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The Peopling of Sub-Saharan Africa: The Case Study of Cameroon

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ABSTRACT This study analyzes the distribution of ten protein genetic polymorphisms in eighteen populations from the most densely inhabited areas of Cameroon. The languages spoken belong to three different linguistic families [Afro-Asiatic (AA), Nilo-Saharan (NS) and Niger-Kordofanian (NK)]. The analysis of variation of allele frequencies indicates that the level of genetic interpopulation differentiation is rather low ($F_{st} = 0.011 \pm 0.006$) but statistically significant ($p < 0.001$). This result is not unexpected because of the relatively small geographic area covered by our survey. This value is also significantly lower than the one estimated for other groups of African populations. Among the factors responsible for this, we discuss the possible role of gene flow. There is a considerable genetic differentiation among the AA populations of north Cameroon as is to be expected because they all originated from the first agriculturists of the farming "savanna complex." The Podowko and Uldeme are considerably different from all the other AA groups, probably due to the combined effect of genetic drift and isolation. In the case of the Wandala and Massa, our analyses suggest that genetic admixture with allogeneous groups (especially with the Kanuri) played an important role in determining their genetic differentiation from other AA speaking groups. The Bantu speaking populations (Bakaka, Bamileke Bassa and Ewondo, NK family, Benué Congo subfamily) settled in western and southern Cameroon are more tightly clustered than AA speaking groups. This result shows that the linguistic affinity among these four populations coincides with a substantial genetic similarity despite their different origin. Finally, the Fulbe are genetically distinct from all the populations that belong to their same linguistic phylum (NK), and closer to the neighboring Fali and Tupuri, eastern Adamawa speaking groups of north Cameroon. Am J Phys Anthropol 110:143–162, 1999.

Cameroon is of considerable anthropological interest for two historical reasons. The peopling of Cameroon involved a process of sedentarization into a few nuclei that is ancient and well-documented. The connections of these earlier people with present-day populations are yet to be understood. In more recent times, Cameroon has been invaded by numerous migratory waves of people of different origin and language, hence this country may be regarded as the first meeting point between the Bantu and Sudanese cultures and peoples.

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The populations of this area display biocultural heterogeneity. There are three distinct habitats between latitudes 2° and 13°N: equatorial forest in the south and central regions, savanna and the Sahel in the northern regions. This environmental heterogeneity led to the development of two different subsistence strategies: the tropical vegecultural systems (yam and palm oil) developed in the forests of southern and central Cameroon and the cereal cultivation (sorghum and millet) developed in the northern regions (Harris, 1976).

In 1985, our research group started a survey on some populations of Cameroon [for a general prospect see Spedini and Bailly (1987) and Destro-Bisol et al. (1990)]. Some genetic and epidemiological data have been presented elsewhere (see Destro-Bisol and Spedini, 1989; Destro-Bisol et al., 1992, 1994; Mencarini et al., 1991; Scozzari et al., 1994). In this paper, we present new data and a final analysis of all protein polymorphisms. The results obtained are discussed in a framework that includes archeological and linguistic knowledge.

THE PEOPLING OF CAMEROON: PRESENT KNOWLEDGE

The first papers on the archaeology, demography, and ethnology of Cameroon's populations appeared a few years after the beginning of the German protectorate in 1884 and publications continued slowly until independence in 1960 (Van Morgen, 1893; Brussaux, 1907; Royer, 1933; Grall, 1936; Millous, 1937; Masson, 1939; Vallois, 1939; Olivier, 1945, 1948; Lalouel, 1949). From 1960 to the present day, francophone and anglophone Africanists have carried out a lot of archaeological, demographic, and linguistic research, whereas anthropological studies were limited to the analysis of some genetic polymorphisms in a few groups (Hiernaux, 1968; Goedde et al., 1979; Bernstein et al., 1980; Constans et al., 1985).

Pre-historic and proto-historic peopling

Paleoanthropological remains in Cameroon are very scanty as in most of central Africa. Two skeletons associated with Later Stone Age (LSA) artifacts (including a single implement of "ax hoe" type and pottery) were found at the Shum Laka rock shelter, on the western plateau (Shaw, 1969). Furthermore, skeletal remains attributed to a young adult about 135 cm tall were recovered near to the Mbi volcano (at 2000-m A.S.L.). Despite their fragmentary status, these remains were used by Warnier (1984) to sustain his theory that "the Negroid type" was present on the plateau between 5000 and 6000 BP. Unfortunately, the absence of original anthropometric data in his paper impairs a critical assessment of this conclusion.

The archaeological surveys in western and northern Cameroon indicate an uninterrupted human presence from at least the final Early Stone Age (ESA) (Lebeuf, 1981; Marliac, 1981; David, 1981; De Maret, 1985; Mveng, 1984; Warnier, 1984; Clist, 1987).

The oldest nucleus of sedentarization was identified in northern Cameroon. Linguistic analyses suggest that stable human settlements were present in the Lake Chad region from at least 6000 BP. Their subsistence was based on farming Sudanic seed (sorghum and bulrush millet), and is described by archeologists as the farming "savanna complex" (Ehret, 1984). These groups gave rise to the "Sao" civilization (Lebeuf, 1981), which are represented at a large number of archeological sites that date back to 1500 BP (McIntosh and McIntosh, 1983) in the southern shores of Lake Chad. Archeological records from these sites suggest that the Sao absorbed pre-existing hunter-gatherer communities and introduced proto-agricultural practices and extensive use of aquatic resources (Lebeuf, 1981). The plain of upper Benoue and the eastern slopes of the Mandara Mountains are other areas of archeological interest. Here sites were found with an impressive quantity of ground and/or polished stones axes, adzes, and pottery of the Neolithic age (Marliac, 1981). In the same area, David (1981) identified some Neolithic settlements dating back to 5000 BP. All this evidence suggests that ". . .during the late second and first millennia BC a mixed farming economy was firmly established in the Chad basin and Mandara mountains. . ." (David, 1981, p84).

A second nucleus of sedentarization was identified in western Cameroon, along the

northern edges of the forest and the mountain slopes of the Nigerian-Cameroon plateau. It is thought to be a proto-Bantu group which originated on the Nigerian-Cameroon plateau around 4000 BP, a date that is thought to mark the linguistic divergence of the Benue-Congo linguistic sub-branch from the Niger-Congo branch (Ehret, 1984). If such is the case, this proto-Bantu settlement would predate the appearance in the same area of the so-called Nok culture (2600 BP), also defined as the "sculptor and metal worker culture" (Alexandre, 1981; Vansina, 1984). During their diffusion through the humid forest, these proto-Bantu groups developed a yam-palm oil economy and fishing with canoes was also of primary importance (David, 1981). A certain degree of admixture between these groups and the Sudanic peoples of north Cameroon occurred at the end of the fourth millennium (Porteres and Barreau, 1981). This led to what Coursey described as the "cross-fertilization of ideas"(Coursey, 1976, p402), as can be seen by the development of crop cultivation in the forest after Bantu contact with agriculturists from the north (David, 1976; Stahl, 1984).

A third nucleus of sedentarization has been identified in the south-central region around the capital Yaounde. The Neolithic settlement of Obobogo dates back to 3000 BP and is regarded as being the oldest farming community of the "forest fringes complex" of the "Neolithic peoples of Guinea" (McIntosh and McIntosh, 1983) or western Bantu (Vansina, 1984). The first proto-Bantu village of central Africa with smelt iron artifacts appeared a thousand years later (De Maret, 1985; Essomba, 1989).

Further contribution to the peopling of Cameroon comes from relatively recent migrations that are described below.

Cameroon's populations today

According to the second population census (1987) in Cameroon, there were 10,490,655 inhabitants, with a density of 22 inhs/km^2 (Demo' 87, 1987). The population is subdivided into more than 200 ethnic groups — a real melting pot (Ki Zerbo, 1972). More than 63% of the total population is rural (Marguerat, 1976).

TABLE 1. The main languages spoken in the north (N), west (W) and central-south (CS) areas of Cameroon

Phylum	Branch	Sub-branch
Afro-Asiatic (N)	Chadic (1)	
Nilo-Saharan (N)	Saharan (2)	
Niger-Kordofanian (N, W, CS)	Niger-Congo (3)	West-Atlantic (3a)
		Adamawa eastern (3b)
		Benué-Congo (3c)

Our survey was carried out in five provinces. The *Extrême Nord* province is inhabited by a total of 1,800,000 individuals, with a maximum density in the Mandara Mountains (140 inhs/km^2) and an average of 50.8 inhs/Km^2. The *Nord* province is inhabited by a total of 832,000 individuals, with an average density of 9.6 inhs/km^2. These two provinces could be considered the domain of the autochthonous animist farmers and of the allogeneous Islamic communities. The *Ouest* province (Bamileke plateau, an altitude of 800–1400 m ASL), is inhabited by a total of 1,370,000 individuals (98.6 inhs/km^2). The Bamileke are the most important group. The *Centre* province is inhabited by a total of 3,533,000 individuals, with a density ranging from 26 to 80.3 inhs/km^2. The *Littoral* province is inhabited by a total of 1,353,000 individuals, with an average density of 80.3 inhs/km^2. The last two provinces are the domain of the Bantu-speaking groups, which are situated in a forest environment; e.g., the plantation areas and around the principal towns (Yaounde, Duala and Nkongsamba).

The last census does not provide information on the total size of each ethnic group. Therefore the following studies were used: (i) Podlewsky (1966), Martin (1970), Boutrais (1973), Boulet and Seignobos (1978) and Hallaire (1991) for the Extrême Nord and Nord provinces; (ii) Barbier et al. (1983), and Champaud (1983) for the Ouest province; Alexandre and Binet (1958) and Champaud (1983) for the Centre and Littoral provinces.

THE POPULATIONS AND THEIR LANGUAGES

According to Greenberg's classification (Greenberg 1963, 1980; Barretau et al., 1984), the languages spoken in Cameroon belong to three phyla or families (Table 1).

The Afro-Asiatic family (1)

The Daba, Mafa, Mada, Podowko, and Uldeme speak a language that belongs to the Chadic branch of the AA linguistic family. Collectively indicated by the French term "Montagnards," they are regarded as to the autochthonous populations of the Mandara Mountains. They are thought to have originated on the plains to the south of Chad Lake, in the region formerly inhabited by the Sao (Lebeuf, 1981). To avoid contact with the Kanem Empire (founded in the 8th century), they moved to the south and in the 13th century they settled in the Mandara Mountains (Martin, 1970; Ki Zerbo, 1977). The Montagnards are presently divided into hundreds of small communities that developed from paleo-Sudanic groups ("paléo-Négritique" according to Bauman and Westerman, 1948) and are geographically close to one another (Boutrais, 1973). They form distinct clans. However, they share the same language and agricultural methods, such as terraced cultivation of sorghum and millet utilizing the hoe (Hallaire, 1991). The development of agricultural techniques that were perfect for a mountain environment enabled them to optimize the exploitation of natural resources (Boutrais, 1973). According to the 1976 census, there are about 400,000 Montagnards since the population increase from 1976 has been counterbalanced by migration (Hallaire, 1991). The Mafa (or Matakam after the Fulfulde term) total 100,000, the Uldeme 6,000, the Mada 10,000, the Podowko 9,600 and the Daba 17,000. From 1920 onwards, the Mafa initiated migrations toward the plains around Mora, so that there are certain quarters that are completely composed of Mafa people within Wandala and Kanuri villages (localities Mora and Memè) and Fulbe villages in the Garua area.

The Wandala (or Mandara after the Fulfulde term) — about 17,000 individuals — partly inhabit the "arrondissement" of Mora and are mostly settled in the Meme village. They are part of the same paleo-Sudanic stock that gave origin to the Montagnards. In the 15th century, they founded a little kingdom which ruled over the Montagnards. They came in contact with the Kanuri and Fulbe peoples, in the seventeenth and eighteenth century respectively, and became completely converted to Islam.

The Guiziga and Massa are two other AA speaking groups of paleo-Sudanic origin. The Guiziga, with a population of 55,000 individuals, are presently dispersed on the eastern plains around Marua, their old capital. The Massa, 75,000 in total, are of animist religion like the Guiziga. They are dispersed along the western and eastern Logone banks in the flood plain downstream between Cameroon and Chad.

The Nilo-Saharan family (2)

The Kanuri (also known as the Bornuans or the Sirata), 25,000 in total, are traders and artisans. They originated from the Bornu (Nigeria) and are thought to be the descendants of the Moslem invaders who arrived in northern Cameroon probably in the 17th century (Boulet and Seignobos, 1978). At present, they are mainly settled in the Mora and Marua areas.

The Niger Kordofanian family (3)

The West-Atlantic subfamily (3a). The Fulbe, also known from the French term "Peuls," total about 183,000 individuals and represent the largest allogeneous ethnic group in northern Cameroon (Podlewski, 1966). Originally nomadic herders, they moved from Nigeria to the Wandala area in different periods from the 18th century onwards (Mohammadou, 1973). After the Djihad in 1806, they founded an empire in the Adamawa plateau, to the north of the Benue River. Once settled in north Cameroon, the Fulbe progressively abandoned sheep-farming and have taken up agriculture. Initially, they remained isolated from autochthonous groups, but later they started a process of cultural assimilation ("fulbization") and imposed their religion (Islam) and language (Fulfulde) on the Fali, Wandala, and other groups. Fulfulde is now the vehicular language in northern Cameroon, a fact that helps in the diffusion of the Fulbe culture in this area. At present, they live mainly in the towns of Marua (60%) and Garua (20%), but are now spreading to rural villages (20%), where they work as farmers. Among the different clans (the Wolarbe, Yillaga, Ferobé

and Bororo), only the Bororo have preserved the traditional Fulbe culture (Mohammadou, 1973).

The Eastern Adamawa sub-family (3b). The Mundang (27,000) and Tupuri (70,000) are dispersed on the plains to the west of the Massa area. They have maintained their paleo-Sudanic tradition and practice an animist religion. The Fali (42,000) are settled along the slopes of the Tinguelin-Kangu and Peske-Boro massifs to the northwest of Garua. After contact with the Fulbe in the 18th century, they acquired the Islamic culture and religion (Mohammadou, 1973). The Tali arrived in northern Cameroon from the Central African Republic in the last century. The migratory flow still continues also today, and is mainly directed toward Garua and its surroundings.

The Benue-Congo sub-family (3c). The Benue-Congo language groups are also referred to as the Bantu groups. The Bamileke — more than one million individuals — inhabit the western plateau known also as the "Bamileke plateau" (Atlas National du Cameroun, 1984). The first nucleus of the Bamileke originated from the Ndobo, who were Sudanic savannah-dwellers who migrated to western Cameroon in the 18th century from the North. Avoidance of contact with the Fulbe was the principal reason for this migration. Others followed this first migration from the south and north (Spedini and Bailly, 1987). The first migrants underwent a high degree of mixing with the Bantu-speakers who were already settled on the plateau (Champaud, 1975). The Bamilekes are of Sudanic origin, and are divided into feudal chiefdoms (chefferies) with a rigid internal hierarchy. The Bandjum, founded in 1790, is thought to be the oldest "chefferie" (Ghomsi, 1972). The Bamileke, the most dynamic ethnic group of Cameroon, have been spreading to other areas since the beginning of the century. This is due to a considerable demographic increase [3% between 1967 and 1976 (Champaud,1983)]. Migration was mostly directed towards the Littoral province, where the Bamileke colonized some rural areas and settled in the Nkongsamba, Duala and Yaundè towns.

The Ewondo (95,000 individuals) are part of the Beti peoples who migrated to central-southern Cameroon from Southern Adamawa in the 17th century (Alexandre, 1981). The Ewondo are settled in the Yaundè surroundings, mainly in forest areas.

The Bassa are settled westward of the area inhabited by the Ewondos. They are considered to be the second population to settle in southern Cameroon after Pygmies (Laburthe, 1981 cited in Essomba, 1991). In the 18th century, the Beti-Fang-Bulu peoples pushed them in their present-day settlements on the right bank of the Sanaga River.

The Bakaka (4,100 individuals) are settled in the Mungo division (Littoral province). Together with the Barekos, Muameuans, Elongs and other groups, they form the so-called "Mbo-Bakossi group," which is believed to have originated from an ancestor called Ngo who came from Mount Manengumba. They suffered a considerable demographic and economic crisis when the Bamileke expanded (Spedini and Bailly, 1987).

AIMS OF THIS STUDY

Our survey was done in the three most densely populated areas of Cameroon, both in the past and present times. The populations were chosen in order to obtain a reliable outline of anthropological and linguistic heterogeneity (see Table 2 and Fig. 1).

The peopling of Cameroon has been characterized by three ancient nuclei of sedentarization and, subsequently, by many different migratory waves of peoples of different origin and language. This predicts a high genetic inter-population heterogeneity. On the other hand, old and new populations underwent a certain degree of gene flow that presumably erased part of their original diversity. Therefore, we first intend to analyze genetic differentiation among the populations examined and the relationships of the measures of differentiation with linguistic and geographic distances.

Almost all the populations examined in the present survey belong to the AA and NK linguistic families. The AA speaking groups may be regarded as the descendants of the

TABLE 2. The populations examined, their language and places of sample collection

Province (chief town)	Place of Collection	Ethnic group	Language[1]	Sample size
Extrême Nord (Marua, 10°37′N; 14°20′E)	Marua, Meme Mora	Daba	1	49
		Guiziga	1	41
		Mada	1	62
		Mafa	1	114
		Massa	1	53
		Podowko	1	34
		Uldeme	1	65
		Wandala	1	187
		Kanuri	2	52
		Fulbe	3a	47
Nord (Garua, 9°20′N; 13°25′E)	Banay, Garua, Pitoa	Fali	3b	330
		Fulbe	3a	193
		Mundang	3b	85
		Tali	3b	68
		Tupuri	3b	101
Ouest (Bafussam 5°15′N; 10°20′E)	Bafussam, Bandjum Mbuda	Bamileke	3c	1056
Littoral (Nkongsamba, 4°55′N; 9°55′E)	Bakwat, Ebone, Nkongsamba, Manengole	Bakaka	3c	280
		Bamileke	3c	210
Centre (Yaundè, 3°55′N; 11°25′E)	Febé, Mbot-Makak, Yaundè	Bassa	3c	183
		Ewondo	3c	169

[1] The number in this column refers to the linguistic classification reported in Table 1.

first agriculturists of the farming "savanna complex" (Lebeuf, 1981). Therefore, they probably started their expansion around 6000 BP (Ehret, 1984). As a consequence of their ancient expansion and because they are scattered over a wide geographic area, one would expect such groups to be considerably differentiated. However, by viewing single populations, one may understand the role played by drift and and/or admixture in determining genetic differentiation among the AA groups.

Among the four Bantu groups examined, the Bakaka and Bassa may be regarded as descendants of the third nucleus of sedentarization (De Maret, 1985; Essomba, 1989, 1991), whereas the Bamileke and Ewondo arrived in western and central Cameroon, respectively, only in relatively recent times (in the 18th and 17th centuries, respectively. The adoption of the Bantu language is a recent event for these two populations, since they originated from the broad and heterogeneous group of Sudanic populations. The Bamileke incorporated some autochthonous Bantu groups during their migrations and settlement in western Cameroon. The Ewondo underwent a certain degree of gene admixture with neighboring Bantus. Therefore, it is of anthropological interest to evaluate whether the Bamileke and Ewondo are also genetically related to the Bakaka and Bassa.

Finally, we have considered other allogeneous groups: the Fulbe, Tali, and Kanuri. In this instance, we also considered an assessment of their genetic similarity to other Cameroon populations. It is known that the Fulbe exerts a strong cultural influence on some neighboring groups. It would be interesting to establish whether this process of Fulbe cultural might have facilitated a process of genetic homogenization. To cast light on this matter, we have also considered three eastern Adamawa speaking populations (the Fali, Mundang, and Tupuri). The lack of reliable historical information makes it difficult to draw any conclusions on the origin of eastern Adamawa groups. However, these populations have adsorbed the Fulbe culture to different degrees. Thus, they may be useful in assessing the genetic effects of the fulbization process.

MATERIALS AND METHODS

A total of 3,379 blood samples were collected in K_3EDTA tubes during different expeditions led by one of us (G.S.), from 1985 to 1992. Only unrelated donors born in the same village as their parents and in apparent good health were considered. The samples were stored at −20°C within 12 hr

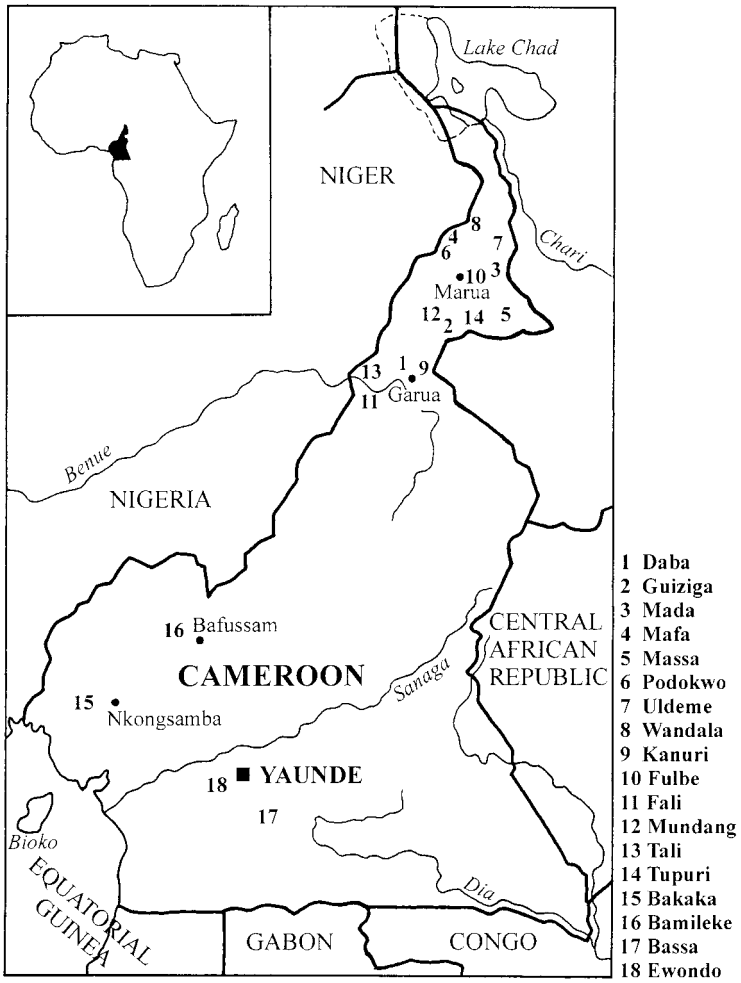

Fig. 1. Geographic map of Cameroon showing the location of the groups examined. Populations are numbered according to the sequence adopted in Table 2.

of collection, and then were flown on ice to the laboratory of Anthropology of the University of Rome "La Sapienza" and stored at −30°C before undergoing electrophoresis.

Laboratory analyses

Erythrocyte and serum polymorphisms (the abbreviation is followed by the reference to the electrophoretic technique used) analyzed were: 6-phosphogluconate dehydrogenase (6-PGD; Sonneborn et al., 1972); acid phosphatase locus 1 (ACP1; Destro-Bisol and Ranalletta, 1988); α_1-antitrypsin (A1-AT; Pascali and De Mercurio, 1981); carbonic anhydrase locus II (CAII; Noppinger and Morrison, 1981); esterase D (ESD; Destro-Bisol and Spinella, 1989); glyoxalase locus I (GLOI; Meera Khan and Doppert, 1976); group specific component (GC; Pascali et al., 1984); glutathione peroxidase (GPX1; Meera Khan et al., 1984); phosphoglucomutase locus 1 (PGM1; Destro-Bisol and Spinella, 1989); transferrin (TF; Pascali et al., 1988). 6-PGD, CAII, GLOI and GPX1 were typed by conventional electrophoresis on gelled cellulose acetate strips (Cellogel). A1-AT, ACP1, ESD, GC, PGM1, and TF were analyzed by isoelectric focusing on polyacrylamide gels. For CAII, GLOI, GPX1, ACP1, ESD, and PGM1 polymorphisms, 0.05 M

dithiotreitol (DTT) was used as a lysis solution to avoid mistypings resulting from protein denaturation.

Data analyses

Allele frequencies were obtained directly by gene counting. For the sake of brevity, observed and expected phenotype frequencies are not reported here, but are available in electronic form at the e-mail address of the senior author (G.S.).

Given the small sample size of some population samples, an exact test was used to assess the congruence between observed genotypic proportions and those predicted by the Hardy-Weinberg equilibrium (HWE) (Guo and Thompson, 1992; Rousset and Raymond, 1995).

The values of the Wright's (1943, 1965) indexes F_{it}, F_{is}, and F_{st} were obtained by means of the Fstat program (Goudet, 1996) which computes unbiased estimates of *F*-statistics (Weir and Cockerham, 1984) and their degree of significance by using permutations (Excoffier et al., 1992).

Genetic relationships between populations were calculated by the method of Harpending and Jenkins (1973). The genetic distances, with this method, are derived from a relationship (*R*) matrix, which is the normalized covariance matrix of allele frequencies across populations. The analysis was performed locus by locus, and the data was then averaged over all alleles. According to Workman et al. (1973), all alleles were weighted equally without taking into account the number of alleles per locus.

To visualize the genetic relationships among the groups examined, we analyzed the genetic distance matrix by principal component (PC) and cluster analysis. In the second case, the unweighted pair-group method using arithmetic averages (UPGMA) was used (Sneath and Sokal, 1973). Even though it is one of the oldest clustering methods (Sneath and Sokal, 1973), UPGMA performs well even with relatively high errors in distance measurements. In this study, UPGMA provided more easily interpretable results than other clustering methods [e.g., neighbor joining trees (data not shown)].

To analyze the relationships between genetic similarity (*R* matrix values) and geographic and linguistic distance matrices, we computed Spearman's ρ correlation and partial correlation coefficients. This method was preferred to Pearson's product moment correlation "*r*" since it assumes only a monotonic relationship, not a linear one, between the variables (Pollard 1977, Relethford, 1985). While Spearman's ρ was preferred for methodological reasons, it is worth noting that values obtained from our data set with the two methods were very similar, and most of the differences were due to a slightly greater value of Spearman's ρ coefficients (data not shown). This substantial similarity between the values obtained with the two methods is important since it allows a direct comparison between our results and those provided by studies in which the product moment correlation coefficients were used (see the Discussion section). Furthermore, no substantial difference between the two methods was observed also when the product moment correlation coefficients were calculated using different dissimilarity index values between distinct linguistic families (data not shown). This indirectly indicates that our method for assessing the relationships between linguistic and genetic diversity is relatively robust to variation in the weight given to language-family differences (see Poloni et al., 1997).

Probabilities of correlation between matrices were derived by using a directional hypothesis as required by basic models of genetic population structure, i.e., that the correlation between genetic affinity, linguistic, and geographic distances should be negative, but positive between linguistic and geographic distances. Probability values were assessed using the Mantel's test (Mantel, 1967; Relethford, 1990). As suggested by Jackson and Somers (1989), the number of permutations was fixed at 10,000 to minimize fluctuation of probability values. Geographic distances were calculated (in kilometers) by measuring the distance of line of the road between the main villages. Linguistic distances were obtained as follows: (i) groups speaking a language of the same sub-branch were assigned a distance of 1; (ii) groups speaking a language of the same branch were assigned a distance of 2; (iii) groups speaking a language of the same family

were assigned a distance of 3; (iv) groups speaking languages belonging to distinct families were assigned a distance of 4. Partial correlations were evaluated using the software developed by de Vries et al. (1993).

RESULTS

Hardy-Weinberg equilibrium and variation of allele frequencies

No consistent pattern of deviation from the Hardy-Weinberg equilibrium (HWE) was observed. In fact, only a few statistically significant p-values were obtained, and they were not associated with specific populations or polymorphisms. Among the ten loci analyzed, p-values <0.05 were encountered at seven loci (ACP, CAII, GLO, GPX1, PGM1, A1-AT, and GC). A maximum of four statistically significant departures from HWE was found for the GC locus (Daba, $p = 0.026$; Guiziga, $p = 0.038$; Bakaka, $p = 0.006$; Bamileke, $p = 0.001$), and a minimum of one case was observed for the PGM1 (Mada, $p = 0.05$) and TF loci (Bassa, $p = 0.003$). Two cases were found for ACP1 (Fulbe, $p = 0.019$; Mundang, $p = 0.024$), CAII (Wandala, $p = 0.045$; Tali, $p = 0.002$), GPX1 (Wandala, $p = 0.024$; Bamileke, $p = 0.017$) and A1-AT (Uldeme, $p = 0.043$; Tali, $p = 0.002$).

The allele frequencies at the 10 loci examined are reported in the Appendix. Table 3 shows some parameters for the distribution of the 28 alleles among the 18 populations examined. This considerable intergroup variability is associated with an extended range of allelic frequencies for most of the loci analyzed. Interestingly, the Podowko and Uldeme alone account for about one-third (15 out of 46) of the values at the extremes of frequency ranges. Locus-by-locus comparisons of phenotype frequencies among all populations showed a marked genetic variation (chi square test; p-value from 0.010 for GPX1 to 0.000 for 6-PGD). G_{st} coefficients of gene differentiation (Nei, 1973) point to significant genetic variations ($P < 0.001$) for all the loci examined.

TABLE 3. Allele frequency statistics

Locus and alleles	Mean	Standard deviation	Allele frequency range Min.	Max.
Erythrocyte polymorphisms				
6-PGD				
A	0.9191	0.0428	0.806	0.971
C	0.0809		0.029	0.194
ACP				
A	0.1892	0.0446	0.097	0.279
B	0.8002	0.0471	0.697	0.903
R	0.0107	0.0084	0.000	0.026
CAII				
1	0.9452	0.0326	0.858	0.990
2	0.0548		0.010	0.142
ESD				
1	0.8943	0.0516	0.750	0.969
2	0.1057		0.031	0.250
GLO				
1	0.3929	0.0502	0.280	0.475
2	0.6071		0.525	0.720
GPX1				
1	0.9410	0.0264	0.857	0.979
2	0.0590		0.021	0.143
PGM1				
1+	0.6548	0.0586	0.483	0.771
1−	0.1460	0.0408	0.076	0.227
2+	0.1526	0.0456	0.085	0.267
2−	0.0466	0.0261	0.015	0.125
Serum polymorphisms				
A1-AT				
M1	0.9056	0.0339	0.824	0.955
M2	0.0154	0.0089	0.000	0.038
M3	0.0679	0.0269	0.030	0.129
S	0.0111	0.0097	0.000	0.030
GC				
1F	0.8323	0.0341	0.785	0.912
1S	0.0998	0.0319	0.036	0.171
2	0.0679	0.0237	0.000	0.095
TF				
C1	0.8718	0.0453	0.793	0.970
C2	0.0772	0.0364	0.015	0.169
C3	0.0022	0.0046	0.000	0.018
D1	0.0488	0.0190	0.015	0.080

Ethnic endogamy

As a preliminary step to the analysis of genetic structure, we collected information on mating behavior. For this purpose, each blood donor was requested to recall his/her parents ethnic group. The results obtained are reported in Table 4. The endogamy rate ranges from 86.96 to 100% (Table 7). The groups with the highest values were the Bamileke, the five Montagnard groups and the Tupuri. Ethnic pride is an important factor in determining endogamy among the Bamileke. In fact, as indicated by our data, mixed marriages are mostly limited to Bamileke females who lose all contact with their natal group after marriage. At the same time, Bamileke males resident in the Littoral province return to the Bamileke plateau to marry. As far as the Montagnards are concerned, geography is one of the main factors in determining endogamy. The moun-

TABLE 4. Endogamy in the examined populations[1]

Propositus' and father's ethnic group	Total marriages	Mixed marriages	Endogamy rate (%)	Mother's ethnic group
Daba	48	1	97.92	Fulbe
Guiziga	38	4	89.47	Fali, Fulbe, Mundang, Fali
Mada	62	0	100.00	
Mafa	110	0	100.00	
Massa	50	3	94.00	Fulbe, Haussa, Tupuri
Podowko	33	0	100.00	
Uldeme	65	0	100.00	
Wandala	171	16	90.64	Mafa, Mada, Mundang (3), Kanuri (8), Fulbe (3)
Kanuri	46	6	86.96	Gambai, Fulbe (2), Kotoko, Mafa, Mandara ,
Fulbe	233	7	97.00	Daba, Fali (3), Guiziga, Haussa, Mundang
Fali	324	7	97.84	Arabis Choa, Fulbe (5), Mafa
Mundang	83	2	97.59	Guiziga, Mbun
Tali	67	1	98.51	Mbun
Tupuri	99	0	100.00	
Bakaka	278	4	98.56	Bamileke (4)
Bamileke	1298	1	99.92	Eton
Bassa	179	4	97.77	Baganga, Ewondo, Ngambe, Yabassi
Ewondo	167	2	98.80	Bassa (2)

[1] In this and subsequent tables, populations are ordered as in Table 2.

tainous environment that has always sheltered them from migrations of groups coming from the north, makes contact with other groups difficult. Among the Tupuri endogamy also has an historical reason, since it was established to avoid any contact with the Fulbe and earlier invaders.

The lowest endogamy was observed among the Kanuri (86.96%), Guiziga (89.47%) and Wandala (90.64%). The high mobility of Kanuri traders may explain their exogamic behavior. It is interesting to note the high level of intermarriage between the Wandala and Kanuri.

F-statistics

The extent to which the marital behavior and the subdivision of the population influences genetic diversity was examined by using Wright's hierarchical inbreeding coefficients F_{it}, F_{is}, F_{st} (Wright, 1943, 1965). These parameters represent the probability of identity of alleles of individuals relative to the total population (F_{it}) and relative to the sub-population (F_{is}), while F_{st} is the probability of identity by descent between random alleles from each sub-population relative to those of the total population. These coefficients are related by the following formula:

$$F_{st} = (F_{it} - F_{is})/(1 - F_{is})$$

The results obtained for the overall data set are reported in Table 5. Taking all the eighteen populations into consideration produced a F_{it} estimate of 0.019 which is larger than zero with a statistically significant probability ($p = 0.0001$). Also F_{st} (mean value = 0.011) is larger than zero with a statistically significant probability ($p < 0.0001$) and is slightly higher than F_{is} (mean value = 0.009). Therefore, the analysis of *F*-statistics relative to the complete data set suggests that genetic diversity is low but statistically significant.

To study possible relationships between linguistic affiliation and genetic differentiation, we analyzed the AA and NK speaking groups separately (Table 6). The F_{it} estimates among the AA and NK speakers were distributed around a positive value of 0.025 and 0.016, respectively. Such a difference is mainly due to F_{is}, which is considerably higher among AA (mean value 0.018) than among NK groups (mean value 0.007), but both values are not statistically larger than zero. On the contrary, F_{st} values were very similar in NK and AA speakers (0.009 versus 0.008). This indicates a more marked effect of within-population inbreeding among AA populations, although the evidence that only the F_{st} values are larger than zero with a statistically significant probability suggests the inter-population differentiation is the predominant force in both the linguistic groups.

TABLE 5. Wright's F-statistic coefficients calculated on the global data set[1–3]

Locus	F_{it}	Prob. F_{it} not >0	F_{is}	Prob. F_{is} not >0	F_{st}	Prob. F_{st} not >0
6-PGD	−0.018	0.8479	−0.038	0.9861	0.020	**<0.0001**
ACP	0.056	**0.0003**	0.049	**0.0024 > *p* > 0.0021**	0.008	**<0.0001**
CAII	0.046	**0.0061**	0.038	0.0327 > *p* > 0.0171	0.008	**<0.0001**
ESD	0.016	0.1842	0.001	0.5084 > *p* > 0.4163	0.016	**<0.0001**
GLO	−0.009	0.6982	−0.027	0.9408 > *p* > 0.9328	0.018	**<0.0001**
GPX1	0.039	0.0162	0.034	0.0480 > *p* > 0.0249	0.005	**0.0004**
PGM1	0.023	0.0301 > *p* > 0.0300	0.017	0.0967 > *p* > 0.0871	0.006	**<0.0001**
A1-AT	0.043	**0.0028**	0.037	0.0112 > *p* > 0.0088	0.006	**<0.0001**
GC	0.012	0.2027	0.006	0.3536 > *p* > 0.3245	0.007	**<0.0001**
TF	0.005	0.3569	−0.009	0.7394 > *p* > 0.7047	0.014	**<0.0001**
All loci	0.019	**0.0001**	0.009	0.0575	0.011	**<0.0001**

[1] Probability values were calculated with a total of 10,000 permutations.
[2] Significant values according to a Bonferroni criterion (Hochberg 1988) are in **bold type.**
[3] In this and subsequent tables, genetic markers are ordered as in Table 3.

TABLE 6. Wright's F-statistic coefficients in Afro-Asiatic (AA) and Niger-Kordofan (NK) linguistic groups of Cameroon[1,2]

	F_{it}		F_{is}		F_{st}	
Locus	AA	NK	AA	NK	AA	NK
6-PGD	−0.033	−0.032	−0.033	−0.035	0.001	**0.003**
ACP	0.023	**0.062**	0.013	**0.056**	0.010	**0.007**
CAII	0.031	0.044	0.023	0.040	0.007	**0.005**
ESD	0.031	0.015	−0.000	0.007	**0.031**	**0.008**
GLO	0.012	−0.020	0.016	−0.037	−0.004	**0.016**
GPX1	0.065	0.034	0.049	0.032	**0.017**	**0.002**
PGM1	0.027	0.023	0.016	0.017	**0.011**	**0.006**
A1-AT	0.045	0.043	0.039	0.037	0.007	**0.007**
GC	0.056	0.003	0.055	−0.006	0.001	**0.009**
TF	0.018	0.001	0.004	−0.015	**0.014**	**0.016**
All loci	0.025	**0.016**	0.018	0.007	**0.008**	**0.009**

[1] Probability values were calculated with a total of 10,000 permutations.
[2] Significant values according to a Bonferroni criterion (Hochberg 1988) are in **bold type.**

Kinship and genetic differentiation

To evaluate the genetic affinities among the populations analyzed we performed a kinship analysis using the method of Harpending and Jenkins (1973). In this method, the weighted sum of all elements of the R matrix is zero; therefore positive r values indicate closer genetic similarity than average and negative values of r indicate less genetic similarity than average. The diagonal elements of the R matrix (r_{ii}) are the genetic distances of each population from the "centroid," defined as the average allele frequencies over all populations.

The kinship matrix is reported in Table 7. More than half of the r_{ij} pairwise values (88 out of 153) are negative and also the positive ones are generally not far from zero. This indicates an overall low genetic affinity among the 18 ethnic groups. The highest positive r_{ij} values are found between the Podowko and Mada (0.0153) and the Tali and Ewondo (0.0134). The Podowko and Mada have a common paleo-Sudanic origin, and, therefore, their genetic similarity may reflect their common evolution. The most negative values are found not only between groups that are geographically separated and belonging to different linguistic branches [Uldeme and Ewondo (−0.0134); Uldeme and Bakaka (−0.0132)], but also between two AA speaking groups from North Cameroon [Uldeme and Daba (−0.0161)].

The diagonal elements of the R matrix (local kinship values) indicate the degree of isolation of each population. The Uldeme and Podowko (0.043) display the highest values (0.045 and 0.043 respectively), whereas the other AA speaking groups present markedly lower local kinship values

TABLE 7. Kinship matrix[1]

	Daba	Guiziga	Mada	Mafa	Massa	Podowko	Uldeme	Wandala	Kanuri	Fulbe	Fali	Mundang	Tali	Tupuri	Bakaka	Bamileke	Bassa	Ewondo
Daba	.0123																	
Guiziga	−.0058	.0144																
Mada	−.0009	−.0026	.0163															
Mafa	−.0017	−.0014	.0065	.0085														
Massa	−.0059	.0022	.0001	.0041	.0139													
Podowko	.0057	−.0047	.0153	.0044	.0021	.0370												
Uldeme	−.0161	.0106	−.0001	.0003	.0042	−.0032	.0459											
Wandala	.0001	.0005	.0053	.0012	.0033	.0087	−.0058	.0077										
Kanuri	−.0055	.0030	−.0015	.0015	.0038	.0020	.0114	−.0006	.0141									
Fulbe	−.0033	−.0004	−.0015	−.0046	−.0044	−.0024	.0085	−.0014	.0010	.0102								
Fali	.0032	−.0022	−.0074	−.0019	−.0030	−.0125	−.0036	−.0054	−.0012	−.0003	.0116							
Mundang	−.0030	.0021	.0043	.0037	.0032	.0025	.0034	.0027	−.0011	−.0007	−.0030	.0067						
Tali	.0068	−.0068	−.0064	−.0046	−.0073	−.0096	−.0127	−.0045	−.0094	.0014	.0049	−.0026	.0220					
Tupuri	−.0015	.0008	−.0035	−.0001	.0003	−.0102	.0018	−.0026	.0001	.0014	.0054	−.0005	.0005	.0070				
Bakaka	.0047	−.0015	−.0062	−.0032	−.0030	−.0079	−.0132	−.0009	−.0076	−.0012	.0030	−.0023	.0062	−.0006	.0138			
Bamileke	.0026	.0005	−.0078	−.0053	−.0032	−.0085	−.0076	−.0024	−.0007	−.0003	.0040	−.0063	.0024	.0001	.0069	.0115		
Bassa	.0035	−.0029	−.0044	−.0029	−.0040	−.0102	−.0105	−.0028	−.0032	−.0031	.0041	−.0058	.0063	.0011	.0050	.0087	.0132	
Ewondo	.0049	−.0058	−.0056	−.0047	−.0066	−.0084	−.0134	−.0031	−.0062	.0011	.0042	−.0035	.0134	.0003	.0079	.0053	.0079	.0122

[1] Derived by the method of Harpending and Jenkins (1973).

with an extended range of variation (from 0.0085 to 0.0163). Only in the case of the Wandala is there an apparent relationship between the local kinship value (0.0077) and the percentage of mixed marriages (9.35%). Eastern Adamawa speaking groups show relatively low values (from 0.0067 to 0.0116), with the exception of the Tali (0.0220). This is in agreement with the theory that groups that settle on the plains are more easily subject to genetic admixture than those that settle in a mountainous environment. Regarding the Tali, their relatively high degree of isolation is not surprising if one considers that they arrived in Cameroon very recently. On the other hand, the value estimated for the to Tupuri (0.0070) is somewhat unexpected if you consider their high ethnic endogamy. Intermediate local kinship values (from 0.0115 to 0.0138) are found among the Bantu groups. In the case of the Bamileke, their ethnic endogamy would predict a higher degree of isolation than that observed. However, it may be argued that both the assimilation of autochthonous Bantu groups during their process of colonization of the Plateau and their large population size might have protected Bamileke from the genetic consequences of isolation. Finally, it is interesting to note that local kinship values in the Fulbe and Kanuri (0.0102 and 0.0141, respectively) are not as high as expected if you consider their linguistic isolation. This suggests that a certain degree of genetic admixture has occurred with neighboring groups.

The reduction of the multidimensional R matrix onto a two-dimensional eigenvector plot helps illustrate the genetic relationships among the groups examined (Fig. 2). The first principal component (PC) accounts for 56.86% of the total variance and is clearly influenced by geography. Populations living in the Extreme Nord province are generally at one extreme and those of the Ouest, Centre, and Littoral provinces are at the opposite side, with most of the populations of the Nord province in the middle. The AA and eastern Adamawa groups are more widely scattered than the Bantu groups. The only ethnic group belonging to the Nilo-Saharan family, the Kanuri, is placed near to the neighboring Guiziga

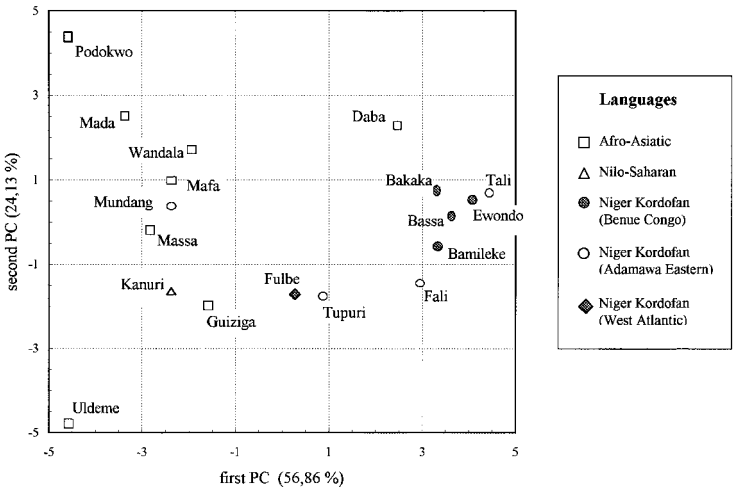

Fig. 2. Principal component representation of the genetic relationships among the populations examined.

and Massa. It is interesting to note that the Fulbe, who are the most historically diverse from all the other groups, appear to be approximately equidistant from the AA and other NK groups. The second PC (accounting for 24.13 % of the total variance) emphasizes the diversity of the Podowko and Uldeme also from other AA groups and, again, the relative homogeneity of the Bantu groups.

Figure 3 illustrates a dendrogram obtained by applying the unweighted pair group method using arithmetic averages (UPGMA) to the genetic similarity coefficients estimated according to Rogers (1972). The cophenetic correlation of 0.803 indicates that the dendrogram is a reliable representation of the information provided by all the analyzed loci. Using Euclidean genetic distances derived from the R matrix (Harpending and Jenkins, 1973) and other genetic distance methods (Rogers, 1972; Wright, 1978) we obtained results very similar to those described here (data not shown). The main result of this analysis is that the AA and NK populations cluster separately, with the Daba and Mundang being the only exceptions. Furthermore, it may be observed that genetic differentiation is higher among the AA populations, but it is also evident that the difference is mainly due to the greater differentiation of the Podowko and Uldeme, which represent one single point cluster. It is interesting that the Wandala are more similar to the Kanuri than to the other groups of paleo-Sudanic origin. As observed in the PC analysis, the Bantu populations are those most genetically coherent. The eastern Adamawa speakers appear to be markedly differentiated from Bantu groups with the Tali being the only exception. However, the position in the dendrogram of the latter group is not easily interpretable because their migratory flow still continues today, and sampling processes could, therefore, influence their genetic structure. The Fulbe are found in the same cluster of two of the three Adamawa speaking groups who live in their same area (the Tupuri and Fali). However, these two groups maintain some genetic similarity despite the different degree of genetic admixture with the Fulbe.

To analyze the differentiation among AA populations in more detail, a separate analysis excluding NK populations from calculations was carried out (Fig. 4). Also in this case, the value of cophenetic correlation (0.740) is satisfactory. For the Montagnard groups, the dendrogram emphasizes the differentiation of the Podowko, Uldeme, and Daba from the Mada and Mafa. It is also interesting to note that Mada, Mafa, Massa, and Wandala have remained relatively similar. This can be clearly seen by their position

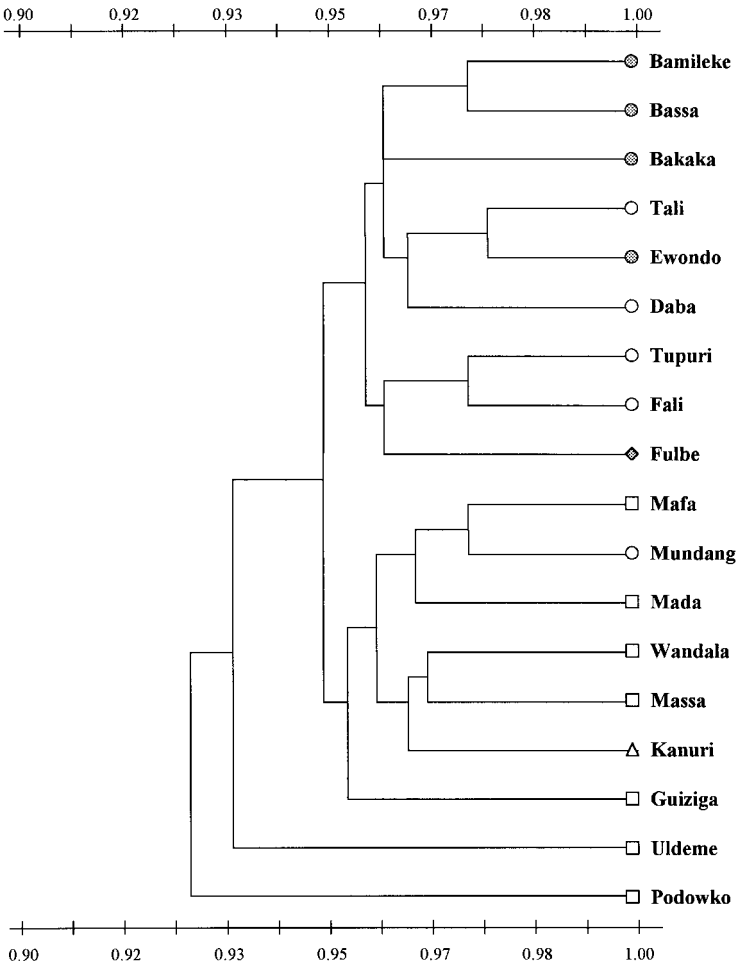

Fig. 3. UPGMA dendrogram based on genetic similarity coefficients estimated according to Rogers (1972) relative to the 18 populations examined. The same symbols as in Fig. 2 were used.

in two clusters which originate from the same node.

Correlation between genetic, geographic, and linguistics distances

Correlation and partial correlation coefficients (Spearman's ρ) between genetic, geographic and linguistic matrices are reported in Table 8. The correlation between any two given matrices showed the expected sign and were all highly significant, indicating that both geography and language are important determinants of genetic affinity among the populations examined. As shown in Table 8, 8.2 and 15.8% of the genetic variance is explained, respectively, by geography and language. Furthermore, the partial correlation between genetics and language ($r_{sGEN \times LIN(GEO)} = -0.299$; $p = 0.0025$) and between genetics and geography ($r_{sGEN \times GEO(LIN)} = -0.158$; $p = 0.0065$), show that the language-family relationship between populations contributes more than their geographic location to the genetic differentiation.

Given their geographic dispersal and linguistic heterogeneity, a separate analysis for NK speakers was carried out. In this case 25.5% of the genetic variation was explained by geography and the two matrices were highly significantly correlated ($p = 0.011$). When language was kept constant, partial correlation between genetics and geography

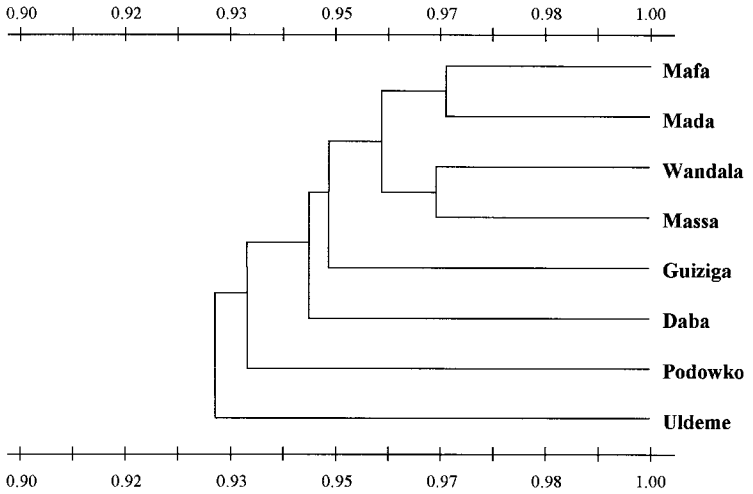

Fig. 4. UPGMA dendrogram based on genetic similarity coefficients estimated according to Rogers (1972) relative to the AA speaking groups.

TABLE 8. Spearman rank correlations for genetic (GEN), geographic (GEO), and linguistic (LIN) matrices calculated on the global data set

Matrices compared	Correlation (r_s)	Significance p (Mantel test)	Proportion of the variance explained (%)
Correlations			
GEN × GEO	−.286	.0013	8.2
GEN × LIN	−.397	.0013	15.8
GEO × LIN	.315	.0015	9.9
Partial correlations			
GEN × GEO (LIN)	−.158	.0065	2.5
GEN × LIN (GEO)	−.299	.0025	8.9

was again statistically significant (p = 0.0431), whereas when geography was kept constant the p-value was well in excess of 0.05 (p = 0.2215). Considering the moderate Spearman rank correlation between genetics and linguistics (r_s = 0.376) and the insignificant correlation between genetics and language when geography is kept constant (p = 0.2215), it appears that most of the genetic differentiation in the NK group is geographically patterned.

DISCUSSION

The archeological, historical and linguistic information reviewed in the present paper suggests that the peopling of Cameroon stems from three ancient nuclei of sedentarization followed by later migratory waves of peoples of different origin and language. Although our study cannot provide an accurate test of this hypothesis, our results are not in contrast with this view and provide additional information. In fact, it is evident that a certain differentiation occurs between the most ancient (AA populations) and most recently arrived populations (NK speaking groups). Considering the data set as a whole, language contributes more than geography to genetic differentiation. On the other hand, geography seems to have played a more important role than language on genetic differentiation among the NK populations.

A study of variation at the RH and GM loci in Sub-Saharan Africa reported relatively high correlation and partial correlation coefficients between genetics and language ($r_{GEN \times LIN}$ = 0.316 and $r_{GEN \times LIN(GEO)}$ = 0.321 for the RH system; $r_{GEN \times LIN}$ = 0.568 and $r_{GEN \times LIN(GEO)}$ = 0.505 for the GM system) (Excoffier et al., 1987). The values of the RH system from that study are comparable to ours, whereas results of the GM system are markedly higher. The lower level of correlation between language and genetics observed in the present study may be explained by gene flow between linguistically heterogeneous but neighboring populations. This is the case in the admixture between Fulbe and other groups of the Nord and Extrême Nord provinces or between Wan-

dala and Kanuri (see below). By contrast, the GM data set of Excoffier et al. (1987) populations are mostly geographically separated, and the correlation between language and geography has probably been less influenced by genetic exchange between linguistically diverse groups.

Within-group inbreeding seems to have played a lesser important role in determining the genetic differentiation. In fact, the mean F_{is} estimate for the global data set (0.009) and for the AA and NK populations (0.018 and 0.007) were not statistically different from zero and also considerably lower than those reported for groups with an acclaimed endogamic mating system (e.g., Das et al., 1996).

F_{st} may be used to compare genetic differentiation within different groups of populations. However, it is not always easy to compare F_{st} values obtained in independent studies. The estimates of F_{st} are very sensitive to the mode of clustering of populations (Jorde, 1980) and there may be also variations depending on the number of loci analyzed. Despite these caveats, it is evident that the F_{st} value we estimated (0.011) is approximately halfway between the European populations extremes (0.0002–0.0136; Jorde, 1980; Jorde et al., 1982) and the Indian castes (0.0438; Papiha, 1996) and the Yanomana (0.065; Ward, 1973). Furthermore, our value is lower than that calculated for all of sub-Saharan Africa (0.035; Cavalli-Sforza et al., 1994). Somewhat unexpected is the fact that our F_{st} is markedly lower than those calculated on less linguistically heterogeneous populations such as the populations belonging to the western branch of the Niger Congo languages (0.0211 ± 0.0017) and the broad and narrow Bantu (0.0157 ± 0.0014; Cavalli-Sforza et al., 1994). The difference between our value and these two estimates is also statistically significant when the standard errors are taken into account. This may be explained by three reasons. First, the F_{st} values reported by Cavalli-Sforza et al. (1994) were calculated on populations scattered on a geographic area considerably wider than that covered by our survey. Second, the heterogeneity of the Bantu groups studied by Cavalli-Sforza et al. (1994) is probably also due to admixture with the Pygmies and speakers of Khoi-San language (see Cavalli-Sforza et al., 1994), whereas only a limited genetic admixture occurred between some of the examined Bantu groups (the Bakaka, Bassa, and Ewondo) and the Pygmies living in southern Cameroon. Finally, taking into consideration the exogamic behavior of some AA populations (Fulbe, Kanuri, and Wandala), the homogenizing effect of gene flow is likely to be a further contributing factor. This may be also true for NK populations, since the lack of correlation between linguistic and genetic distances observed for these populations may result from gene flow across linguistic boundaries.

Given a presumable continuity with the first agriculturists of the farming "savanna complex," we observed a considerably high differentiation among the populations belonging to the AA linguistic family. This is clearly illustrated by the dispersal of AA populations on the PC graph and by the fact that they show the deepest branches in the UPGMA dendrogram. In comparison with NK populations, within-group inbreeding seems to have played a more important role in determining genetic diversity. The Podowko, Uldeme, and Daba are highly differentiated from each other and from other Montagnard populations. Combining the information provided by kinship analysis with data obtained on variation of allele frequencies, it appears that genetic drift and isolation are responsible for this in the Podowko and Uldeme, while data on mixed marriages indicate that such behavior still persists today. This is a plausible theory if one considers that the Podowko and Uldeme are organized in small communities settled in a mountainous environment, conditions which have probably impaired gene flow from other groups. Also in the case of the Mafa and Mada, data collected on mixed marriages suggest a high ethnic endogamy, but this is not accompanied by the other features observed in the Podowko and Uldeme. In fact, they are the most tightly clustered populations among all the AA speaking groups (Fig. 4) and kinship analysis indicates that their degree of isolation is markedly lower than that of the Podowko and Uldeme. Another interesting case is that of the Wandala and

Massa. Here, our analyses suggest that genetic admixture with allogeneous groups played an important role in determining their genetic differentiation from other AA speaking groups. This can be seen in the UPGMA dendrogram of Fig. 3, where these groups are more similar to the Kanuri than to other AA groups. Their high exogamy also supports this hypothesis, as does data on mixed marriages that indicate a high level of intermarriage between the Kanuri and Wandala.

Both PC and UPGMA analyses clearly show that the Bantu populations are considerably more tightly clustered than the AA and eastern Adamawa populations. This finding is consistent with the widely accepted view that the Bantu expansion is thought to have occurred more recently than the AA speaking groups, approximately 4000 BP (Ehret, 1980; David, 1982). However, given the Sudanic origin of the Bamileke and Ewondo, this implication is of particular interest. It suggests that the processes leading to the formation of the present-day Bamileke ethnic group and the gene admixture (Ewondo) have erased part of the original genetic diversity among the four Bantu groups. Thus, it appears that the common linguistic affiliation of the four populations coincides with a certain genetic similarity, despite their different origin.

Finally, there is no evidence of a marked genetic similarity between the Tali and their neighboring populations, whereas the effect of gene flow is more evident in the case of the Fulbe. While the situation of the Tali may be easily explained by their very recent arrival in Cameroon, the Fulbe are genetically distinct from all the populations who belong to their same linguistic phylum. This is explained by the fact that the Fulbe have never substantially admixed with other NK populations in Cameroon. Conversely, the Fulbe tend to cluster together with the eastern Adamawa speaking groups of north Cameroon. This is to be expected, since our data show that mixed marriages occur between the Fulbe and their neighboring groups of the Nord and Extrême Nord provinces, and our Fulbe sample is mainly composed (80.4 %) of individuals living in north Cameroon. Finally, given the different degree of cultural integration of the Fulbe with the Fali, Mundang, and Tupuri, our data may help evaluate the influence of the "fulbization" process on inter-population genetic variation. Assuming that culture exerts a strong influence on genetic exchanges, one would expect to find the Fulbe to be genetically closer to the Fali and Mundang than to the Tupuri. However, the PC and UPGMA analyses produced no such results. Therefore, it would appear that the influence of culture on mating choice has not yet been so strong and prolonged to shape the genetic affinities between the Fulbe and Eastern Adamawa speaking groups.

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APPENDIX. Gene frequencies (×100) at ten protein loci in the populations examined

	6-PGD		ACP			CAII		ESD		GLO		GPX1	
	A	C	A	B	R	1	2	1	2	1	2	1	2
Daba	90.6	9.4	20.8	77.1	2.1	91.5	8.5	96.9	3.1	34.4	65.6	95.8	4.2
Guiziga	94.6	5.4	9.7	90.3	0.0	97.2	2.8	85.7	14.3	41.9	58.1	93.2	6.8
Mada	87.7	12.3	27.9	69.7	2.4	99.0	1.0	91.0	9.0	44.8	55.2	91.7	8.3
Mafa	88.5	11.5	22.0	77.1	0.9	96.8	3.2	89.0	11.0	44.3	55.7	95.3	4.7
Massa	88.5	11.5	16.3	82.7	1.0	96.7	3.3	83.7	16.3	43.7	56.3	97.9	2.1
Podowko	80.6	19.4	27.4	72.6	0.0	98.2	1.8	92.2	7.8	40.3	59.7	91.9	8.1
Uldeme	89.7	10.3	14.6	83.9	1.5	95.3	4.7	75.0	25.0	40.6	59.4	85.7	14.3
Wandala	89.5	10.5	17.3	80.6	2.1	98.2	1.8	91.2	8.8	42.4	57.6	95.9	4.1
Kanuri	88.0	12.0	14.1	85.9	0.0	96.6	3.4	83.7	16.3	38.6	61.4	93.5	6.5
Fulbe	94.4	5.6	20.6	78.5	0.9	94.2	5.8	88.1	11.9	38.8	61.2	91.1	8.9
Fali	95.0	5.0	20.4	78.2	1.4	91.6	8.4	89.5	10.5	32.1	67.9	96.3	3.7
Mundang	90.7	9.3	21.6	77.2	1.2	96.2	3.8	87.8	12.2	47.5	52.5	95.1	4.9
Tali	94.8	5.2	20.5	78.8	0.7	85.8	14.2	94.8	5.2	43.3	56.7	94.8	5.2
Tupuri	95.3	4.7	16.7	80.7	2.6	93.8	6.2	86.7	13.3	39.7	60.3	95.4	4.6
Bakaka	97.1	2.9	17.6	82.2	0.2	93.8	6.2	96.2	3.8	38.4	61.6	94.9	5.1
Bamileke	96.4	3.6	14.2	85.6	0.2	94.0	6.0	92.0	8.0	28.0	72.0	95.2	4.8
Bassa	96.2	3.8	17.0	81.3	1.7	92.4	7.6	92.2	7.8	31.1	68.9	95.5	4.5
Ewondo	96.7	3.3	21.8	77.9	0.3	90.1	9.9	94.0	6.0	37.3	62.7	94.6	5.4

	PGM1				A1-AT				GC			TF			
	1+	1−	2+	2−	M1	M2	M3	S	1F	1S	2	C1	C2	C3	D1
Daba	67.0	10.2	10.2	12.5	94.6	1.1	3.2	1.1	81.5	12.0	6.5	87.5	7.3	0.0	5.2
Guiziga	64.1	20.3	12.5	3.1	91.5	1.4	5.7	1.4	82.9	17.1	0.0	87.5	5.6	0.0	6.9
Mada	70.8	14.2	11.7	3.3	93.1	2.6	4.3	0.0	80.7	11.4	7.9	91.2	4.4	0.0	4.4
Mafa	70.7	16.5	8.5	4.3	94.9	0.9	3.7	0.5	83.8	7.1	9.1	82.6	9.6	0.5	7.3
Massa	65.6	12.2	20.0	2.2	90.8	1.0	8.2	0.0	91.0	5.0	4.0	86.4	9.4	0.0	4.2
Podowko	48.3	21.7	26.7	3.3	95.5	1.5	3.0	0.0	80.3	12.1	7.6	97.0	1.5	0.0	1.5
Uldeme	64.1	22.7	10.1	3.1	83.9	2.7	11.6	1.8	83.9	12.5	3.6	80.4	10.7	1.8	7.1
Wandala	62.3	12.3	20.4	5.0	89.3	2.1	6.5	2.1	82.8	10.7	6.5	92.9	4.1	0.0	3.0
Kanuri	65.0	12.5	13.7	8.8	90.0	0.0	10.0	0.0	80.0	11.1	8.9	84.0	8.0	0.0	8.0
Fulbe	58.0	15.0	19.2	7.8	82.4	3.8	12.9	0.9	78.5	12.5	9.0	87.0	9.6	0.6	2.8
Fali	69.1	14.6	12.3	4.0	91.1	0.9	5.5	2.5	82.2	11.8	6.0	79.3	16.9	0.0	3.8
Mundang	65.0	18.6	13.5	2.9	88.0	1.2	7.8	3.0	82.1	11.1	6.8	86.4	6.2	0.0	7.4
Tali	70.0	11.0	13.0	6.0	88.5	1.5	8.5	1.5	82.8	9.4	7.8	90.9	6.8	0.0	2.3
Tupuri	66.5	13.8	15.4	4.3	91.9	2.0	5.6	0.5	79.4	11.3	9.3	81.1	14.2	0.0	4.7
Bakaka	61.0	14.9	20.7	3.4	89.9	1.3	6.3	2.5	91.2	3.6	5.2	84.6	8.8	0.0	6.6
Bamileke	66.2	15.8	14.8	3.2	90.3	2.3	7.0	0.4	87.0	6.6	6.4	89.9	6.6	0.2	3.3
Bassa	77.1	7.6	13.8	1.5	94.2	1.2	4.6	0.0	84.7	7.1	8.2	90.3	3.7	0.9	5.1
Ewondo	67.8	8.9	18.2	5.1	90.0	0.3	7.9	1.8	83.3	7.2	9.5	90.1	5.6	0.0	4.3