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Interethnic Genetic Differentiation: GM Polymorphism in Eastern Senegal

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Summary

Analysis of GM polymorphism has been performed on 1,806 individuals representing three sympatric ethnic groups—Bedik, Fulani, and Mandenkalu—of eastern Senegal. Haplotype frequencies estimated by maximum likelihood have been used to compute common genetic pools between the three samples and a number of other sub-Saharan African populations. Despite extreme linguistic and sociocultural differentiations and very high levels of endogamy, especially in the Bedik and Niokholo Mandenkalu, the three populations share about 90%–95% of their haplotype frequencies in a system which commonly provides strong genetic differentiations. This supports the view that, despite its importance at a large continental scale level, as it is discussed for a set of populations from many regions of sub-Saharan Africa, sociocultural differentiation usually has little effect on local genetic diversity.

Introduction

This work is a contribution to a multidisciplinary comparative study of the three ethnic groups dwelling in a hilly area of eastern Senegal, the Bademba or Niokholo hills, located in the district of Bandafassi, Kedougou, close to the borders of Mali (east) and Guinea (south) (fig. 1). Extensive information about these people and their neighbors has been collected and published in the field of social anthropology (Dupire 1963, 1970; Gessain 1963; Gomila 1971; Pison 1982). Some data have been intensively studied in specialized fields such as anthropometrics, nutrition, and ethnomedicine.

The Niokholo area was also chosen as a pilot zone for intensive demographic and population genetics studies. Much has already been published in this field, either monographs about one of the three populations (Bouloux et al. 1972; Langaney et al. 1972, 1979; Langaney 1974; Langaney and LeBras 1972) or comparative and interethnic relationship studies (Langaney and Gomila 1973; Lalouel and Langaney 1976). Further work is coming; we present here the overall results of the comparative study of the seric IGH immunoglobulin polymorphism, which provide new and reliable insights into genetic differentiations in West Africa.

The general question about genetic diversity is, Can social and cultural barriers lead to genetic differentiation in neighboring people? The GM system, with measurable haplotype frequencies and high polymorphism throughout the world, was likely to be one of the most suitable to answer such a question.

Material and Methods

Population Samples

In the mid 1970s, 1,500 Bedik, 1,200 Niokholo Mandenkalu, and 3,500 Bande Fulani were dwelling in Bandafassi hills. Our plan was to collect blood from at least 70%–80% of the adults in the two first populations and from a comparable subset of 1,200 Fulani. The Bedik and the Mandenkalu were cooperative if not enthusiastic about giving blood samples. Unfortunately, though very hospitable, the Bande Fulani were very

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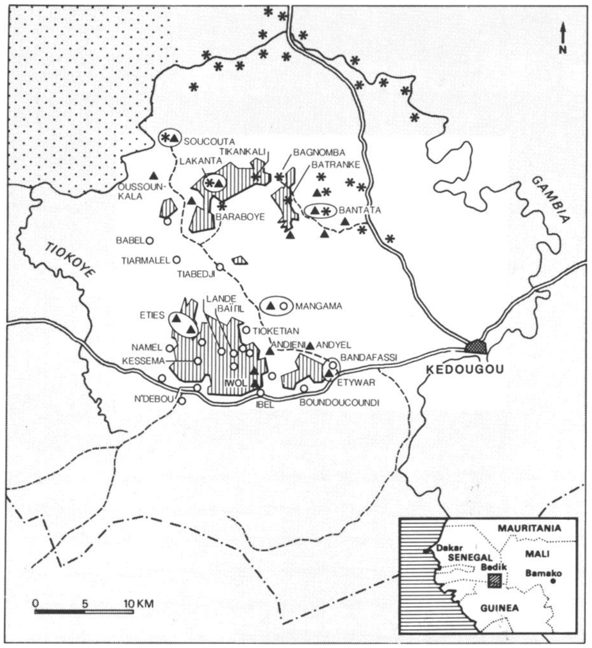

Figure 1 Map of Bandafassi district of Kedougou, showing localization of Bedik (▲), Fula (○), and Mandenka (∗) villages.

reluctant to give blood samples. Children and women especially became anxious just about the thought of a syringe, and the effort to sample them was given up. While we collected the expected family and pedigree data from the others, we obtained an almost random sample of Fulani men from all villages to ascertain gene frequencies, with almost no haplotype transmission control. The final sample sizes according to GM typing were 880 Bedik, 557 Mandenkalu, and 369 Fulani.

History and Demography

The 1,500 Bedik were the last descendants of the reputed first settlers of the area. They are known to belong to the broader Tenda ethnolinguistic group, whose settlements are extended from Senegal to Guinea. Coniagui, Badyaranké, Tenda Boïni, Tenda Mayo, and Bassari are the other members of this group. The Bedik have been present in the Niokholo hills since at least the 13th century and are said to have migrated from the eastern Manding area. Nothing else is known about their remote past; the earliest period which can be ascertained for their cultural differentiation is given by the 6,000 B.C. estimation for the beginning of their Niger-Congo linguistic family differentiation, as estimated from linguistic data (Ehret 1984).

The Bedik territory was invaded by the Mandenkalu during the Mali Empire (14th century). Mandenkalu from the Niokholo belong to the Mande linguistic family, which is thought to be the first to differentiate from the set of Niger-Congo speakers (Pellegrini 1987). The Niokholo Mandenkalu dwell in the northeast of the hills and farther north. Several hundred thousand people constitute the broad Mandenka community of Mali, Guinea, and Senegal, but, in contrast to most of the Mandenkalu, Niokholo Mandenkalu are not Muslims but monotheist pagans.

The Fulani are thought to have a Saharan or/and East African origin (Excoffier et al. 1987), but no historical data exist to support it. Their first known settlement in the Fouta Djallon dates to the 15th century. The Bande Fulani settled in the southeastern part of the Niokholo area at the end of the 18th century, living peacefully until the end of the 19th century. At this time, the Fouta Djallon Fulani invaded the whole country, fighting the Mandenkalu and almost exterminating the Bedik population. The Muslim Bande Fulani, admixed with the Bedik from the time of their first communities, developed an ambiguous attitude toward the warring parties: they did not collaborate with their Fouta Djallon neighbors but took many Bedik, Mandenkalu, and others as slaves whom they later assimilated. The cultural consequence is that their Islam is often very "africanized" by their former pagan slave tradition.

Demographic data show a rapid annual increase in population size for the three tribes: about 1% annually from 1970 to 1981 for the Mandenkalu and 1.2% annually between 1975 and 1980 for the Fulani. A rapid increase has been observed in the Bedik since 1975. A former census by Gomila had shown a constant census of 1,500 people from 1962 to 1975, and the population was then stationary; but from 1975 to 1981 the census increased by more than 200 people. A demographic survey showed that this was the joint consequence of three developments: (1) infant care information by catholic nurse-nuns, (2) measles vaccination both by governmental action and by the nuns, and (3) reduction of birth intervals. The last of these developments occurred because, whereas traditionally intercourse had been prohibited before weaning or death of a previous child, this tradition was given up, especially in Catholic-converted or roadside villages; therefore many new births occurred 1–2 years after the birth of a surviving baby, instead of 3–4 years later, as had been the case previously. So the Bedik began increasing rapidly, owing both to mortality decrease and to fertility increase.

Social Structures

Figure 1 gives the map of the main villages of the three sympatric populations. Coresidence exists between Bedik and Mandenkalu in two very small remote villages (Soucouta and Lakanta) and between Bedik and Fulani in one medium-size village (Etywar). The residence structure is, in fact, highly complex, with numerous hamlets of complex affiliations and frequent secondary dwellings in remote fields during the rainy season. Moreover, the Fulani and Mandenkalu have always been very mobile, and the Bedik now move more and more. Ascertainment of the precise origins of these people was thus only possible through our history and pedigree records, collected throughout the area.

The three populations are patrilocal. Bedik and Mandenkalu are usually exogamous according to patrilineage (with very few exceptions), while Fulani very often marry between patrilineal first cousins or classificatory equivalents. According to different patterns of sexual behavior in the remote and near past, illegitimate conceptions may have been possible, but not very frequent, by Mandenkalu or Fulani in Bedik populations and were the exception—or even excluded—in the other combinations. Fulani commonly receive wives from the others, and Mandenkalu from other Mandenkalu. But in the last case, almost all 11% of immigrant women come from the Gambia River section of the pagan Niokholo Mandenkalu who were excluded from the survey. So Bedik and Mandenkalu can be considered as strictly endogamous from a demographic point of view, while the Fulani are partially exogamous.

Assimilation by Fulani of Bedik or Mandenkalu slaves was frequent long ago, but more recently it has been reduced to very few migrations of wives from the other two tribes (one Mandenka and nine Bedik women were counted in 1980). Intermarriage is limited to family exchange or coresidence in villages between Bedik and Fulani: a Muslim man can marry a pagan girl, but a Muslim girl may not marry a pagan man, unless he is Islamized and Fulanized, which is very rare. Intermarriage between Bedik or Fulani and Mandenkalu is the exception (one Fula and two Bedik wives are known among Mandenkalu). Similarly, according to our data only nine "foreign" women have married Bedik men. Three of them were Mandenkalu but with a Bedik mother, while the others, said to be "Dialonke," were in fact descendants of Bedik people who emigrated to the Fouta Djallon during the Fulani war, at the end of the 19th century.

The effects of an ancient immigration common to the Bedik and the Mandenkalu is more difficult to ascertain. Several lineages known as Bapen in the Bedik and as Kankata in the Mandenkalu villages are the witnesses of the extinction of an ethnic group whose last refugees are said to have come from the Fouta Djallon a century ago (Ferry 1967). The Bapen language has not been spoken for at least half a century, and the demographic and genetic impact that this immigration has had on the pedigrees is limited to very few individuals and their descendants, mostly in two villages.

The social structure and behavior patterns of these populations are, then, distinct enough to maximize both the effects of origin on their gene pools and the ongoing ethnic isolation in a common environment and to answer our question.

GM Typing

Sera from 1,806 blood samples were collected, frozen, and studied in the serum-grouping laboratory of the Centre d'Hémotypologie of the C.N.R.S. (Toulouse). More samples were collected but could not be properly studied after partial hemolysis.

All samples were tested for allotypes IGH G1M 1, G1M 2, G1M 3, G1M 17, G3M 5, G3M 6, G3M 10, G3M 11, G3M 13, G3M 14, and G3M 21. All Fula and Mandenkalu samples were also tested for G1/3M 28 and G3M 15; G3M 15 positives were further tested for G3M 16. All Fula sera but only selected Bedik and Mandenka samples were tested for G3M 24. Table 1

Table 1

Nomenclatures of GM allotypes Tested in Present Study, and Reagents Used

	NOMENCLATURE		REAGENT USED	
LOCALIZATION	Alphanumeric	Numeric	Antiserum	Coat
IgG1 G1M	A	1	Lap Don	Mill
	X	2	Bon	
	F	3	Lab Dem	Juk
	Z	17	Caz	Mayn
IgG1,3 G1/3M	G5	28	Lla	
IgG3 G3M	B0	11	Gag	
	B1	5	Pag	Dail
	B3	13	Bet	Val
	B4	14	Bon G84[a]	
	B5	10	Mol	
	C3	6	Ser Ouel[b] Lok	2781[b] 2781[b] Rok
	C5	24	HodSF[c]	2781[b]
	S	15	Pyg87	Puh[c]
	T	16	SF[c]	
	G	21	Blaz	Mar

[a] Reference: D. Brazier, London.

[b] Reference: E. van Loghem, Amsterdam.

[c] Reference: M.S. Schanfield, Washington, DC.

gives the list of reagents used, which were all human SNagg and exchanged and referenced at the WHO International Rouen Workshop (1974).

Haplotype Frequency Estimations

Phenotype distributions were computed and interpreted into haplotype-distribution hypotheses. Haplotype frequencies were estimated using a maximum-likelihood standard procedure based on the Hardy-Weinberg equilibrium hypothesis.

Pedigrees were available for the three populations. But paternity concept and adoptions prevent their use in a biological sense in the Bedik case. The Fula pedigrees could have been more significant, but the reluctance of women and children to give blood samples prevented their use in testing transmission hypotheses. In the Mandenka case, social and biological paternity and maternity fit almost perfectly, when checked by using GM and other genetic markers with a transmission testing algorithm (Langaney and Nadot 1973). This confirms that the postulated haplotypes were those actually transmitted in the Mandenka case and probably transmitted in the other two populations (A. Langaney, unpublished data).

Common Genetic Pools and Distance Analyses

Common genetic pools between our three Senegalese samples—and a choice of already published data on other sub-Saharan populations—were computed using the formula $P_{ij} = \Sigma_{(k=1,\,m)} \min(f_{ik},f_{jk}) \times 100$, where f_{ik} and f_{jk} are the kth frequencies observed in populations i and j, respectively, in a haplotype distribution defined by m elements. P_{ij}'s, which represent shared percentages of gene frequencies between two populations, have already demonstrated their efficiency for the study of RH, GM, and HLA polymorphisms in human populations (Sanchez-Mazas et al. 1986; Excoffier et al. 1987; Sanchez-Mazas and Langaney 1988). They are related to the genetic distance, $D_{ij} = \frac{1}{2}\, \Sigma_{(k=1,m)}\, |f_{ik} - f_{jk}|$, which is very similar to the "mean character difference" distance coefficient described by Cain and Harrison (1958). It was proved to be a mathematical distance by Gregorius (1978). It is used in our present study to plot human population-genetic differentiations by means of principal coordinate analyses (Gower 1967).

Results

Table 2 gives the phenotype distributions, and table 3 gives the maximum-likelihood haplotype frequency estimates for the three population samples. The fit to Hardy-Weinberg equilibrium was good at the .05 level for Mandenka and Fula distributions but not for Bedik ($.02<P<.01$), who show an excess of homozygotes for GM*1,17 10,11,13.

Common Haplotypes

As expected on the basis of other sub-Saharan population-genetic data (for review, see Excoffier et al. 1987), by far the most common haplotype found in the three populations is GM*1,17 *5** (*5** = mosaic 5,10,11,13,14), followed by GM*1,17 5,6,11,24. Compared with GM*1,17 5,6,11,24, the haplotype GM*1,17 5,6,10,11,14, also usually found in sub-Saharan Africans, assumes rather low frequencies in Senegalese. This feature may represent a more general west-African differentiation, as attested by previous reports from Nigeria (van Loghem et al. 1978), Gambia (Steinberg and Cook 1981), and Burkina Faso (Huizinga 1969). It is to be noted, however, that this haplotype also assumes low frequencies among Khoisan (Steinberg et al. 1975) and has not been observed in Nilo-Saharans (Hiernaux 1976; Langaney et al. 1978) or in pygmies (Cavalli-Sforza et al. 1969; G. Jaeger, personal communication). GM*1,17 10,11,13,5, which is known to be very frequent in Khoisan (actually, existing data on Khoisan populations cannot differentiate between haplotypes GM*1,17 10,11,13,15 and GM*1,17 10,11,13,15,16, as no test was performed for the allotype G3M 16), is commonly suggested to represent Khoisan admixture in South African Bantu populations, where it was detected at variable frequencies (Jenkins et al. 1970). Although this hypothesis explains in part GM*1,17 10,11,13,15 frequency clines in South Africa, our results suggest that this haplotype may have a different source in west Africa, where Khoisan populations are nonexistent. It has also been found in east Africans (Steinberg 1973), thus leading to the conclusion that it is very widely distributed (though with variable frequencies) in sub-Saharan Africa. Genetic-drift mechanisms may be responsible for its very high frequencies in recently admixed but long-time isolated Khoisan populations and for its disappearance or its low frequencies in many other African tribes. Finally, GM*1,17 21 is present in the three Senegalese samples, as in east Africans, Khoisan, and some Bantu populations; this adds further evidence that this haplotype is not strictly extra-African, as has been suggested by Steinberg and Cook (1981).

Tests for G1/3M 28 in the Mandenkalu and Fulani samples show that most haplotypes are split according to the presence or absence of this allotype. This is in

Table 2

GM Phenotype Distributions for Three Population Samples

			POPULATION		
G1M	G1/3M[a]	G3M[a]	Bedik	Mandenkalu	Fulani
1,17		5,10,11,13,14	473	94	105
1,17	28	5,10,11,13,14		207	94
1,17	28	5,10,11,13,14,15		31	19
1,17	28	5,10,11,13,14,15,16			1
1,17	(28)	5,10,11,13,14,21	22	7	4
1,3,17		5,10,11,13,14	...	...	2
1,3,17	28	5,10,11,13,14	...	...	2
1,3,17	28	5,10,11,13,14,21	...	...	1
1,17	28	5,14	...	...	1
1,17	28	5,11[b]	...	1	...
1,17		5,6,10,11,13,14	295	91	25
1,17		5,6,10,11,13,14,24			54
1,17	28	5,6,10,11,13,14		70	11
1,17	28	5,6,10,11,13,14,24			24
1,17		5,6,10,11,13,14,15		1	...
1,17	28	5,6,10,11,13,14,15		2	4
1,2,17		5,6,10,11,13,14	1	...	...
1,17		5,6,10,11,13,(15)	17	1	...
1,17	28	5,6,10,11,13,15,(24)		12	3
1,17		5,6,10,11,14	14	5	1
1,17		5,6,10,11,14,24			5
1,17	28	5,6,10,11,14,24		...	1
1,17	28	5,6,10,11,14,21	...	...	1
1,17		5,6,11,(24)	42	20	8
1,17	28	5,6,11,(24)		9	...
1,17	(28)	5,6,11,21,(24)	5	3	1
1,17	28	5,6,11,14,24	...	...	2
1,17	(28)	10,11,13,(15)	11	2	...
1,17	28	10,11,13,15,21	...	1	...
Total			880	557	369

[a] Allotypes in parenthesis were positive when tested.

[b] Negative with antisera Ser, Ouel (anti-G3M 6), and HodSF (anti-G3M 24) and positive with antiserum Lok (anti-G3M 6).

agreement with Nigerian data (van Loghem et al. 1978) from which we have estimated frequencies for haplotypes including G1/3M 28 (table 3). Similar ranges of frequencies are found between the three west-African populations, G1/3M 28 being more frequently negative in the haplotypes carrying G3M 5. The greatest difference is observed between Fulani and the other two samples, whose G1/3M −28:G1/3M+28 ratios are very similar (table 4).

Uncommon Haplotypes

GM*1,17 5,14, which has been established in the Fulani, has been found to occur sporadically in sub-Saharan Africans and especially in Khoisan (Jenkins et al. 1970; Steinberg et al. 1975). This haplotype could be present but hidden in the other Senegalese samples, as well as in other sub-Saharan populations; it is not easily detectable in low sized samples (as is the case for most of the available GM data), owing to the presence of GM*1,17 5* and GM*1,17 5,6,10,11,14. GM*3 5* and GM*1,17 10,11,13,15,16 found in the Fulani could be a very limited clue to their different origin, as well as an admixture event.

Common Genetic Pools

P_{ij}'s have been computed for 18 sub-Saharan population samples (listed in table 5) on the basis of already published data and our present study (table 6). The results have been used for a principal coordinate analysis plotted in figure 2.

Table 3

GM Haplotype Frequencies Estimated by Maximum Likelihood for Four Population Samples

	POPULATIONS IN PRESENT STUDY			VAN LOGHEM ET AL.'S (1978) NIGERIAN POPULATION
HAPLOTYPE	Bedik ($N = 879$[a])	Mandenka ($N = 556$[b])	Fulani ($N = 369$)	($N = 214$)
GM*1,17 5*[c]	.668	.414	.527	.440
GM*1,17 5*,28		.306	.189	.238
GM*1,17 5,6,11,24	.210	.177	.144	.180
GM*1,17 5,6,11,24,28		.024	. . .	.023
GM*1,17 5,6,10,11,14	.034	.022	.060	.052
GM*1,17 5,6,10,11,14,28		. . .	.006	.009
GM*1,17 10,11,13,15	.073	.003	. . .	. . .
GM*1,17 10,11,13,15,28		.044	.035	.051
GM*1,17 10,11,13,15,16,28			.001	. . .
GM*1,17 21,28	.015	.010	.010	. . .
GM*1,17 21		. . .	. . .	.007
GM*1,17 5,14,28	. . .	. . .	.021[d]	. . .
GM*3 5*	. . .	. . .	.007	. . .
Total	1.000	1.000	1.000	1.000
χ^2	16.6	25.8	34.1	19.53
df	6	13	26	16

[a] One rare phenotype—GM 1,2,17 5,6,10,11,13,14—was excluded.

[b] One rare phenotype—GM 1,17 28 5,11 (Lok +)—was excluded.

[c] Necessary to explain three phenotypes—two GM 1,17 28 5,6,11,14,24 and one GM 1,17 28 5,14.

P_{ij}'s between the three tribes are fairly high, with Fulani and Bedik being more distant from each other (P_{ij} = 89%) than they are from Mandenkalu (P_{ij} = 93% and 95%, respectively). However, the three values lie in the common range of all west-African populations, which appear to be quite homogeneous according to GM frequencies, as is well illustrated in figure 2. This west-African group is clearly separate from but very close to the Bantu-speaker family, whose broader heterogeneity is apparently due to Khoisan admixture for some South African tribes such as Bechwana (Botswana) and Xhosa (Republic of South Africa). Unfortunately, east-African populations are represented by a unique sample, as no other good data were available. Nevertheless, our analysis reveals a high degree of genetic differentiation between—and a low degree of genetic differentiation within—broad cultural areas in sub-Saharan Africa, represented by (1) East Africans,

Table 4

G1/3M −28:G1/3M +28 Frequency Ratios for Three Common Haplotypes in West African Samples

	−28: +28 RATIO		
SAMPLE	GM*1,17 5*	GM*1,17 5,6,11,24	GM*1,17 5,6,10,11,14
214 Nigerians (van Loghem et al. 1978	1.8	7.8	5.8
556 Mandenkalu (present study)	1.3	7.4	(Only −28)
369 Fulani (present study)	2.8	(Only −28)	10.0

Table 5

Population Samples Used for Analysis of Common Genetic Pools Between Sub-Saharan Populations

Population	*N*	Location	Linguistic Family	Reference
Babinga pygmies	162	Central African Republic	"Pygmy"	Cavalli-Sforza et al. 1969
Bechwana..............	155	Botswana	Bantu Sotho	Jenkins et al. 1970
Bedik	880	Senegal	West Atlantic	Present study
Fulani, Peul	369	Senegal	West Atlantic	Present study
Keneba.................	822	Gambia	West Atlantic	Steinberg and Cook 1981
Khoikhoi	149	Namibia	Khoisan	Steinberg et al. 1975
Kuambi	119	Ovamboland	Bantu Ovambo	Jenkins et al. 1970
Kurumba	150	Burkina Faso	Voltaic	Huinzinga 1969
Malinke	557	Senegal	Mande	Present study
Mbukushu	115	Angola	Bantu Kavambo	Jenkins et al. 1970
Mlozi, Lozi	189	Zambia	Bantu Sotho	Jenkins et al. 1970
Ndebele	103	Republic of South Africa	Bantu Nguni	Jenkins et al. 1970
Nigerians (Yoruba)	214	Nigeria	Kwa	van Loghem et al. 1978
San, !Kung, Dobe	394	Botswana	Khoisan	Steinberg et al. 1975
Sara Majingay	255	Chad	Central Sudanic	Hiernaux 1976
Shangana	153	Mozambic	Bantu Tonga	Jenkins et al. 1970
Sidamo.................	140	Ethiopia	Eastern Cushitic	Steinberg 1973
Xhosa..................	214	Republic of South Africa	Bantu Nguni	Jenkins et al. 1970

Table 6

***P_{ij}*'s for 18 Sub-Saharan Populations**

	POPULATION[a]																	
POPULATION[a]	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
1																		
2	89																	
3	95	93																
4	87	90	93															
5	95	94	98	92														
6	96	93	95	88	95													
7	79	83	84	91	83	80												
8	82	86	87	94	86	83	97											
9	51	52	48	44	50	52	40	40										
10	78	77	74	71	76	78	67	67	57									
11	84	92	88	92	89	88	89	92	49	75								
12	85	90	85	83	86	89	80	83	53	78	91							
13	91	90	89	86	91	93	77	80	58	83	88	92						
14	87	87	84	81	86	88	77	77	59	84	86	93	95					
15	65	64	60	57	63	64	53	53	68	85	61	64	69	70				
16	92	91	92	87	91	96	79	82	53	79	90	92	94	89	65			
17	50	48	47	44	48	47	40	40	59	64	41	42	47	48	78	44		
18	40	36	37	33	38	37	29	29	47	54	31	31	37	38	67	33	71	

[a] 1 = Bedik; 2 = Fulani; 3 = Mandenkalu; 4 = Keneba; 5 = Kurumba; 6 = Nigerians; 7 = Sara; 8 = Babinga; 9 = Sidamo; 10 = Bechwana; 11 = Kuambi; 12 = Mbukushu; 13 = Lozi; 14 = Shangana; 15 = Xhosa; 16 = Ndebele; 17 = Khoi; 18 = San.

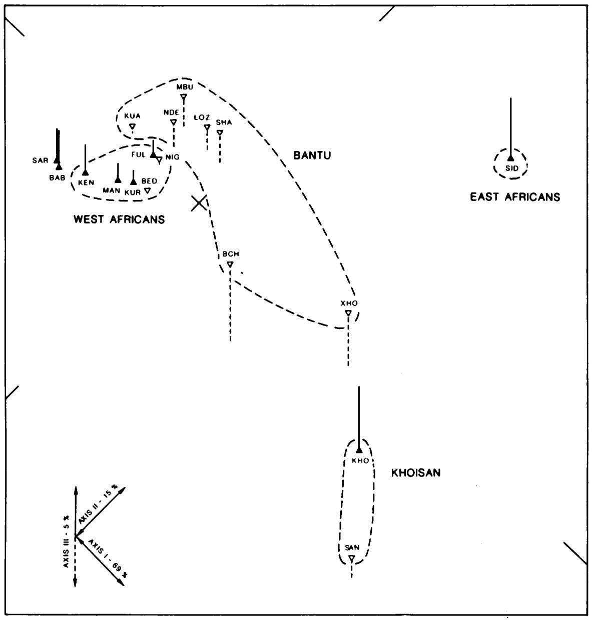

Figure 2 Principal coordinate analysis for 18 populations of sub-Saharan Africa. Genetic distances (see text) were computed from eight GM haplotype frequencies: GM*1,17 21; GM*1,2,17 21; GM*3 5*; GM*1,17 10,11,13,15; GM*1,17 5,6,11,24; GM*1,17 5,6,10,11,14; GM*1,17 5,14; and GM*1,17 5*. Total information on axes I–III = 89%. Unbroken lines = above plane; dotted lines = under plane. Dotted clusters correspond to linguistic families.

(2) Khoisan, and the (3) other populations belonging to west-African, Bantu, Nilo-Saharan, and pygmy groups.

Discussion

The GM system is known to provide the lowest shared percentages of common isoactive genes among the commonly tested immunological systems (Sanchez-Mazas et al. 1986). At the continental level of sub-Saharan Africa, these values fall to some 30% between the most distant groups (e.g., between San and some other populations). These great genetic differentiations appear to be closely related to the geographical distances separating the places of settlement of broad cultural groups (east Africans, west Africans, Bantu, and Khoisan). In a previous study (Excoffier et al. 1987), we were able to show that these genetic links were more precisely explained by linguistic relationships: according to sub-Saharan peopling history as it has been suggested by most linguists, west-African and Bantu populations were differentiated from a Niger-Congo superfamily at quite recent times compared to both East Africans and Khoisan. This is in good agreement with their genetic distances, with Bantu and west Africans being very close to each other. Moreover, the place of Niger-Congo differentiation is believed to cover an area including present-day Nigeria and Congo, and this may also be evidenced by our results, in which Nigerians appear to be genetically intermediate between west Africans and Bantu. So we can conclude that long geographical distances, together with deep sociocultural barriers separating population groups during several millenia, should appear, as in this case, in the genetic structures of present-day sub-Saharan Africans.

This is not the case when we consider within-group differentiations, except when strong admixture events are evidenced between fairly different genetic structures—such as between some Bantu and Khoisan—for which historical data are well documented. The very high P_{ij}'s (95%) found between Mandenkalu and Bedik, and the fact that these tribes have remained isolated from each other, underline the absence of any genetic differentiation between them in this system as well as in erythrocyte blood groups (Y. Marty, personal communication). Bedik bottleneck during the Fouta Djallon Fula war have probably had little or no effect on their genetic structure. Even between the Fulani and the other two groups, a P_{ij} of 90% is very close to most values found within the west-African group, in spite of the former's far different, Saharan or east-African origin. So the drastic cultural differences between the three populations of the present study are by no means paralleled by any significant genetic differentiation. It is puzzling both to see that long-term endogamy did not induce any significant drift differentiation between tribes in this system (or in the other systems tested) and to measure the same level of genetic homogeneity of GM throughout Africa. The easy explanation of unidentified migration is excluded in our survey, and rare illegitimate conceptions are restricted to the Bedik case in the past. Moreover, genetic similarity over long distances—e.g., between populations in Senegal and Nigeria—is not likely to be explained by migrations.

The fact that a large part of the Fula Bande ancestors were former Mandenka, Bambara, or Bedik "Fulanized" slaves or even Bedik wives of a Fula founder (Dupire 1963) may account for a large part of this similarity. Nevertheless, one cannot help comparing these results with those obtained in similar studies comparing the Lebanese communities (Lefranc et al. 1978), the Amazonas Indians (Gershowitz and Neel 1978; Neel et al. 1980), or others in which extreme cultural differentiation and political cleavage cut through a fairly homogeneous continuum of population gene frequencies.

Populations in which cultural barriers have been tight and long enough to prevent gene flows between sympatric populations are real but quite uncommon. Even the 3-century "apartheid" system of Twaregs such as the Kel Kummer or the Kel Diniq, a system corroborated by highly reliable pedigrees (Chaventré 1983), did not prevent the former gene admixture from their neighbors. So, in the most common cases, neighboring populations should be considered as stepping-stones in gene-frequency clines through more or less homogeneous areas, whatever the ethnic and/or linguistic specificities might be. This has been established in different areas—e.g., in Europe (Menozzi et al. 1978; Sokal et al. 1988), Micronesia (Morton and Lalouel 1973*a*, 1973*b*), and Melanesia (Imaizumi and Morton 1970)—and between minority nationalities in China (Ai et al. 1987; Matsumoto 1988). It seems also to be justified in Africa, either locally, as we have demonstrated here, or at the continental level (Excoffier et al. 1987).

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