ANNALS OF HUMAN BIOLOGY, 1994, VOL. 21, NO. 4, 335–345

Gm and Km allotypes in Wayampi, Wayana and Emerillon Indians from French Guiana

J. M. DUGOUJON†, E. GUITARD†, M. T. SENEGAS†, P. GRENAND‡ and E. BOIS*

†Centre de Recherches sur le Polymorphisme Génétique des populations humaines, Toulouse, France
‡Département Société, Urbanisme, Développement, Paris, France
*Unité de Recherches d'Epidémiologie Génétique, Paris, France

Received 16 April 1993; revised 11 November 1993

Summary. We have studied 506 Amerindians from three French Guiana groups: 194 Wayampi, living in Trois-Sauts, and 100 in the Camopi area; 47 Emerillon also living in the Camopi area and 165 Wayana on the Litani and Maroni rivers. All samples were tested for G1m(1,2,3,17), G3m(5,6,10,11,13,14,15,16,21,24,28) and Km(1) by the classical method of hemaglutination inhibition. The phenotype and haplotype distributions are presented and have been subjected to factorial correspondence analysis. Two Gm haplotypes are common: $Gm^{1,17;21,28}$, and $Gm^{1,2,17;21,28}$, but with an important variation in frequency. A rare haplotype, probably the result of a genetic anomaly: $Gm^{1,17;21R,28}$, is frequent in the Emerillon (17%). These populations show no evidence of Black or Caucasian admixtures.

1. Introduction

The allotypic markers of human immunoglobulins (Ig) are inherited differences located on the heavy chains of IgG (Gm), IgA (Am), IgE (Em) and light chain Kappa (Km). Each epitope is restricted to one of the IgG (IgG1, IgG2 and IgG3) or IgA (IgA2) subclasses and found on the constant regions (CH1, CH2, or CH3 domains). Km allotypes are variants of all Ig classes and subclasses. In most cases, allotypes have been associated with specific amino-acid sequences (Schanfield and van Loghem 1986). Genes encoding the heavy chains of Ig are closely linked on chromosome 14, at band q 32·33 (Shander, Martinis and Croce 1980, Hobart, Rabbits, Goodfellow, Solomon, Chambers, Spurr and Powey 1981, Cox, Markovic and Teshima 1982, Lefranc, Lefranc and Rabbits 1982, Lefranc, Lefranc, de Lange, Out, van der Broek, van Nieu Woop, Radl, Helal, Chaabani, van Loghem and Rabbits 1983), Kappa light chains are localized on chromosome 2, at band 2p12 (McBride, Hieter, Hollis, Swan, Otey and Leder 1982).

Population and family studies in different human populations have demonstrated the existence of large differences both in the frequency and combinations of allotypes (haplotypes) (Steinberg and Cook 1981). So, the allotypic systems (particularly the most polymorphic of them, Gm), are very useful genetic markers for anthropological studies and human genetics. Besides the identification of populations (diversity, genetic affinities), we can evaluate admixture or gene flow from other populations by the presence of either unique haplotypes or differences in the frequencies of haplotypes. Major ethnic groups are characterized by a set of haplotypes; differences between them are both qualitative and quantitative. Uncommon haplotypes that may have arisen either by recombination (crossing-over), conversion, deletion or mutation exist in any population (about 1% of the total phenotypes) (van Loghem and Natvig 1970). All these events creating new genetic material are due to internal homology in the structure of domains and cluster arrangements. Several unusual IGHG haplotypes have been characterized at molecular level (Lefranc *et al.* 1982, 1983, Chaabani, Bech-

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Hansen and Cox 1985, Bech-Hansen and Cox 1986, Bottaro, de Marchi, de Lange, Boccazzi, Caldesi, Gallina and Carbonara 1989).

Many studies have been reported on Amerindian populations showing the usefulness of Gm and Km polymorphisms for the evaluation of their genetic relationships (Fernet, Larrouy and Ruffié 1964, Geerdink, Nijenhuis, van Loghem and Li Fo Sjoe 1974, Daveau, Rivat, Langaney, Afifi, Bois and Ropartz 1975, Gershowitz and Neel 1978, Black, Santos, Salzano, Callegari-Jacques, Weimer, Franco, Hutz, Rieger, Kubo, Mestriner and Pandey 1988, Salzano, Black, Callegari-Jacques, Santos, Weimer, Mestriner, Pandey, Hutz and Rieger 1988). However, some of the hitherto published Gm studies have considered only a few Gm allotypes.

We report here the results of the Gm and Km typing of three populations: Wayampi, Emerillon and Wayana. We will also review the present knowledge concerning these genetic systems of Ig in the Amerindian populations of the neighbouring countries of Brazil and Surinam.

2. Material and methods

2.1. Populations

The three Amerindian groups (Wayampi, Emerillon and Wayana) live in the interior of French Guiana (2·3N, 53·0W, altitude 95 m), an Amazonian lowland with a tropical rainy climate and a tropical rainforest (figure 1).

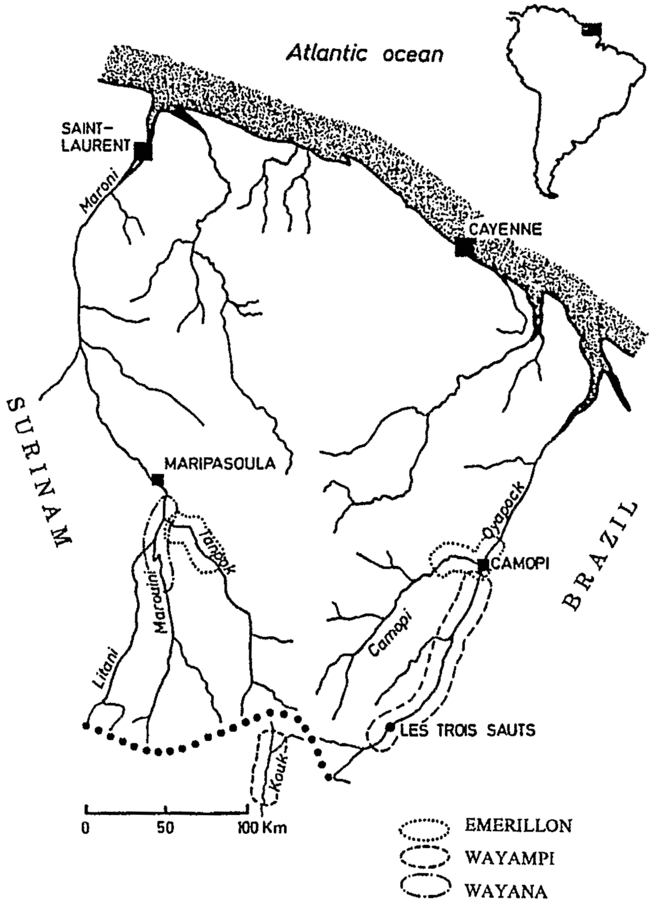

Figure 1. French Guiana. Geographical distribution of the Emerillon, Wayampi and Wayana.

They have a culture and a way of life adapted to their survival in the tropical rainforest (Grenand and Grenand 1979). They practice slash and burn agriculture, hunting, fishing and gathering. The three groups developed in a similar way with no non-Indian admixture until the last two decades, but with continuous intertribal marriages, including individuals of now extinct groups. The population dramatically diminished in size following their first contacts with Europeans. A few decades ago, they seemed to be nearing extinction and adopted isolation as a way of survival. Their numbers are now on the increase. Pedigrees up to nine-ten generations were ascertained from ethnological studies.

The Wayampi

They came from the lower Amazonian region in Brazil at the end of the 18th century (Grenand 1980), and belong to the Tupi-Guarani language group. A census taken in 1985 showed them to number 501 persons living in two communities along the upper reaches of the Oyapock river, on the Eastern border: 283 inhabit three villages in the Trois-Sauts area in the extreme south of the country and are in touch with a small group of Brazilian Wayampi, some 30 of whom came to Guiana 20 years ago and 218 live in the Camopi area in two villages half way down the Oyapock. The Wayampi villages are permanently occupied and there is a high degree of endogamy among the population and only very limited cross-breeding with non-Indian groups.

The Emerillon

They are Tupi-Guarani like the Wayampi and were already in the region in the 16th century and at the time of our study numbered 124 persons in the Camopi area, on the Oyapock and Maroni rivers. About 50 other Emerillon live on the Waki and Tampock, both tributaries of the Maroni river. The two communities keep very close relations with each other and narrowly escaped extinctions in the 50's when they came to number only 53 persons.

The Wayana

The Wayana speak a Carib language. They are 550 in number and are spread out in some ten villages on the upper Maroni and the Litani. This ethnic group, almost completely isolated till the middle of the 19th century, has been less affected by epidemics and is today the most important group among the Indian tribes of the hinterland. Another group live on the Tapahoni in Surinam. The three groups keep a very close relationship. They are semi-nomadic and used to leaving their river to go and live with some distant relations on another river hundreds of km away (5–10% of the population every year). The Wayana system of family relationship is based upon preferential marriages between classificatory non-cousins that should result in a theoretically very high degree of consanguinity, which is, however, counterbalanced to a large extent by the necessity of finding sons-in-law from outside the village, the ideal consisting in keeping in the village as many sons as possible and attracting sons-in-law from outside (Rivière 1984). The Wayana, however, refuse to be influenced by other populations.

2.2. *Material*

Sera from 506 individuals belonging to the three groups were analysed as follows: 194 Wayampi living in Trois-Sauts and 100 living in the Camopi area (i.e. 59% of the whole population), 47 Emerillon living in the Camponi area (38% of population) and

165 Wayana living on the Litani and Maroni rivers (30% of population). These samples were collected on dry silicone tubes (Vacutainer, Becton-Dickinson, France). The samples were then forwarded to Paris in isothermic boxes with refrigerating packs. Sera (with 0·02% N3 Na) were kept at −30°C until typing.

2.3. *Methods*

Gm and Km typing. All the samples were tested for G1m (1,2,3,17), G3m (5,6,10,11,13,14,15,16,21,24,28) and Km(1). G2m(23) was not tested because it would not have been informative. All antisera were of human origin, except for anti-G3m (21R) R.224.23 (rabbit origin). The reagents are listed in table 1. We used the classical hemagglutination inhibition method on opaline plates (Field and Dugoujon 1989).
Statistical analysis. Haplotype frequencies were estimated using maximum likelihood [Edwards 1984]. Using Gm and Km haplotype frequencies, we have performed a correspondence factorial analysis, based on the chi-2 distance (Benzecri and Benzecri 1980).

Table 1. Reagents used for Gm and Km allotype determination.

Chain	Genetic Marker			
	Allotype nomenclature†			
Gm	Numerical	Alphabetic	Anti-allotype	Coating antigen (anti-D)
γ_1	G1m(1)	G1m(a)	Lap.	Mae.
	G1m(2)	G1m(x)	Sub.	Mae.
	G1m(3)	G1m(f)	Lab., Omo., Dem.	Mok.
	G1m(17)	G1m(z)	Caz.	May.
γ_3	G3m(5)	G3m(b1)	Pag.	Eyc.
	G3m(10)	G3m(b5)	Des.	Eyc.
	G3m(11)	G3m(b0)	Feu.	Eyc.
	G3m(13)	G3m(b3)	Bet.	Eyc.
	G3m(14)	G3m(b4)	Blan., Rou.	Eyc.
	G3m(15)	G3m(s)	2624‡, 1590591	4095‡
	G3m(16)	G3m(t)	JT169*	4095‡
	G3m(21)	G3mg1)	Blaz.	Ant.
	G3m(21R)	G3m(g1)	R224-23§, Lac.	Ant.
	G3m(28)	G3m(g5)	Lla.	Ant.
Km				
K	Km(1)	Km(1)	Por.	Mok.

Reagents gifts by: ‡E. v. Loghem and G. de Lange, *H. Matsumoto, §L. Rivat.

†Nomenclature according to proposals of the World Health Organization meeting on Human Immunoglobulin Allotypes, Rouen, 1974. W.H.O. *Journal of Immunogenetics*, 1976, 3, 357–362.

3. Results

The Gm and Km phenotype distribution are presented in table 2 and the derived haplotype frequencies in table 3. We observed seven phenotypes which can be explained by the existence of four haplotypes: the Gm$^{1,17;21*}$ haplotype is the most frequent in each tribe, varying from 0·55 (Emerillon) to 0·82 (Wayampi from Trois-Sauts), then the Gm$^{1,2,17;21*}$ with a frequency from 0·13 (Emerillon) to 0·24 (Wayana). Therefore, these two haplotypes represent in all cases (other than the Emerillon) more than 90% of the total Gm haplotype frequency. A third Amerindian haplotype, of Mongoloid origin, Gm$^{1,17;10,11,13,15,16}$ appears with the highest frequency in the Emerillon, but it is again found in the Wayampi and Wayana. This haplotype is also found at 6% in the neighbouring Wayampi from Camopi, suggesting intertribal marriages. The strikingly high frequency of the unusual haplotype $Gm^{1,17;21R,28}$ (which lacks the G3m (21) allotype) in Emerillon (0,17) is probably related to the small size of their population resulting in a high degree of consanguinity. In the Km system, the Wayampi from Trois-Sauts and Camopi have the same high frequency of Km^1 (0·61). In contrast, the Emerillon and Wayana have a higher frequency of Km^3 than Km^1 (respectively 0·86 and 0·65).

Table 2. Gm and Km phenotype distributions in the Guiana populations.

	Tupi–Guarani								Karib	
	Wayampi						Emerillon		Wayana	
	Trois-Sauts		Camopi		Total					
Phenotypes Gm system	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.
1,17;21*	132	131·9	62	64·3	194	196·7	25	26·0	91	90·8
1,2,17;21*	61	60·9	28	29·1	89	90·2	10	10·4	68	67·8
1,17;10,11,13,15,16,21*	1	1	4	4·6	5	5·3	4	5·4	5	4·8
1,2,17;10,11,13,15,16,21*	0	0·2	2	1·0	2	1·2	1	1·2	1	1·6
1,17;10,11,13,15,16	0	0·0	3	0·1	3	<0·1	3	0·5	0	0
1,17;10,11,13,15,16,21R,28	0	0·0	1	0·4	1	0·2	4	1·8	0	0
1,17;21R,28	0	0·0	0	0·5	0	0·4	0	1·7	0	0
Total	194	194·0	100	100·0	294	294·0	47	47·0	165	165·0
Chi-2	0·0002		0·127		0·074		0·411		0·001	
df	1		1		1		1		1	
Km system										
1	165	165·0	85	85·0	250	250·0	12	12·0	95	95·0
−1	29	29·0	15	15·0	44	44·0	35	35·0	70	70·0
Total	194	194·0	100	100·0	294	294·0	47	47·0	165	165·0

21* = 21,21R,28; 5* = 5,10,11,13,14

Table 3. Gm and Km haplotype frequencies

	Tupi–Guarani				Karib
	Wayampi			Emerillon	Wayana
	Trois-Sauts	Camopi	Total		
Gm haplotypes					
1,17;21*	0·824	0·714	0·771	0·550	0·744
1,2,17;21*	0·172	0·163	0·169	0·126	0·237
1,17;10,11,13,15,16	0·003	0·065	0·024	0·159	0·018
1,17;21R,28	0·001(1)	0·057	0·036	0·165	NE
Km haplotypes					
1	0·613	0·613	0·613	0·137	0·349
3	0·387	0·387	0·387	0·863	0·651

(1): Would become zero with infinite iterations; NE:non estimated.

Factorial analysis of correspondence based on chi–2 distance favours the frequency differences of the less represented variables (figure 2). In the first group, the Emerillon can be distinguished well separated from other populations and characterized by a high frequency of the haplotypes $Gm^{1,17;21R,28}$ and $Gm^{1,17;10,11,13,15,16}$; in the second group the proximity of the Wayampi of Trois-Sauts and Camopi can be seen (high frequency of Km^1 and $Gm^{1,17;21*}$): these two groups are distinct from the Wayana, characterized by the highest frequency of the $Gm^{1,2,17;21*}$ haplotype.

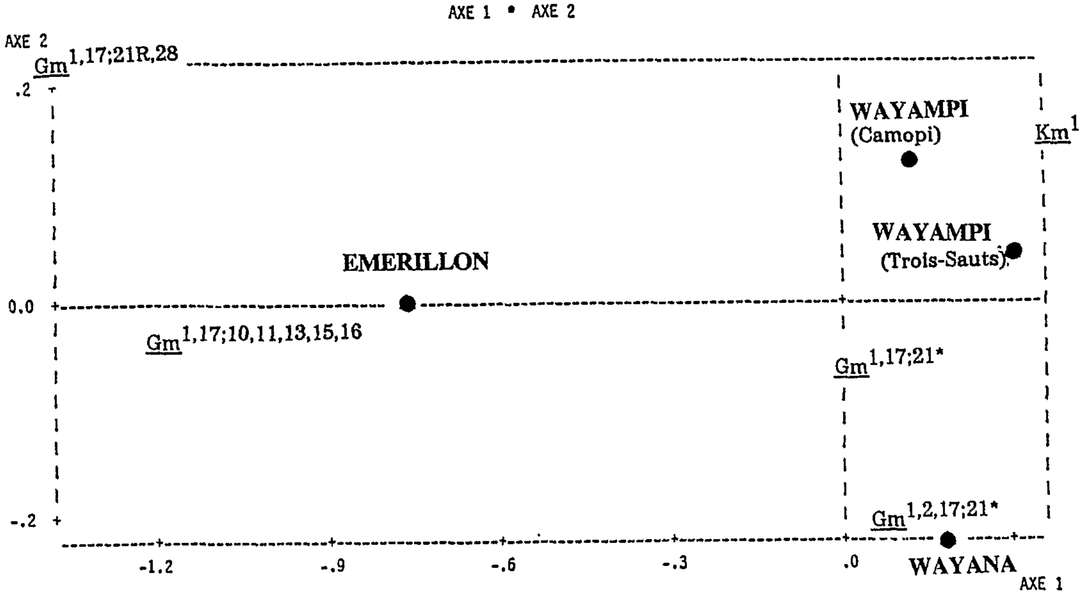

Figure 2. Factorial analysis of correspondence on three Guiana populations.

The Wayampi, Emerillon and Wayana tribes show no evidence of black or Caucasian admixture, unlike other Amerindian populations of French Guiana, Surinam or Brazil (Fernet *et al.* 1964, Geerdink *et al.* 1974, Daveau *et al.* 1975, Gershowitz and Neel 1978, Black *et al.* 1988, Salzano *et al.* 1988, Dugoujon, Senegas, Burali and Guitard 1990). In the latter, we note the presence of the Gm$^{1,17;5*}$, Gm$^{1,17;5,6,11,24}$, Gm$^{1,17;5,6,10,11,14}$ and Gm$^{1,17;10,11,13,15}$ African haplotypes (table 4).

4. Discussion

As has been previously noted, only two Gm haplotypes (Gm^{1,17,21*} and Gm$^{1,2,17;21*}$) are common in Amerindians, but an important variation of frequency of the two haplotypes is found. In such small populations with high levels of inbreeding, the Gm and Km polymorphisms show all the variability caused by founder effects and genetic drift. Some haplotypes of low frequency (like Gm$^{1,17;10,11,13,15,16}$), could be eliminated from the genetic pool of these populations, and others become highly prevalent (Gm$^{1,17;21*}$ and Gm$^{1,2,17;21*}$). Besides, otherwise rare or 'private' haplotypes, resulting probably from a genetic anomaly in the region coding for the heavy chains of Ig become frequent. This is the case for Gm$^{1,17;21R,28}$, present in 19% of the Emerillon.

These populations have been investigated for three decades for several genetic markers: red cell antigens, serum proteins and red cell enzymes, HLA antigens, rare electrophoretic variants (Larrouy, Marty and Ruffie 1964, Bois 1967, Geerdink *et al.* 1974, Seger, Tchen, Feingold, Grenand and Bois 1978, Tchen, Seger, Grenand and Bois 1976, Tchen, Bois, Feingold, Grenand and Degos 1978a, Tchen, Bois, Seger, Grenand, Feingold and Feingold 1978b, Tchen, Seger, Bois, Grenand, Fribourg-Blanc and Feingold 1978c, Tchen, Seger, Bois and Neel 1980, Tchen, Bois, Lanset and Feingold 1981). According to the systems or alleles, they confirm the results provided by Gm and Km allotypes.

Numerous authors support the hypothesis that there were three distinct waves of migration from northeast Asia into the Americas: Paleo-Amerindians, 30,000 to 40,000 years ago, Neo-Amerindians or Na Dene between −20,000 to −13,000, and

Table 4. Gm and Km haplotypes in neighbouring Amerindian populations from Brazil and Surinam.

		Gm								Km		
	Number tested	1,17;21	1,2,17;21	1.17;10,11,13,15,16	1,3;5* or 3;5*	1,17;5*	1,17;5,6,11,24	1,17;5,6,10,11,14	1,17;10,11,13,15	1	3	Reference
KARIB												
Galibi(1)	156	0·47	0·36	0·12	<0·01	-	0·05	-	-	0·34	0·66	Dugoujon, *et al.*, 1990
Wayana(2)	192	0·75	0·24	0·02	-	-	-	-	-	0·36	0·64	Geerdink, *et al.*, 1974
Apalai-Wayana(3)	93	0·74	0·17	-	-	0·09	-	-	-	0·40	0·60	Salzano, *et al.*, 1988
Wayana(4)	376	0·64	0·33	0·03	-	-	-	-	-	0·40	0·60	Geerdink, *et al.*, 1974
Tiriyo(5)	95	0·74	0·23	0·02	-	-	<0·01	<0·01	-	0·53	0·47	Gershowitz and Neel, 1978 Salzano, *et al.*, 1974
Karib(6)	130	0·53	0·25	<0·01	0·04	0·05	0·07	0·01	0·04	0·41	0·59	Geerdink, *et al.*, 1974
Karib(7)	124	0·54	0·21	<0·01	<0·01	0·07	0·10	-	0·08	0·32	0·68	Geerdink, *et al.*, 1974
TUPI												
Urubu-Kaapor(8)	159	0·55	0·39	<0·01	-	0·06	-	-	-	0·49	0·51	Black, *et al.*, 1988
Asurini(9)	153	0·82	0·17	-	0·01	-	-	-	-	0·54	0·46	Black, *et al.*, 1988
Parakana(10)	134	0·91	0·09	-	-	-	-	-	-	0·50	0·50	Black, *et al.*, 1988
ARAWAK												
Palikur(11)	266	0·60	0·39	-	<0·01	<0·01	-	-	-	0·67	0·33	Dugoujon, *et al.*, 1990
Matsiguenga(12)	204	0·68	0·28	-	0·01	-	0·03	-	-	0·54	0·46	Dugoujon, *et al.*, 1990
Arawak(13)	93	0·63	0·32	<0·01	0·02	0·03	<0·01	-	-	0·32	0·68	Geerdink, *et al.*, 1974
Arawak(14)	100	0·68	0·21	-	0·01	0·07	0·03	-	<0·01	0·44	0·56	Geerdink, *et al.*, 1974

(1) Karib tribe living on the coast of French Guiana, on the Mana estuary. (2) Settlements of Alaparu (near the border of Brazil, on the upper Corantijne river) and Pelulu Tepu (upper Tapanahony river) in Surinam, but they are probably Tiriyo tribes. (3) They result from a fusion between the Wayana and the Apalai, two Karib tribes, at the end of the past century, in the region of the Paru de Leste river (border of Brazil with Surinam and French Guiana). (4) Settlements of Puleowine (on the Tapanahony river) and Kawenhakan (on the Lawa river, near the border of French Guiana). (5) This group is located at the margins of the river Paru de Oeste (1°57′N, 55°49′W), Brazil. (6) This tribe (the same tribe as (1)) lives in Surinam (Bernhardsdorp), in the tropical forest, near Brokopondo lake. (7) Karib tribe (the same tribe as (1)) living in Bigi Poika, on the Saramaka river, in Surinam. (8) The Urubu-Kaapor (speaking a language close to the Wayampi) are settled in a reservation in the state of Maranhao, Brazil. (9) The Asurini tested are divided between two villages: Trocara (about 150 individuals) and Koatinemo (about 54 individuals), Brazil. (10) Group living at Bom Jardim, Brazil. (11) Arawak tribe living along the estuary of Oyapok, French Guiana. (12) This population lives in the area of Koribeni, on the Haut-Urubamba river, Peru. (13) Settlement from Powaka, Surinam. (14) Settlement from Matta, Surinam.

Eskimo-Aleut 9000 years ago. Some of them: Salzano and Steinberg 1965, Sukernik and Osipova 1982, Williams, Steinberg, Gershowitz, Bennett, Knowler, Pettitt, Butler, Baird, Dowda-Rea, Burch, Morse and Smith 1985 base their opinion upon Gm data; others: O'Rourke and Suarez 1985, Salzano and Callegari-Jacques 1988, O'Rourke, Mobarry and Suarez 1992 upon demographic, ethnological or archaeological observations. Such a length of time is sufficient to have permitted micro-evolutionary differentiation. More recent studies carried out on native Amerindians have revealed differences between the Indian populations of North, Central and South America. Callegari-Jacques, Salzano, Constans and Maunières 1993, have shown a north-south and southwest-northeast clinal difference. The two haplotypes mainly responsible are Gm$^{1,2,17;21*}$ and Gm$^{1,17;10,11,13,15,16}$. If we take into account the language groups, we notice that the Eskimos and the Na-Dene cluster together and are different from the other populations, particularly from the Amerindian tribes located in North America. Differences were also observed between tribes from Mexico and the homogeneous group of Chibchan-Paezan located in Central America. The results are in keeping with the ones obtained by Hazout, Guasp, Loirat, Maurières, Larrouy and Dugoujon 1993, using the 'mobile site method' which draws up genetic-similarity maps, combining genetic and geographic distances. The genetic profile of the different waves of migration are essentially marked by Gm$^{1,17;21*}$ and Gm$^{1,2,17;21*}$ haplotypes for Paleo-Indians, Gm$^{1,17;21*}$, Gm$^{1,2,17;21*}$ and Gm$^{1,17;10,11,13,15,16}$ for the Na Dene and Gm$^{1,17;21*}$ and Gm$^{1,17;10,11,13,15,16}$ for the last migration of Eskimo Aleut. Shanfield (1992) has also examined the variation of Gm and Km over the two Americas and argues for a fourth Gm pattern for later North American non-Nadene populations characterized by the highest frequencies of Gm$^{1,17;21*}$. Furthermore, recent analysis also based on Gm haplotype diversity (Mourrieras, Dugoujon, Buffat and Hazout, in preparation), allows the interpretation of this distorted geographic map in terms of local genetic diversity and possible population migrations. It shows that the same group of northern Amerindians stands apart, but also one can note the position of the Guiana tribes distributed along the atlantic coast, and particularly the Emerillon well separated from other populations. Their genetic proximity with Brazilian tribes belonging to the same linguistic classification (Equatorial—Tucanoan) is to be noticed. The Amerindian tribes living today in French Guiana belong to population groups spreading far outside the boundaries of the 'French Departement'. The Wayana, for instance, are linked with a great number of ethnological groups living from the Orenoco in the west to the Amazonian basin in the south. The Wayampi and the Emerillon are the Tupi-Guarani populations from Brazil and Paraguay that have pushed their way farthest north. These tribes tend to drift toward the northern regions of Central America (Panama, Costa Rica and Mexico). Analyses carried out on the mtDNA (cf Szathmary's review 1993) confirm the validity of the three migrations hypothesis.

All the Gm haplotypes found in these Amerindian populations occur in Chinese, Japanese and other Mongoloid groups (Matsumoto 1988, Zhao and Lee 1989). The Gm$^{1,17;10,11,13,15,16}$ haplotype is now found with its highest frequency among northern Baikal Buritas, Eskimos, Mongolians and Siberians. In Amerindian populations it is relatively rare and, like Gershowitz and Neel (1978), we can demonstrate by genealogical studies that in some cases it has been introduced by intertribal admixture. This haplotype has probably been present since ancient times. The high frequency of Gm$^{1,17;21*}$ and Gm$^{1,2,17;21*}$ also characterizes all the Mongoloid populations from southeast and east Asia, particularly the northern group. We observe a genocline with a point of contact between Koreans and Mongolians. The southern group is marked by a high frequency of Gm$^{1,3;5*}$ and the centre of dispersion has been identified as the Guangxi and Yunnan areas in the southeast of China. This haplotype is not found in our Amerindian populations. However, we can speculate about its presence in all Arawak Indians and some Karib or Tupi tribes (table 4) with a frequency of about 1%. In most cases we cannot differentiate it from the Gm$^{3;5*}$ Caucasian haplotype (because of its frequent association with Gm$^{1,\pm 2,17;21*}$).

The genetic variation on the American continent has been structured primarily by isolated local populations drifting independently. The micro-differentiation observed between the Wayampi of Trois-Sauts and the Wayampi of the Camopi area is due to drift or, most probably, to admixture with Emerillon. The Guiana tribes have a genetic profile similar to the Paleo-Indians' except for the Emerillon who have a high frequency of the abnormal Gm$^{1,17;21R,28}$ and of Gm$^{1,17;10,11,13,15,16}$, the latter as our genealogical studies have shown having been brought by the neighbouring Wayampi tribe. Their high frequency can be explained by the small number of people in that tribe and the resulting consanguinity. The demographic evolution, at first dramatic, may partially explain the genetic data. For four centuries, they have had to go through sociological readjusting, splitting, regrouping as is often the case with small populations (conflicting alliances, migrations), but the genetic evolution is mostly due to the very strong external constraint (imposed upon them by nature).

Acknowledgements

The authors thank P. Maurières for technical assistance in the genetic analysis, L. Hillat and D. Sicre for secretarial services, and Dr J. Clayton for reading the manuscript and comments.

References

BECH-HANSEN, N.T., and COX, D.W., 1986, Duplication of the human immunoglobulin heavy chain gamma-2 gene. *American Journal of Human Genetics*, **38**, 67–74.

BENZECRI, J.P., and BENZECRI, F., 1980, *Pratique de l'analyse des données* (Paris: Dunod).

BLACK, F.L., SANTOS, S.E.B., SALZANO, F.M., CALLEGARI-JACQUES, S.M., WEIMER, T.A., FRANCO, M.H.L.P., HUTZ, M.H., RIEGER, T.T., KUBO, R.R., MESTRINER, M.A., and PANDEY, J.P., 1988, Genetic variation within the Tupi linguistic group: new data on three Amazonian tribes. *Annals of Human Biology*, **15**, 337–351.

BOIS, 1967, Les Amérindiens de la Haute-Guyane Française—anthropologie, pathologie, biologie. *Editions du CRNS*, (Paris: Desclée), 180 pp.

BOTTARO, A., DE MARCHI, M., DE LANGE, G., BOCCAZZI, C., CALDESI, F., GALLINA, R., and CARBONARA, A.O., 1989, New types of multiple and single gene deletions in the human Ig CH locus. *Immunogenetics*, **29**, 44–48.

CALLEGARI-JACQUES, S.M., SALZANO, F.M., CONSTANS, J., and MAURIERES, P., 1993, Gm haplotype distribution in Amerindians: Relationship with geography and language. *American Journal of Physical Anthropology*, **90**, 427–444.

CHAABANI, H., BECH-HANSEN, N.T., and COX, D.W., 1985, A multigene deletion within the immunoglobulin heavy chain region. *American Journal of Human Genetics*, **37**, 1164–1171.

COX, D.W., MARKOVIC, V.D., and TESHIMA, I.E., 1982, Genes for immunoglobulin heavy chains and for alpha 1 anti-trypsin are localized to specific regions of chromosome 14q. *Nature*, **297**, 428–430.

DAVEAU, M., RIVAT, L., LANGANEY, A., AFIFI, N., BOIS, E., and ROPARTZ, C., 1975, Gm and Inv allotypes in French Guiana Indians. *Human Heredity*, **25**, 88–92.

DUGOUJON, J.M., SENEGAS, M.T., BURALI, C., and GUITARD, E., 1990, Les marqueurs allotypiques Gm et Km des immunoglobulines et la structure génétique de quelques isolats amérindiens. *Approche pluridisciplinaire des isolats humains*. (Paris: INED), Congrès et colloques n° **3**, 106–130.

EDWARDS, A.W.F., 1984, *Likelihood* (Cambridge: Cambridge University Press).

FERNET, P., LARROUY, G., and RUFFIE, J., 1964, Etude hémotypologique des populations Indiennes de Guyane Française. II Les groupes sériques du système Gm. *Bulletin des Membres de la Société Anthropologique de Paris*, **7**, 119–123.

FIELD, L. L., and DUGOUJON, J. M., 1989, Immunoglobulin allotyping (Gm, Km) of GAW 5 families. *Genetic Epidemiology*, **6**, 31–34.

GEERDINK, R. A., NIJENHUIS, L. E., VAN LOGHEM, E., and LI FO SJOE, E., 1974, Blood groups and immunoglobulin groups in Trio and Wayana Indians from Surinam. *American Journal of Human Genetics*, **26**, 45–53.

GERSHOWITZ, H., and NEEL, J. V., 1978, The immunoglobulin allotypes (Gm and Km) of twelve Indian tribes of Central and South America. *American Journal of Physical Anthropology*, **49**, 289–302.

GRENAND, F., and GRENAND, P., 1979, Les populations Amérindiennes de Guyane. *Atlas de la Guyane* (Paris: ORSTOM-C.N.R.S.), p. 160.

GRENAND, P., 1980, Introduction à l'étude de l'univers Wayampi. *Langues et civilisations à tradition orale* (Paris: SELAF).

HAZOUT, S., GUASP, G., LOIRAT, F., MAURIERES, P., LARROUY, G., and DUGOUJON, J. M., 1993, A new approach for interpreting the genetic diversity in space: 'Mobile site method'. Application to Gm haplotype distribution of twenty seven Amerindian tribes from North and Central America. *Annals of Human Genetics* **57**, 221–237.

HOBART, M. J., RABBITTS, T. H., GOODFELLOW, P. N., SOLOMON, E., CHAMBERS, S., SPURR, N., and POWEY, S., 1981, Immunoglobulin heavy chain genes in humans are located on chromosome 14. *Annals of Human Genetics*, **45**, 331–335.

LARROUY, G., MARTY, Y., and RUFFIE, J., 1964, Etude hémotypologique des populations indiennes de la Guyane française. I. Les groupes érythrocytaires. *Bulletin des Membres de la Société Anthropologique de Paris*, **7**, suppl. **11**, 107–117.

LEFRANC, M. P., LEFRANC, G., and RABBITTS, T. H., 1982, Inherited deletion of immunoglobulin heavy chain constant regions in normal individuals. *Nature*, **300**, 760–762.

LEFRANC, M. P., LEFRANC, G., DE LANGE, G., OUT, T. A., VAN der BROEK, P. J., VAN NIEU WOOP, J., RADL, J., HELAL, A. N., CHAABANI, H., VAN LOGHEM, E., and RABBITTS, T. H., 1983, Instability of the human immunoglobulin heavy chain constant region locus indicated by different inherited chromosomal deletions. *Molecular Biology and Medicine*, **1**, 207–217.

MCBRIDE, O. W., HIETER, P. A., HOLLIS, G. F., SWAN, D., OTEY, N. C., and LEDER, P., 1982, Chromosomal location of human Kappa and lambda immunoglobulin light chain constant region genes. *Journal of Experimental Medicine*, **155**, 1480–1490.

MATSUMOTO, H., 1988, Characteristics of Mongoloid and neighbouring populations based on the genetic markers of human immunoglobulins. *Human Genetics*, **80**, 207–218.

MOURRIERAS, B., DUGOUJON, J. M., BUFFAT, L., and HAZOUT, S., (in preparation) Association between a distorted geographic map and a genetic system for interpreting the genetic diversity in space: application to Gm haplotypes of Native American populations.

O'ROURKE, D. H., MOBARRY, A., and SUAREZ, B. K., 1992, Patterns of genetic variation in Native America. *Human Biology*, **64**, 417–434.

O'ROURKE, D. K., and SUAREZ, B. K., 1985, Patterns and correlates of genetic variation in South Amerindians. *Annals of Human Biology*, **13**, 13–31.

RIVIERE, P., 1984, *Individual Society in Guiana: Comparative Study of Amerindian Social Organization* (Cambridge: Cambridge University Press), 127 pp.

SALZANO, F. M., BLACK, F. L., CALLEGARI-JACQUES, S. M., SANTOS, S. E. B., WEIMER, T. A., MESTRINER, M. A., PANDEY, J. P., HUTZ, M. H., and RIEGER, T. T., 1988, Genetic variation within a linguistic group: Apalai-Wayana and other Carib tribes. *American Journal of Physical Anthropology*. **75**, 347–356.

SALZANO, F. M., and CALLEGARI-JACQUES, S. M., 1988, *South American Indians. A case study in evolution* (Oxford: Clarendon Press).

SALZANO, F. M., and STEINBERG, A. G., 1965, The Gm and Inv of Indians from Santa Catarina, Brazil. *American Journal of Human Genetics*, **17**, 273–279.

SALZANO, F. M., WOODAL, J. P., BLACK, F. L., WEITKAMP, L. R., and FRANCO, M. H. L. P., 1974, Blood groups, serum proteins and hemoglobins of Brazilian Tiriyo Indians. *Human Biology*, **46**, 81–87.

SCHANFIELD, M. S., 1992, Immunoglobulin allotypes (Gm and Km) indicate multiple founding populations of native Americans: Evidence of at least four migrations to the New World. *Human Biology*, **64**, 381–402.

SCHANFIELD, M. S., and VAN LOGHEM, E., 1986, Human immunoglobulin allotypes. In *Handbook of Experimental Immunology*, Vol. 3: *Genetics and Molecular Immunology*, edited by D. M. Weir (London: Blackwell Scientific Publications), 94.1–94.18.

SEGER, J., TCHEN, P., FEINGOLD, N., GRENAND, F., and BOIS, E., 1978, Homozygosity of Adenylate Kinase allele 3: Two cases. *Human Genetics*, **43**, 337–339.

SHANDER, M., MARTINIS, J., and CROCE, C. M., 1980, Genetics of human immunoglobulins: Assignment of the genes for μ, α, γ immunoglobulin chains to chromosome 14. *Transplantation Proceedings*, **12**, 417–420.

STEINBERG, A. G., and COOK, C. E., 1981, *The distribution of the human immunoglobulin allotypes* (Oxford: Oxford University Press).

SUKERNIK, R. I., and OSIPOVA, L. P., 1982, Gm and Km immunoglobulin allotypes in Reindeer Chukchi and Siberian Eskimos. *Human Genetics*, **61**, 148–153.

Szathmary, E. J. E., 1993, mtDNA and the peopling of the Americas. *American Journal of Human Genetics*, **53**, 793–799.

Tchen, P., Bois, E., Feingold, N., Grenand, F., and Degos, L., 1978a, Histocompatibility antigens in two American Indian tribes of French Guiana. *Tissue Antigens*, **11**, 315–319.

Tchen, P., Bois, E., Lanset, S., and Feingold, N., 1981, Blood group antigens in the Emerillon, Wayampi, and Wayana Amerindians of French Guiana. *Human Heredity*, **31**, 47–53.

Tchen, P., Bois, E., Seger, J., Grenand, F., Feingold, N., and Feingold, M., 1978b, A genetic study of two French Guiana Amerindian populations. I. Serum proteins and red cell enzymes. *Human Genetics*, **45**, 305–315.

Tchen, P., Seger, J., Bois, E., Grenand, F., Fribourg-Blanc, A., and Feingold, N., 1978c, A genetic study of two French Guiana Amerindian populations. II. Rare electrophoretic variants. *Human Genetics*, **45**, 317–326.

Tchen, P., Seger, J., Bois, E., and Neel, J. V., 1980, Is there a PGM1-4 allele specific to Amerindian populations? *Human Genetics*, **53**, 229–231.

Tchen, P., Seger, J., Grenand, P., and Bois, E., 1976, Variants électrophorétiques rares des protéines adénylate kinase 1, phosphoglucomutase 1 et 2 et transferrine dans deux populations de Guyane française. *C. R. Academie des Sciences Paris*, **286**, 1817.

Van Loghem, E., and Natvig, J. B., 1970, Uncommon Gm gene complexes. *Vox Sanguinis*, **18**, 421–434.

Williams, R. C., Steinberg, A. G., Gershowitz, A. G., Bennett, P. H., Knowler, W. C., Pettitt, D. J., Butler, W., Baird, R., Dowda-Rea, L., Burch, T. A., Morse, H. G., and Smith, C. G., 1985, Gm allotypes in Native Americans: Evidence for three distinct migrations across the Bering Land Bridge. *American Journal of Physical Anthropology*, **66**, 1–19.

Zhao, T., and Lee, T. D., 1989, Gm and Km allotypes in 74 Chinese populations: a hypothesis of the origin of the Chinese nation. *Human Genetics*, **83**, 101–110.

Address correspondence to: J. M. Dugoujon, C.R.P.G.-C.N.R.S., Hopital Purpan, Avenue de Grande Bretagne, 31300 Toulouse, France.

Zusammenfassung. Wir haben 506 Amerindianer aus 3 verschiedenen bevolkerungsgruppen Franzosisch-Guyanas untersucht: 194 Wayampi mit wohnsitz in Trois-Sauts und 100 aus der umgebung von Camopi, 47 Emerillon ebenfalls aus der umgebung von Camopi und 165 Wayana, die an den ufern der flusse Litani und Maroni leben. Alle seren wurden mit der klassischen methode der hamagglutinations-inhibierung auf die allotypen Glm(1,2,3,17), G3m(5,6,10,11,13,14,15,16,21,24,28) und Km(1) getestet. Die phanotypishen und haplotypischen verteilungen sind vorhanden und werden einer faktoriellen korrespondenzanalyse unterzogen. Zwei Gm-haplotypen sind gemeinsam: $Gm^{1,17;21,28}$ und $Gm^{1,2,17;21,28}$, allerdings mit erheblichen unterschieden in der frequenz. Ein seltener haplotyp, wahrscheinlich das resultat einer genetischen anomalie: $Gm^{1,17;21R,28}$, ist haufig bei den Emerillon zu finden (17%). Diese populationen zeigen keine anziechen fur kreuzungen mit Negroiden oder Kaukasiern.

Résumé. Nous avons analysé 506 Amérindiens provenant de trois populations de Guyane française: 194 Wayampi résidant à Trois-Sauts et 100 dans les environs de Camopi, 47 Emerillon résidant aussi dans les environs de Camopi et 165 Wayana sur les bords des rivières Litani et Maroni. Tous les sérums ont été testés pour les allotypes Glm(1,2,3,17), G3m(5,6,10,11,13,14,15,16,21,24,28) et Km(1) par la méthode classique de l'inhibition de l'hémaglutination. Les répartitions phénotypiques et haplotypiques sont présentées et soumises à une analyse factorielle de correspondance. Deux haplotypes sont communs: $Gm^{1,17;21,28}$ et $Gm^{1,2,17;21,28}$, mais avec d'importantes variations de fréquences. Un haplotype rare, résultant probablement d'une anomalie génétique: $Gm^{1,17;21R,28}$ est fréquent chez les Emerillon (17%). Ces populations ne montrent aucune évidence de métissage Africain ou Caucasoide.