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The genetic diversity of three peculiar populations descending from the slave trade: Gm study of Noir Marron from French Guiana

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Abstract

The *Noir Marron* communities are the direct descendants of African slaves brought to the Guianas during the four centuries (16th to 19th) of the Atlantic slave trade. Among them, three major ethnic groups have been studied: the Aluku, the Ndjuka and the Saramaka. Their history led them to share close relationships with Europeans and Amerindians, as largely documented in their cultural records. The study of Gm polymorphisms of immunoglobulins may help to estimate the amount of gene flow linked to these cultural exchanges. Surprisingly, very low levels of European contribution (2.6%) and Amerindian contribution (1.7%) are detected in the Noir Marron gene pool. On the other hand, an African contribution of 95.7% redraws their origin to West Africa ($F_{ST} \leqslant 0.15$). This highly preserved African gene pool of the Noir Marron is unique in comparison to other African American populations of Latin America, who are notably more admixed. ***To cite this article: N. Brucato et al., C. R. Biologies 332 (2009).***

Keywords: Gm polymorphism; French Guiana; African American; Slave trade; Admixture

1. Introduction

As the colonization of America began, the economic exploitation of this continent became the major goal of Europeans, and the slave trade was created to provide the required working force. During the 16th and 19th centuries, an estimated 11 million Africans were enslaved to work in plantations. Up to 200,000 slaves were sent to the newly established regions of French Guiana and Surinam (former Dutch Guiana), near Brazil [1]. At first, the majority of slaves came from West Africa: Equatorial Guinea and Angola, followed by the historical areas of the Slave Coast (now Togo, Benin), the Biafra (Nigeria, Cameroon) and finally the Gold Coast (Ghana), the Ivory Coast and the Senegambia (Senegal, Guinée-Bissau, Sierra Leone, Liberia, Guinea). To prevent rebellion during the crossing of the Atlantic Ocean,

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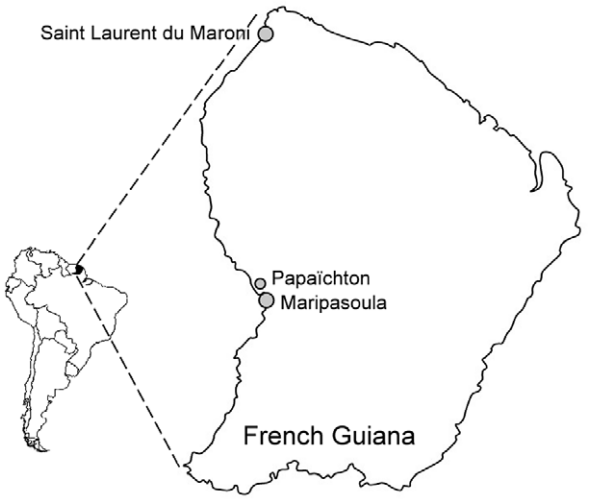

Fig. 1. Geographical location of the three Noir Marron populations studied.

the slave traders took care to break all familial and ethnic structures, and to maintain a certain proportion of male and females [2].

Despite the precautions of the Europeans settlers, many slaves managed to escape, taking refuge in the dense equatorial forest, and reconstructed communities known as the *Noir Marron* (or Bushinengué) with their own cultural identities. However, they were subsequently enslaved, particularly in Dutch Guiana, and many of their villages were destroyed. In this environment, they met Amerindians, with whom relationships fluctuated. However, the population size of the Noir Marron still increased, and slowly the colonial forces were compelled to sign peace treaties with some of them. Between 1760 and 1849, six Noir Marron communities were officially recognized: the Saramaka, the Ndjuka, the Aluku, the Paramaka, the Matawai and the Kwinti. Today, the first three groups are the most numerous. They represent about 30,000 individuals living on French soil, and are widely present along the Maroni River and in major cities (Fig. 1). They are an essential component of the large melting-pot of this region, in which several other ethnic groups also live, such as Amerindians, Asians, Europeans and Creoles [3].

The Noir Marron communities each have their own cultural particularities which differentiate them from each other, but despite the difficulties related to their environment and the fact that they originated from several African ethnic groups, they created a homogeneous culture based on multiple sources, and many cultural similarities can still be observed among them [4,5]. Each ethnic group has an endogamic marital structure, maintaining exogamic practices between their own clans, like in many West African populations. Their religion is likewise preserved, with a pantheon resembling that of Akan's in West Africa. However, more extended cultural exchanges are obvious on examination of their languages, which take their roots in Dutch, for the Ndjuka and the Aluku, and in Portuguese, for the Saramaka. Similarly, on studying their adaptation to the Amazonian forest, many techniques have been learned from Amerindians: for example the construction of housing or canoes, in which the Saramaka have acquired specific skills.

Due to this cultural diversity and knowing their historical origins, interbreeding within the Noir Marron communities can be expected to be seen, as is the case for many African American populations in Latin America [6]. On the other hand, clear signatures of their African ancestry are expected from their endogamy. No genetic study has ever been conducted on the Noir Marron.

This study proposes the first genetic insights into the origin of three Noir Marron populations and aims at examining whether ethnical and cultural diversity can be linked to genetic diversity, using the Gm immunoglobulin polymorphism. Gm allotypes are polymorphic antigenic markers on the immunoglobulin gamma constant regions, not present in all individuals [7]. Four systems of allotypic antigens have been described so far: Gm, Am, Em, and Km [8–12]. Gm antigenic determinants are present on the heavy chains of three of the four subclasses of IgG (IgG1, IgG2, and IgG3) [13,14]. Gm allotypes are encoded by IGHG genes that are closely linked on chromosome 14 (14q32.33) and are inherited [15]. Data on Gm allotypes of human immunoglobulins in African populations and other populations have been previously reported [16–24]. The Gm system has been frequently studied in human populations, due to its heterogeneous haplotype frequencies among populations [25–27], and is thus very useful to assess genetic relationships among populations in a given geographic area [28–30] or from different geographic areas [23,31, 32]. Its high power of discrimination is relevant for the aims of this study.

2. Materials and methods

2.1. Population samples

This study is based on 177 plasma samples originating from individuals belonging to three out the four Noir Marron populations present in French Guiana. These samples comprising 88 plasma from Djuka, 47 from Aluku, and 42 from Saramaka were collected

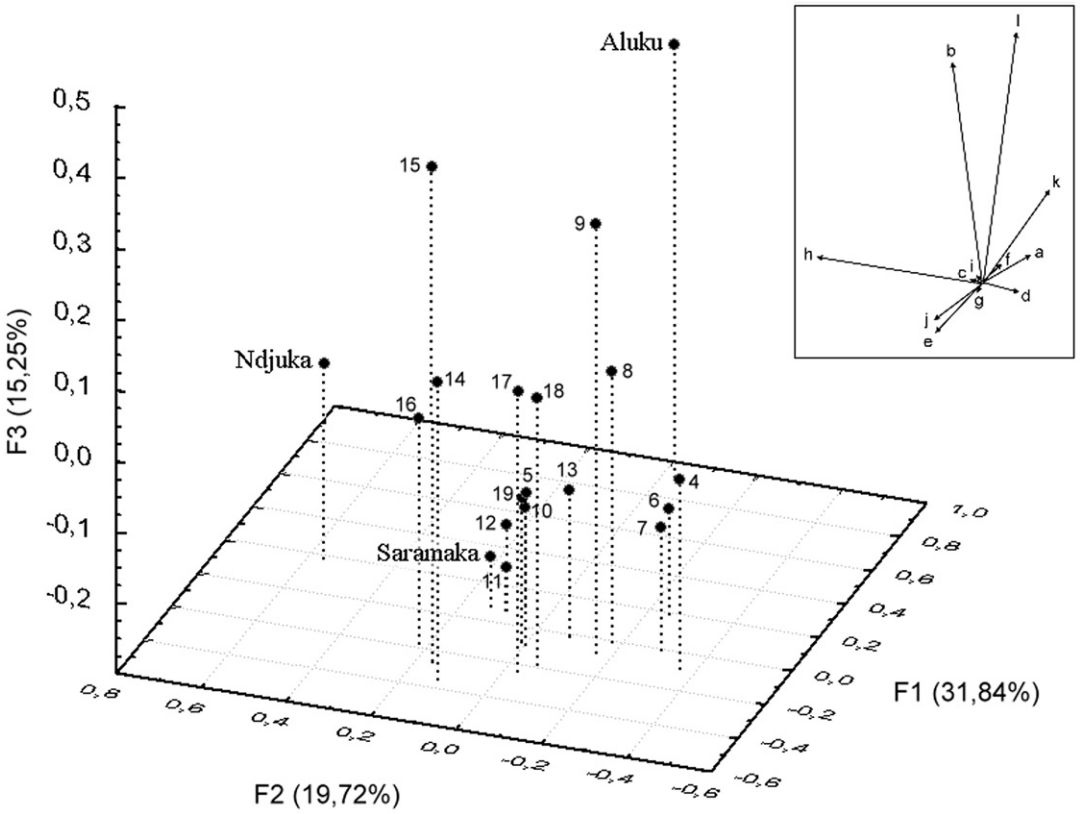

Fig. 2. Factorial Correspondence Analysis in three dimensions based on Gm haplotype frequency of seventeen West African and three Noir Marron populations. 1: Aluku; 2: Ndjuka; 3: Saramaka (French Guiana, present study); 4: Dogon; 5: Bobo; 6: Bwa (Mali); 7: Mandenka; 8: Fulani (Senegal); 9: Abron; 10: Yacouba; 11: Baoule; 12: Ahizi (Ivory Coast); 13: Yoruba (Nigeria); 14: Mandara; 15: Fulbe; 16: Fali; 17: Bamileke; 18: Bassa; 19: Ewondo (Cameroon) (personal data from J.M. Dugoujon). Vectors of genotypes shown in the right frame: a: Gm21, 28; 1, 17; ..; b: Gm5, 10, 11, 13, 14; 3; ..; c: Gm5, 10, 11, 13, 14; 1, 17; ..; d: Gm5, 10, 11, 13, 14; 1, 17; ..(+Gm28); e: Gm10, 11, 13, 15; 1, 17; ..; f: Gm10, 11, 13, 15; 1, 17; ..(+Gm28); g: Gm5, 6, 10, 11, 14; 1, 17; ..; h: Gm5, 6, 10, 11, 14; 1, 17; ..; i: Gm5, 6, 11, 24; 1, 17; ..; j: Gm5, 6, 11, 24; 1, 17; ..(+Gm28); k: Gm5, 14; 1, 17; ..(+Gm28); l: others (Gm10, 11, 13, 15, 16; 1, 17; .. for the Noir Marron).

during former collaborative studies on such populations living in Saint-Laurent du Maroni and Maripasoula/Papaichton in the Maroni river area [33–35]. The location of these populations is shown in Fig. 1. Informed consent was obtained for all participants and we followed human experimentation guidelines from the Commission nationale de l'informatique et des libertés (CNIL) and the Comité consultatif de protection des personnes dans la recherche biomédicale (Necker Hospital, Paris).

2.2. Gm immunoglobulin allotypes

All the plasma were tested for G1m (1, 2, 3, 17), G2m (23), G3m (5, 6, 10, 11, 13, 14, 15, 16, 21, 24) and Gm(28) immunoglobulin allotypic markers by using a classical haemagglutination inhibition method [36]. The reagents used are described by Dugoujon et al. [37] and Giraldo et al. [38]. The Gm haplotypes are presented using the International System for Human Gene Nomenclature (ISGN) (G3m, G1m, and G2m order) and are set in simplified forms [14]. Allotypes are separated by commas, and the subclasses are separated by semicolons [14,39]. The notation ".." indicates that the sample was tested for G2m (23) but found to be negative for this allotype, and 5* stands for 5, 10, 11, 13, 14. Gm(28) is presented separately from the other polymorphisms because it has been shown that it is not necessarily located on the gamma 3 chain in African populations [24].

2.3. Statistical analyses

Gm haplotype frequencies were estimated from the phenotypic distributions of the three populations tested by a standard maximum likelihood procedure using the program Genef2, which is Lathrop's modification

Table 1
Gm phenotype distributions in the three Noir Marron population samples. All p-values >0.01.

Gm phenotypes G1m;G2m;G3m	Aluku ($N = 47$)		Ndjuka ($N = 88$)		Saramaka ($N = 42$)	
	Observed	Expected	Observed	Expected	Observed	Expected
3; ..; 5, 10, 11, 13, 14	0	0.02	0	0.01	0	0
1, 3, 17; ..; 5, 10, 11, 13, 14	0	0.55	0	0.92	0	0
1, 3, 17; ..; 5, 10, 11, 13, 14 (+Gm28)	0	0.39	1	0.16	0	0
1, 3, 17; ..; 5, 10, 11, 13, 14, 21 (+Gm28)	0	0.06	0	0	0	0
1, 3, 17; ..; 5, 6, 10, 11, 13, 14, 24	1	0.4	0	0.4	0	0
1, 3, 17; ..; 5, 6, 10, 11, 13, 14, 24 (+Gm28)	0	0	0	0.12	0	0
1, 3, 17; ..; 5, 6, 10, 11, 13, 14	1	0.09	0	0.11	0	0
1, 3, 17; ..; 5, 10, 11, 13, 14, 15 (+Gm28)	0	0.38	0	0.04	0	0
1, 3, 17; ..; 5, 10, 11, 13, 14, 15	0	0	1	0.05	0	0
1, 3, 17; ..; 5, 10, 11, 13, 14, 15 (+Gm28)	0	0	0	0.13	0	0
1, 3, 17; ..; 5, 10, 11, 13, 14, 15, 16	0	0.09	0	0.03	0	0
1, 17; ..; 5, 6, 11, 24	2	1.92	5	3.59	2	1.24
1, 17; ..; 5, 6, 11, 21, 24 (+Gm28)	0	0.61	0	0	0	0.4
1, 17; ..; 5, 6, 10, 11, 13, 14, 24	8	5.19	18	16.28	5	5.98
1, 17; ..; 5, 6, 10, 11, 13, 14, 24 (+Gm28)	3	3.7	9	8.55	3	3.33
1, 17; ..; 5, 6, 11, 24 (+Gm28)	0	0	4	2.42	1	0.48
1, 17; ..; 5, 6, 10, 11, 14, 24	0	0.81	0	2.03	0	1.2
1, 17; ..; 5, 6, 10, 11, 14, 24 (+Gm28)	0	0	0	1.63	0	0.21
1, 17; ..; 5, 6, 10, 11, 13, 15, 24 (+Gm28)	3	3.64	0	0.94	2	0.76
1, 17; ..; 5, 6, 10, 11, 13, 15, 24 (+Gm28)	0	0	0	3.24	1	1.67
1, 17; ..; 5, 6, 10, 11, 13, 15, 16, 24	0	0.81	1	0.61	0	0
1, 17; ..; 21 (+Gm28)	0	0.05	0	0	0	0.02
1, 17; ..; 5, 10, 11, 13, 14, 21 (+Gm28)	0	1.4	0	0	2	1.1
1, 17; ..; 5, 6, 10, 11, 14, 21 (+Gm28)	0	0.13	0	0	0	0.17
1, 17; ..; 10, 11, 13, 15, 21 (+Gm28)	2	0.57	0	0	0	0.29
1, 17; ..; 10, 11, 13, 15, 16, 21 (+Gm28)	1	0.13	0	0	0	0
1, 17; ..; 5, 10, 11, 13, 14	4	3.51	20	18.44	8	7.22
1, 17; ..; 5, 10, 11, 13, 14 (+Gm28)	6	6.79	6	7.2	7	5.37
1, 17; ..; 5, 6, 10, 11, 13, 14	0	1.09	5	4.6	4	2.9
1, 17; ..; 5, 6, 10, 11, 13, 14 (+Gm28)	0	0	3	2.95	0	0.93
1, 17; ..; 5, 10, 11, 13, 14, 15	0	0	2	2.13	0	1.82
1, 17; ..; 5, 10, 11, 13, 14, 15 (+Gm28)	9	8.43	4	6.51	2	4.75
1, 17; ..; 5, 10, 11, 13, 14, 15, 16	0	1.09	0	1.37	0	0
1, 17; ..; 5, 10, 11, 13, 14, 15, 16 (+Gm28)	3	0.78	1	0.25	0	0
1, 17; ..; 5, 6, 10, 11, 13, 15, 16, 24 (+Gm28)	0	0	0	0.18	0	0
1, 17; ..; 5, 6, 10, 11, 14	0	0.09	0	0.29	0	0.29
1, 17; ..; 5, 6, 10, 11, 13, 14 (+Gm28)	1	0.78	0	0.27	0	0
1, 17; ..; 5, 6, 10, 11, 13, 14, 15	0	0	0	0.27	1	0.37
1, 17; ..; 5, 6, 10, 11, 13, 14, 15 (+Gm28)	2	0.77	5	1.01	2	0.63
1, 17; ..; 5, 6, 10, 11, 13, 14, 15, 16	0	0.17	1	0.17	0	0
1, 17; ..; 5, 6, 10, 11, 13, 14, 15, 16 (+Gm28)	0	0	0	0.07	0	0
1, 17; ..; 10, 11, 13, 15	0	0	0	0.06	0	0.12
1, 17; ..; 10, 11, 13, 15 (+Gm28)	1	1.72	2	0.67	2	0.74
1, 17; ..; 10, 11, 13, 15, 16	0	0.09	0	0.1	0	0
1, 17; ..; 10, 11, 13, 15, 16 (+Gm28)	0	0.77	0	0.19	0	0
HW equilibrium (χ^2)		39.44		61.85		18.5
Degrees of freedom		25		28		16
Significance		n.s.		n.s.		n.s.

of Yasuda's algorithm [40]. The hypothesis of Hardy–Weinberg equilibrium was tested in the three populations by the goodness-of-fit chi-square test [41].

Admixture was calculated by an average of three estimation methods: the Bernstein's method [42], the Roberts and Hiorns' estimator [43] and the Maximum Likelihood estimation using Leadmix v.1.0 [44] as detailed by Schanfield [45]. Three parental populations were considered, each composed of two reference groups: African (Mandenka from Senegal [21]

Table 2
Gm haplotype frequencies and gene diversity indices in the three Noir Marron population samples.

Gm haplotype G3m;G1m;G2m	Aluku ($N = 47$)		Ndjuka ($N = 88$)		Saramaka ($N = 42$)	
21, 28; 1, 17; ..	0.032	±0.041	0	–	0.024	±0.046
5, 10, 11, 13, 14; 3; ..	0.021	±0.018	0.011	±0.034	0	–
5, 6, 11, 24; 1, 17; ..	0.202	±0.015	0.202	±0.008	0.172	±0.017
5, 10, 11, 13, 14; 1, 17; ..	0.273	±0.052	0.458	±0.041	0.415	±0.059
5, 10, 11, 13, 14; 1, 17; .. (+Gm28)	0.195	±0.048	0.082	±0.027	0.133	±0.045
5, 6, 11, 24; 1, 17; .. (+Gm28)	0	–	0.059	±0.023	0.031	±0.028
5, 6, 10, 11, 14; 1, 17; ..	0.043	±0.021	0.057	±0.019	0.083	±0.030
5, 6, 10, 11, 14; 1, 17; .. (+Gm28)	0	–	0.022	±0.014	0	–
10, 11, 13, 15; 1, 17; ..	0	–	0.026	±0.013	0.052	±0.028
10, 11, 13, 15; 1, 17; .. (+Gm28)	0.191	±0.041	0.064	±0.019	0.090	±0.034
10, 11, 13, 15, 16; 1, 17; ..	0.043	±0.021	0.017	±0.009	0	–
Gene diversity	0.818		0.735		0.778	

and Yoruba from Nigeria [20]), European (individuals from fourteen French provinces [46] and from Huelva in Spain [47]) and Amerindian (Wayana from French Guiana [48] and Wayampi from French Guiana [49]).

Gene diversity [50] was estimated using the Arlequin v3.01 program [51]. For multivariate and other genetic structural analyses, the following Gm haplotypes were used: Gm21, 28; 1, 17; ..; Gm5*; 3; ..; Gm5*; 1, 17; ..; Gm5*; 1, 17; ..(+Gm28); Gm5, 6, 11, 24; 1, 17; ..; Gm5, 6, 11, 24; 1, 17; ..(+Gm28); Gm5, 6, 10, 11, 14; 1, 17; ..; Gm5, 6, 10, 11, 14; 1, 17; ..; Gm10, 11, 13, 15; 1, 17; ..; Gm10, 11, 13, 15; 1, 17; ..(+Gm28); Gm10, 11, 13, 15, 16; 1, 17; .. . Our results were compared with a Gm database of West African populations (see Fig. 2) composed by 3409 individuals typed for the same markers. Factorial Correspondence Analysis was performed with Rogers' genetic distances using XLStat v.7.5.2 software (Addinsoft) and Statistica v.8.0 (Statsoft) for visualization.

In order to determine whether the Gm haplotypes distributions were statistically different in the populations, pairwise F_{ST} genetic distances [52] were computed between populations and tested for significance by using a non-parametric resampling procedure included in the Arlequin v3.01 program package [51].

3. Results

The Gm phenotype distributions observed in the studied sample of three Noir Marron populations are shown in Table 1. The observed frequencies fit Hardy–Weinberg equilibrium.

These phenotypes can be explained by eleven different Gm haplotypes (Table 2). Two of them are particularly frequent: Gm5*; 1, 17; .. (from 27.3% to 45.8%) and Gm5, 6, 11, 24; 1, 17; .. (from 17.2% to 20.2%). They are common in Sub-Saharan populations, as also haplotypes Gm5*; 1, 17; .. (+Gm28) (from 8.2% to 19.5%), Gm10, 11, 13, 15; 1, 17; .. (+Gm28) (from 6.4% to 19.1%), Gm5, 6, 10, 11, 14; 1, 17; .. (from 4.3% to 8.3%), Gm5, 6, 11, 24; 1, 17; .. (+Gm28) (from 0% to 5.9%), Gm5, 6, 10, 11, 14; 1, 17; .. (+Gm28) (from 0% to 2.2%) and Gm10, 11, 13, 15; 1, 17; .. (from 0% to 5.2%). Among the three last haplotypes, Gm10, 11, 13, 15, 16; 1, 17; .. (from 0% to 4.3%) is common in Asia and America, Gm5*; 3; .. (from 0% to 2.1%) is common in Europe and Gm21, 28; 1, 17; .. (from 0% to 3.2%) is common in the three continents.

Gene diversity is relatively similar among these populations, with 0.818 for the Aluku, 0.735 for the Ndjuka and 0.778 for the Saramaka (Table 2). At the same time, they indicate a high internal diversity for all of them.

The relative contribution of Gm haplotypes coming from Africa, Europe and America was evaluated by the average of the three methods used to estimate admixture (Table 3). Of course, we here considered arbitrary parental populations from African, European and Amerindian origins, which is a simplification, but may give an idea of past admixture events. According to those estimations, the Aluku present 92.4% contribution from Africa, 5.7% from Europe and 1.9% from America. For the Ndjuka, the first value raises to 97.4%, but the other decrease to 2.2% and 0.4%, respectively. The Saramaka show a contribution of 97.4% from Africa and 2.6% from America (none from Europe). In all of these three populations the European and American contributions thus appears to be very low, whereas the original African gene pool is preserved.

A Principle Components Analysis of African populations tested for Gm revealed a high genetic divergence among East, North, South and West Africans, with Noir Marron clustering with the latter (data not

Table 3
Proportions of African, European and Amerindian admixture as estimated by direct counting (Bernstein's methods), Roberts and Hiorns (R–H), Maximum-Likelihood (ML), and averaged over the three methods.

Population	Method	African	European	Amerindian
Aluku	Bernstein	0.973	0.004	0.023
	R–H	0.932	0.041	0.027
	ML	0.868	0.125	0.007
	Average	**0.924**	**0.057**	**0.019**
Ndjuka	Bernstein	0.987	0.001	0.012
	R–H	0.987	0.013	0.000
	ML	0.948	0.051	0.001
	Average	**0.974**	**0.022**	**0.004**
Saramaka	Bernstein	0.964	0	0.036
	R–H	0.977	0	0.023
	ML	0.981	0.001	0.018
	Average	**0.974**	**0**	**0.026**

shown; see [23,53]). The Factorial Correspondence Analysis shown in Fig. 2 represents the population relationships among this last group. A total of 66.88% of the genetic variance is represented by Factors 1, 2 and 3. The Gm10, 11, 13, 15; 1, 17; .. Gm5*; 1, 17; .. and Gm5, 6, 10, 11, 14; 1, 17; .. (+Gm28) haplotypes contribute significantly to Axis 1, Gm5*; 1, 17; .. (+Gm28) to Axis 2 and the Gm5*; 3; .. and both Gm5, 6, 11, 24; 1, 17; .. (+Gm28) to Axis 3. Within the scatterplot, the Ndjuka can be distinguished due to the contribution of Gm5, 6, 10, 11, 14; 1, 17; .. (+Gm28), Gm10, 11, 13, 15, 16; 1, 17; .. and Gm5*; 3; .. . Likewise the Aluku can be distinguished due to the frequency of Gm5*; 3; .., Gm21, 28; 1, 17; .. and Gm10, 11, 13, 15; 1, 17; .. (+Gm28). On the contrary, the Saramaka cluster in the middle of the West African group.

Since the spatial locations of the three Noir Marron populations are different in relation to the West African group, a permutation test was performed to evaluate the significance of the F_{ST}'s (Table 4, supplementary material). Among the three Noir Marron populations, none of the pairwise F_{ST}'s was significant. The highest F_{ST}'s were reached between each of the three Noir Marron populations and the Fulbe from Cameroon ($F_{ST} = 0.150$ for the Aluku, $F_{ST} = 0.059$ for the Ndjuka and $F_{ST} = 0.066$ for the Saramaka, respectively). However, all these F_{ST}'s are low or not significant.

4. Discussion

The aim of this study on the Gm system of three Noir Marron populations was to obtain relevant information about their genetic backgrounds, and to investigate a possible concordance between past gene flow and cultural exchanges between these African slave descendents and both European and Amerindian populations.

The Gm genetic profiles of Aluku, Ndjuka and Saramaka reveal a relative homogeneity among the three populations (Table 1): the estimated genetic diversity is relatively close (Table 2), and pairwise F_{ST} values are not significant among them (Table 3). This suggests that despite cultural variation, the genetic background of these Noir Marron populations is relatively homogeneous. The major characteristic of Noir Marron is the high predominance of frequent African Gm haplotypes (Gm5*; 1, 17; .. , Gm5*; 1, 17; .. (+Gm28), Gm5, 6, 11, 24; 1, 17; .. , Gm5, 6, 11, 24; 1, 17; .. (+Gm28), Gm5, 6, 10, 11, 14; 1, 17; .. , Gm5, 6, 10, 11, 14; 1, 17; .. (+Gm28), Gm10, 11, 13, 15; 1, 17; .. , Gm10, 11, 13, 15; 1, 17; .. (+Gm28)) which rise together to a cumulated frequency of 95.7% (Table 4). According to our admixture scheme, the European contribution would be responsible for only 2.6%, and the Amerindian for 1.7%. This suggests a high level of endogamy.

The congruence between marital practices and genetic results leads to suppose that the Noir Marron populations are still genetically very close to their African ancestors. The Factorial Correspondence Analysis (FCA) shown in Fig. 2 confirms the close relationship between the three Noir Marron populations and West Africans (Mali, Ivory Coast, Senegal, Nigeria and Cameroon). Even if significant F_{ST} values were found between the Noir Marron and some other ethnic groups, they are relatively low ($F_{ST} \leqslant 0.150$, Table 4, supplementary material). All other values were not significant, which is in concordance with the general aspect of the FCA (a homogeneous cluster in the centre). The similarity between the Noir Marron and West African populations is consistent with historical and genetic data indicating a great number of African Americans ancestors in West Africa [1,54,55]. However, a more precise location of their origin is unidentifiable for several reasons. The first one is the low power of discrimination of the Gm system within continental groups, and even more within West Africans. The second one is that the intentional breaking of all ethnic structures by slave traders has certainly blurred the genetic profile of the ancestral African American communities [55]. The third one is that present West African populations may have evolved genetically since the slave trade period.

If the West African contribution represents the majority of the Gm haplotype diversity, the contribution from Europe and America should not be ignored, as in

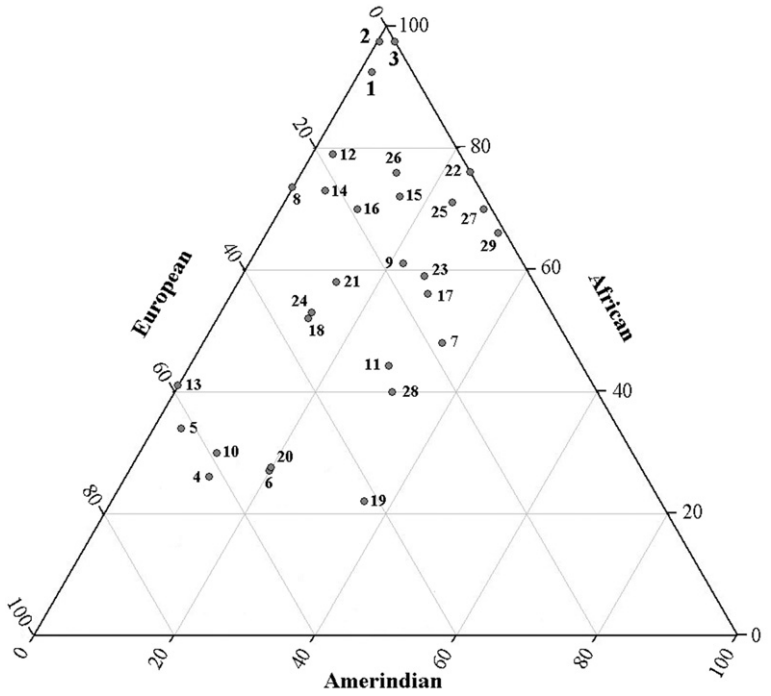

Fig. 3. Triangle plot based on relative autosomal contributions of 29 African–American populations from Latin America. Populations shown: 1: Aluku, 2: Ndjuka, 3: Saramaka (French Guiana) (present study), 4: Punta Gorda (Belize) (Schanfield et al., 1984), 5: Mimbo, 6: Sitio Velho (Arpini-Sampaio et al., 1999), 7: Aracaju (Conceiçao et al., 1987), 8: Pacolval, 9: Curiau (Pante-de-Souza et al., 1999), 10: *Nordestinos* Sao Paulo (Krieger et al., 1965), 11: Afro-Brazilian (Muniz et al., 2008), 12: Trombetas (Schneider et al., 1987), 13: Belem (Schneider and Salzano, 1979), 14: Cameta, 15: Paredao (Bortolini et al., 1995), 16: Porto Alegre (Bortolini et al., 1997), 17: Ribaero Preto (Brazil), 18: Curiepe (Bortolini et al., 1999), 19: Patanemo, 20: Ganga (Castro de Guerra et al., 1993), 21: Panaquire (Castro de Guerra et al., 1996), 22: Churuguara (Loyo et al., 2004), 23: Caracas (Venezuela) (Martinez et al., 2007), 24: Limon (Costa Rica) (Madrigal et al., 2001), 25: Afro-Ecuadoran (Ecuador) (Gonzalez-Andrade et al., 2007), 26: Livingston (Guatemala) (Crawford et al., 1981), 27: Tamahihua (Mexico) (Lisker and Babinsky, 1987), 28: Bluefields (Nicaragua) (Biondi et al., 1988), 29: Melo (Uruguay) (Sans et al., 2002).

all admixed populations. An Amerindian contribution is not surprising in such populations. Refuged in the Amazonian forest, each Noir Marron ethnic group met with many different Amerindian populations during its history; actually, its adaptation to this environment was directly learned from the American autochthons. Taking these events into account, an average contribution of 1.7% is quite low in comparison to what could be expected. Indeed, we should consider in parallel observations made on the Gm system of neighbouring Amerindian populations, the Wayana and the Kaliña. Living near the Aluku, the Wayana have an African contribution of only 3%. An equal bidirectional exchange of genes between these groups should be supposed. On the other hand, percentage likely admixture of 11.6% was estimated for the Kaliña living at the mouth of the Maroni river, and should be due to Creole gene flow [56–58]. These results indicate that the level of gene flow between the Noir Marron and the Amerindians has been particularly low.

A European genetic contribution to African American populations is generally expected [6], considering close relationships during several hundreds of years of slave trade, with possibility of admixture. Gm haplotypes frequent in Europe are indeed present in the Noir Marron populations. However, European contribution appears to be low in the Aluku (5.7%) and is negligible in the Saramaka. Therefore, the genetic European contribution to the Noir Marron is historically very low. Despite four centuries in the Amazonian forest, where they lived near Amerindian and European populations, with whom relationships are attested by cultural exchanges, the Noir Marron have conserved their highly African gene pool for the Gm system.

Even though only one Ancestry Informative Marker (AIM) has been used (i.e. Gm), the conclusion made in this work could be compared to recent studies on other admixed populations [45,59–61]. Due to the high power of discrimination of the Gm system, the identification of

genetic contributions from Europe, America and Africa was found in African Americans.

A triangle plot was achieved to view the relative autosomal contributions of European, Amerindian and African populations to the Noir Marron gene pool and to other African American populations in Latin America (Fig. 3). The Noir Marron cluster is the most African and differs greatly from Brazilian Afro-descendant communities. Moreover, the community of Curiaù [62] could have had the same slave ancestors as the Noir Marron [63]. Coming from the same plantations in Surinam, these slaves would have fled further than the Noir Marron to the Amapa State in Northeast Brazil. If any ethnic segregation between Noir Marron and Curiaù ancestors justifies their separation, the differences observed between their frequencies of contribution can only be explained by their own dynamic of settlement in America. So it seems that historical relationships among neighbouring ethnic groups are the most important determinants of interbreeding, compared to cultural identities.

Cultural exchanges do not seem to be followed by gene flow in this region of the world. This result, due to a strong endogamy, constitutes the uniqueness of African American populations inhabiting Latin America [6]. It is therefore important not to combine all African American within a unique group, because each population has its own genetic background with a unique interbreeding profile. These results are particularly relevant for the inclusion of African American data in forensic, anthropological and pharmacogenetic studies [64–67]. As it was concluded for the Tobago [61], the essentially African ancestry of the Noir Marron may provide an appropriate example to study genetic factors involved in complex diseases or specific resistances. Furthermore, their geographical proximity to the Creoles, who may have close African ancestry as the Noir Marron but with a more admixed genetic profile, could point to French Guiana as a key location for such a study.

5. Conclusion

The Aluku, the Ndjuka and the Saramaka represent three of the major Noir Marron communities inhabiting French Guiana and constitute an original example of African descendant populations in Latin America. Despite a long history in the Amazonian forest, involving cultural exchanges with neighbouring Europeans and Amerindians, the marital practice of endogamy probably prevented gene flow between them. The high conservation of their African gene pool, its homogeneity and its internal diversity indicate that the Noir Marron are a very interesting group if one aims at redrawing the origin of African Americans.

Note

Table 4 is supplied as online supplementary material to this article.

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