (0.02)	
	Gc 2	0.25 (0.08)		0.14 (0.02)	
GPT: Phenotypes:	1	9	8.7	38	49.1
	2-1	22	23.0	136	115.3
	2	16	15.3	58	67.6
Total		47	47	232	232
				$\chi^2_{(2df)} = 7.59$	$P < 0.023$
Gene frequencies (SD):	GPT 1	0.43 (0.05)		0.46 (0.02)	
	GPT 2	0.57 (0.05)		0.54 (0.02)	
PGM_1: Phenotypes:	1	55	55	180	179.4
	2-1	—	—	51	49.5
	2	—	—	3	3.4
	(4/10)-1	—	—	2	4.1
	(4/10)-2	—	—	1	0.6
Total		55	55	237	237

Table 2 (continued)

System		Emerillon		Wayampi	
		Observed	Expected	Observed	Expected
Gene frequencies (SD):	PGM_1 1	1		0.87 (0.015)	
	PGM_1 2	—		0.12 (0.015)	
	PGM_1 (4/10)	—		0.01 (0.005)	
PGM_2: Phenotypes:	1	51	50.7	213	214.8
	6–1	4	4.2	24	22.6
	6	—	0.1	1	0.6
Total		55	55	238	238
Gene frequencies (SD):	PGM_2 1	0.96 (0.02)		0.95 (0.01)	
	PGM_2 6	0.04 (0.02)		0.05 (0.01)	
Tf: Phenotypes:	C	52	52	211	212.6
	D-C	—	—	15	13.2
	D	—	—	—	0.2
Total		52	52	226	226
Gene frequencies (SD):	Tf C	1		0.97 (0.01)	
	Tf D	—		0.03 (0.01)	

For GPT, there is a marked deviation from the Hardy-Weinberg equilibrium in the Wayampi tribe, with an excess of heterozygotes. This phenomenon is unexplained, but may be due only to chance.

Few studies of this system have been made; it is one of the few known to be polymorphic in Amerindian populations. Table 3 summarizes the results which we found in the literature for Amerindians.

The Amerindians are generally considered to have less diverse genetic features than other populations. One measure of this characteristic is the average heterozygosity per locus (Harris, 1966; Lewontin and Hubby, 1966; Lewontin, 1967). We calculated the mean heterozygosity on 5, 7, and 9 loci for 16, 10, and 6

ble 3. GPT system in Amerindians: allele frequencies and heterozygosity

pulation	Total typed	Allele		H	Authors
		GPT_1	GPT_2		
ee Indians (Canada)	194	0.43	0.57	0.49	Lucciola et al. (1974)
nada Indians	69	0.54	0.46	0.50	Chen et al. (1972b)
uvian Indians	44	0.57	0.43	0.49	Chen et al. (1972b)
ra (Chile)	102	0.41	0.59	0.48	Van der Does et al. (1972)
mpi (French Guiana)	232	0.46	0.54	0.50	Present study
rillon (French Guiana)	47	0.43	0.57	0.49	Present study
a (Venezuela)	91	0.47	0.53	0.50	Tchen et al. (1979)

Amerindian populations respectively, from data found in the literature (Tanis et al., 1973, 1977; Vergnes et al., 1976b; Neel et al., 1977) and from our own data. The systems chosen were those which had been studied on the largest number of Central and South Amerindian populations. Table 4 gives the values obtained, together with the values calculated for three African populations and for the French population in order to draw a comparison. The approximate size of the populations is also indicated.

The mean heterozygosity in the Amerindians is inferior to that of the French population. In most cases, it is also inferior to that of the three African populations for which we have recent data, even when compared with the values of the Pygmies, who are similar to the Amerindians in terms of their habitat, mode of life, and genetic isolation.

If one considers that the Amerindians have lived in isolation for more than 20,000 years, this higher homogeneity can be explained by a genetic drift causing the loss of the less frequent alleles. Nevertheless, random genetic drift alone is not a satisfactory explanation for the polymorphism currently observed. In fact, one expects to find a lower heterozygosity in the smaller populations resulting from a more rapid disappearance of the less common alleles, which is not always the case. For example, the Yanomama tribe which is estimated at 15,000 individuals, has a much lower heterozygosity than the Wayampi, who number less than 500.

It should be noted that, when one considers all the loci studied, five of them—Est D, Gc, AcP, PGM_1 (Table 4), and GPT (Table 3)—play a leading role in the variation of mean heterozygosities observed in the Amerindians. These systems also make a preponderant contribution to heterozygosity in all the populations of the world.

One possible explanation for this variation in heterozygosities between different loci is a variation in the molecular evolution rates of different proteins (Harris, 1975). An alternative explanation could be the existence of a balanced polymorphism, or some other action of natural selection in those systems which have a high heterozygosity. While no definite proof of this has yet been found, several studies have been made showing that natural selection may play a role in some of these systems.

In a study on the geographic variability of the red cell PGM_1 and acid phosphatase gene frequencies, Walter (1976) found that the P^a and P^b alleles showed significant correlations with the mean annual temperatures of the various human biotopes. He concluded that these correlations may reflect the operation of factors acting selectively in the AcP system. PGM_1 alleles did not show a comparable correlation. In this system, selection might act by incompatibility effects (Ananthakrishnan et al., 1973), but this would be contrary to the maintenance of a polymorphism.

For the Gc system, Mourant et al. (1976) showed in an empirical study that the frequency of Gc 2 allele is generally 'low in areas of high insolation and high where there is little sunshine.' This study followed the discovery by Daiger et al. (1975) that the Gc proteins of human plasma act as the carriers of vitamin D. Even if it is unproved that Gc distribution is causally related to sunlight intensity, this may be an explanation for a natural selection in the Gc system.

Table 4. Heterozygosity at various loci

Population	(Authors)	Locus					Total of the 5 loci	Mean of the 5 loci
		AK_1	6-PGD	AcP 1	PGM_1	PGM_2		
Yanomama	(1)	0	0	0.02	0.10	0	0.12	0.024
Makiritare	(1)	0	0	0.10	0.27	0	0.37	0.074
Piaroa	(1)	0	0	0.35	0.38	0	0.73	0.146
Macushi	(2)	0	0	0.05	0.29	0	0.34	0.068
Wapishana	(2)	0	0.02	0.11	0.35	0	0.48	0.096
Cayapo	(1)	0	0	0.39	0.35	0	0.74	0.148
Guaymi	(3)	0	0.16	0.34	0.10	0	0.60	0.120
Jicaque	(4)	0	0	0.51	0.01	0	0.52	0.104
Mataco	(4)	0	0	0.10	0.37	0	0.47	0.094
Chorote	(4)	0	0	0.15	0.38	0	0.53	0.106
Chipaya	(4)	0	0	0.32	0.09	0	0.41	0.082
Sirionos	(4)	0	0.37	0.01	0.50	0	0.88	0.176
Aymara	(4)	0	0	0.33	0.36	0	0.69	0.138
Emerillon		0	0	0.20	0	0.08	0.28	0.056
Wayampi		0.06	0	0.24	0.23	0.10	0.63	0.126
Cuiva	(5)	0	0	0.47	0	0	0.47	0.094
Obamba (Gabon)	(6)	0	0.07	0.37	0.30	0.03	0.77	0.154
Bateke (Gabon)	(6)	0	0.13	0.36	0.30	0.01	0.80	0.160
Pygmies	(6)	0	0.04	0.19	0.29	0.11	0.63	0.126
France	(6)	0.07	0.05	0.50	0.39	0	1.01	0.202

Authors: (1) Tanis et al. (1973); (2) Tanis et al. (1973) and Neel et al. (1977); (3) Tanis et al. (1977);

For GPT, following the finding of a significant deviation from the expected Hardy-Weinberg equilibrium in the Wayampi tribe, we checked the data given by Blake (1976) for 69 population groups. We found significant deviations in nine cases: three with an excess of heterozygotes and six with an excess of homozygotes. The reasons for these discrepancies are unclear.

If there is some kind of natural selection in the systems mentioned above, those with low heterozygosity would be selectively neutral. For them, homogeneity would have been reached fairly rapidly by a random genetic drift in most of the Amerindian populations, the heterozygosity observed nowadays at these loci being maintained by mutation pressure or being a vestige of an initial polymorphism of the Amerindians' ancestors.

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ADA	Tf	Total of the 7 loci	Mean of the 7 loci	Est D	Gc	Total of the 9 loci	Mean of the 9 loci	Population size
0	0	0.12	0.017	0.24[a]	0.23	0.59	0.066	15,000
0	0	0.37	0.053	0.35[a]	0.28	1	0.111	2000
0	0.17	0.90	0.129	—	0.30	—	—	?
0	0	0.34	0.049	0.43	0.12	0.89	0.099	4000
0	0	0.48	0.069	0.32	0.30	1.10	0.122	2000
0	0	0.74	0.106	—	0.47	—	—	1500
0	0.13	0.73	0.104	0.04	—	—	—	30,000
								500
								?
								?
				—	0.13	—	—	<1000
								1000
				—	0.30	—	—	800
0	0	0.28	0.040	0.42	0.49	1.19	0.132	<200
0	0.06	0.69	0.099	0.21	0.50	1.40	0.156	<500
0	0	0.47	0.067	0	—	—	—	<500
0	0.11	0.88	0.126	0.14	—	—	—	8000
0	0.07	0.87	0.124	0.13	—	—	—	10,000
0	0.22	0.85	0.121	0.29	0.14	1.28	0.142	?
0.08	0.02	1.11	0.159	0.20	0.41	1.72	0.191	$\simeq 50 \cdot 10^6$

(4) Vergnes et al. (1976b); (5) Tchen et al. (1979); (6) J. Seger (unpublished); [a] Mestriner et al. (1976)

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