

## Differentiation of modern sub-Saharan African populations: craniometric interpretations in relation to geography and history

*Différenciation des populations contemporaines de l'Afrique sub-Saharienne : interprétations craniométriques en relation avec la géographie et l'histoire*

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**DIFFERENTIATION OF MODERN SUB-SAHARAN AFRICAN POPULATIONS:  
CRANIOMETRIC INTERPRETATIONS IN RELATION TO GEOGRAPHY AND HISTORY**

**DIFFÉRENCIATION DES POPULATIONS CONTEMPORAINES DE L'AFRIQUE SUB-SAHARIENNE :  
INTERPRÉTATIONS CRANIOMÉTRIQUES EN RELATION AVEC LA GÉOGRAPHIE ET L'HISTOIRE**

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ABSTRACT

In order to explore the biological effects on skull morphology of both geography and history, craniomandibular variation was re-evaluated in modern African populations, using the largest sample of metrical data available so far. This work focused on a both large-scale and long-term event such as the Bantu-speakers expansion that probably shaped, during last 5,000 years, the present biological diversity within sub-Saharan Africa. It was attempted to see whether, despite geographical diversification, there has been any traces left from this major dispersal such as a homogenization due to a founder effect phenomenon. The sample was subdivided into four geographical units (Western Africa, Central Africa, Eastern Africa, Southern Africa) and two historic foraging groups (Pygmies, KhoiSan). Multivariate statistics were performed using up to twelve metric traits. Multiple discriminant function analyses showed that geographical differentiation of populations appeared to be quite variable (41% up to 80.1% individuals correctly classified into their group of origin), depending on the number of groups included and parts of the skull analysed. Patterns of variation also revealed that it was possible to observe slight traces of a homogenization process due to a common origin resulting from the Bantu-speakers expansion. However, craniometric results remained difficult to interpret in relation to the effects of only one historical event, as the latter is probably superimposed by other sources of diversity (geographical barriers, recent population admixtures, nature and size of sample).

*Keywords:* Africa, microevolution, Bantu-speakers expansion, skull, metrics.

RÉSUMÉ

*Afin d'explorer les effets biologiques de la géographie et de l'histoire sur la morphologie du crâne, la variation crano-mandibulaire a été réévaluée dans des populations africaines contemporaines avec l'échantillon de données le plus large possible. Ce travail s'est intéressé plus particulièrement à un évènement de très grande amplitude, tel que l'expansion des populations de langue bantoue, qui ont probablement contribué largement durant les derniers 5000 ans à la formation de la diversité présente en Afrique sub-saharienne. Nous avons tenté d'observer si, malgré une diversification géographique, des traces de cette migration majeure, telles qu'une homogénéisation due à un effet fondateur, sont encore présentes. L'échantillon a été subdivisé en quatre unités géographiques (Afrique occidentale, Afrique centrale, Afrique orientale, Afrique australe) et deux groupes historiques de chasseurs-cueilleurs (Pygmées, Khoisan). Des statistiques multivariées ont été réalisées avec un nombre maximum de douze traits métriques. Des analyses de fonctions discriminantes multiples ont démontré que la différenciation géographique des populations était assez variable (41 % à 80,1 % d'individus correctement classifiés dans leur groupe d'origine), en fonction du nombre de groupes inclus et des parties du crâne analysées. Les tendances de la variation ont aussi révélé qu'il était possible d'observer des traces subtiles d'un processus d'homogénéisation dû à une origine commune et résultant de l'expansion des populations de langue bantoue. Cependant, les résultats craniométriques restaient difficiles à interpréter en relation avec les effets d'un seul évènement historique, étant donné que ces derniers sont probablement superposés à d'autres sources de diversité (barrières géographiques, mélanges récents de populations, nature et taille de l'échantillon).*

*Mots-clés :* Afrique, micro-évolution, expansion bantouphone, crâne, anthropométrie.

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## INTRODUCTION

The present research attempts to evaluate the morphological variability in African populations as expressed in the skull, focusing on the effects of both geography and a specific historical phenomenon on population diversity. Africa has been chosen here to study human diversity, as it provides on a worldwide scale, one of the highest levels of both biological and cultural diversity (Murdock 1959; Hiernaux 1980; Cavalli-Sforza *et al.* 1994; Relethford, Harpending 1994): for example, already within only sub-Saharan Africa, it is peopled nowadays by more than three thousands ethnic groups, who are mainly Bantu-speaking. African peoples occupy a wide range of habitats and rely on various types of subsistence strategies developed through time. As a consequence, according to Hiernaux (1976), marked biological differences that were generally enhanced by a high ethnic endogamy, were created among populations.

Evolution is the result of various complex factors, and both geography and history are key-elements in understanding present biological diversity. While biological processes such as genetic and phenotypic adaptations are central to understanding human evolution, it is also essential to link these to major historical events such as the Bantu-speakers expansion.

In the last 10,000 years, microevolutionary processes became increasingly complex, especially in high density populations such as agriculturists, who replaced and/or assimilated low density hunter-gathering populations. In particular, the expansion of Bantu-speakers, who have been related to the emergence of food production in Western-Central Africa and throughout sub-Saharan Africa in the last 5,000 years (Vansina 1995), probably left some biological traces in the present diversity as suggested by genetics (Cavalli-Sforza *et al.* 1994; Bandelt *et al.* 1995; Pereira *et al.* 2001; Underhill *et al.* 2001). For example, it could have facilitated a process of homogenization due to, not only a founder effect phenomenon but also an acceleration of genetic admixture between different groups, and therefore a decrease of both genetic drift and isolation.

However, this dispersal cannot be explained by a simple microevolutionary model. In fact, according to Hiernaux (1980), other factors (selective pressures, population admixture) could also have played an important role in the phenomenon. Therefore, in relation to all these aspects, craniometric diversity in sub-Saharan Africa needs firstly to be re-assessed multivariately with a

very large set of modern individual data ( $N = 957$ ). It will help to provide better knowledge of variation on an intra-continental level and possibly more detailed information about history, in comparison to previous studies that used mainly population means (Howells 1989; Froment 1998). It will be also attempted whether it is still possible to determine the effects of a major event such as the Bantu-speakers migration within modern sub-Saharan Africa.

## PREVIOUS CRANIOMETRIC WORK

In all recent craniometric studies, the main question that is raised is whether it is possible to detect subtle decreases and increases in gene flow through levels of diversity in skull morphology. According to the results already obtained from modern populations (Howells 1989; Froment 1992a; Lahr 1996), the geographical variation suggests that despite an "apparent" homogeneity on a worldwide scale sub-Saharan Africans cannot be described as sharing a single morphology. The present morphological polymorphism observed in Africa (Hiernaux 1976) is far beyond "racial" categories proposed in the past (Leakey 1935; Coon 1971).

Geography is a key-element in understanding population differentiation both on a worldwide scale and within a continent. Through skull morphology, it has been explored previously by three main recent studies (Hiernaux 1976; Howells 1989; Froment 1998), showing that not only vault features but also various facial ones, are responsible for both inter- and intra-regional differences within sub-Saharan Africa.

Firstly, by using a wide range of characters in relation to not only anthropometry (including craniometry) and genetics, but also various social, cultural and environmental factors, Hiernaux (1966, 1968, 1974, 1976) was the first to bring some light on the inter- and intra-population variability in sub-Saharan Africa. His multivariate analyses were based on a very large sample of individual data from living populations comprising 267 ethnic groups of known origin. And, they showed that variation is a quasi-continuum phenomenon.

Secondly, using four population means (Teita, Dogons, Zulu, Bushman) ( $N = 373$ ), Howells (1989) noted that, on a worldwide scale, sub-Saharan African crania were characterized by the following morphological features and variables: narrow cranial base; very convex frontal; narrow and short face; large breadth across nose, eyes and face; and face bowed forward without nasal prominence.

Thirdly, in comparison to the previous author, Froment (1992a, b, 1998) evidenced better the regional diversity present within sub-Saharan Africa, especially Western Africa. In fact, he used a larger data set of population means obtained from compiled publications ( $N = 531$ ) that were more representative of all regions. He observed marked differences in maximum cranial breadth between the two following groups of regions: Southern Africa (Zulu) and Western Africa (various Cameroonians) with broadest crania, and Eastern Africa (Teita) and other areas of Western Africa (Ashanti) with narrowest crania. Froment (1998) also re-evaluated some of the metric traits (dolichocephaly, platyrrhinia, low orbits, alveolar prognathism) used by Chabeuf (1959) to define sub-Saharan African populations. Also, his study showed that only half of the crania studied (42% for Eastern Africa and 8% for Western Africa) had a long, high and narrow vault (or dolichocephaly) and a large nose (or platyrrhinia).

Multivariate analyses of both Howells (1989) and Froment (1992a, b) agreed on the following points: in contrast to the observations of Hiernaux (1976), the variation within sub-Saharan Africa was not entirely continuous, as significant differences were observed between regions; and these marked geographical differences were well shown especially when using two cranial variables related to both bizygomatic breadth of face and nasal breadth.

#### THE EXPANSION OF BANTU-SPEAKERS

In order to introduce the historical background of the present paper, the dispersal of the Bantu-speakers is presented in detail, and its effects are discussed in the light of various results obtained from different fields of research.

This expansion is one of the greatest population movements in the history of the world and a complex historical event that concerns all sub-Saharan Africa with at present more than 250 million Bantu-speakers. It is also part of much wider phenomena, both linguistic and "cultural"—the establishment of the whole linguistic phylum to which the Bantu-speakers belong, and the emergence of several food production strategies. However, a single approach is not sufficient to understand the microevolutionary processes, which shaped diversity of African populations today. This is why the Bantu-speakers dispersal has been and is still presently an arena where Linguistics, Archaeology, Genetics and Biological Anthropology try to reconcile their findings.

#### Linguistic data

The term "bantu" is an entirely linguistic concept, grouping peoples into a cluster of closely related languages. It also does not mean a category (or single entity) because of its linguistic diversity. The Bantu languages belong to the largest linguistic phylum (Niger-Kordofanian including Niger-Congo), as well as to the largest linguistic sub-set in Africa (Guthrie 1962; Greenberg 1964; Heine 1980; Blench 1997). The Niger-Congo sub-phylum is spoken from Western to Southern Africa throughout most of two thirds of sub-Saharan Africa, and it has ramified into several branches. The eastern group (Benue-Congo) includes the Bantoid languages from which the Bantu originated.

The Bantu languages are also relatively young in evolutionary terms (Blench 1997). They have been dated in a very approximate manner by Lexicostatistics (Bastin 1980; Heine 1980; Bastin *et al.* 1983; Coupey 1989): the latter uses lexical variability (especially basal vocabulary) to reconstruct the affinities of languages and it can also attempt to find a constant through linguistic evolution for dating the linguistic splits. For example, Bastin *et al.* (1983) after having discarded borrowed elements, analysed the proportions of conservation/innovation within Bantu languages, using especially shared innovations to define sub-groups and date their splits (*e.g.*, conservation/innovation proportion of around 86% and 14% respectively in one millennium) (Swadesh 1955). These authors found that the 300 to 600 Bantu languages correspond to a huge continuum of dialects with very small differences between them. This observation implies that language differentiation was a process of splits between dialects occurring simultaneously in a relatively short time and starting around 5,000 years ago (if the chronological scale of Swadesh is applied) (Heine 1980). The meaning itself of the word "bantu" supports this fact: these languages were probably called "bantu" meaning "people", because of the frequent occurrence of this word in the whole group (Comrie *et al.* 1997).

The nature of this linguistic phenomenon is closely linked to a "wave model" (Vansina 1995). The process of language differentiation operated from an ancestral mother language, the so-called "proto"-Bantu localized in North-Western Cameroon (Grassfields), a region where the highest degree of "archaism" and diversity in Bantu languages is found (Bastin *et al.* 1983). Looking at the geographical coherence of the Bantu-speaking "world", it

can be admitted intuitively that the spread of migrants was mainly southwards.

Concerning both geographical origin and routes of this dispersal, there are several linguistic models (Guthrie 1962; Greenberg 1964; Heine 1980; Bastin *et al.* 1983). The common broad lines are, as follows: after a first differentiation and dispersal from a primary Bantu centre, there were several secondary centres of expansion from which western and eastern streams directed towards the south followed by fissions within each main subdivision. In particular, the model of Bastin *et al.* (1983) viewed the two waves of migration as nearly simultaneous phenomena. In contrast to the latter, Heine (1980) proposed a later eastern wave, originating from a secondary western Congo centre. This is supported by the fact that Eastern Bantu languages are less diverse than the Western-Central group, suggesting therefore a more recent evolution (Heine 1980; Ehret 1997; Holden 2001). Models of the exact route of the Bantu-speakers dispersal are never definitive, especially when the shape of linguistic trees changes according to the number of languages included. Nevertheless, most linguists, like archaeologists, agree that this expansion did not necessarily follow a regular pattern.

Finally, there are a few cautionary remarks to be done about all these inferences derived from Linguistics. Firstly, the occurrence of a parallel linguistic innovation is possible and it does not imply genealogical relationship. Secondly, there is also no absolute dating, as the rate of linguistic change is not always constant (Coupez 1989). And finally, although lexicostatistics can yield a "preliminary genetic classification" (Vansina 1995) of the Bantu languages, the language trees cannot be confused with population trees.

### Archaeological data

The archaeological approach can provide material and chronological evidence supporting the phenomenon of the Bantu-speakers expansion in terms of "culture". Other improved models of dispersal can be built, but this time with the advantage of being confronted by linguistic data. Furthermore, in contrast to Linguistics, Archaeology can provide an absolute chronological background: once mapped, radiocarbon dates can reflect past human occupation on both regional and continental scales. However, in Archaeology, the meaning of the word "bantu" is based on many assumptions.

Firstly, the latter is related to the nature of an archaeological remain itself (de Maret 1989). It is not possible to relate an artefact to a linguistic group.

Secondly, according to archaeological evidence, the "cultural" meaning of the word "bantu" is closely related to the process of sedentism (de Maret 1977; Clist 1991). Since the last 5,000 years, an increasing number of sites with traces of sedentism (pottery, domesticated plants and animals, later iron production) have been observed in Africa (de Maret 1989; Phillipson 1994; Vansina 1995). This phenomenon in sub-Saharan Africa has approximately the same time-depth as the linguistic Bantu-speakers expansion described above. Archaeological evidence and radiocarbon dates (much more accurate than those derived from linguistics) also suggest that this dispersal started in West-Central Africa during the transitional period of the Later Stone Age-Iron Age (around 4,000-1,000 B.C.). And, it occurred most probably after the first appearance of pottery and farming and before the first signs of metallurgy (de Maret 1989; Vansina 1995).

Thirdly, archaeologists have therefore inferred that the cultural meaning of the word "bantu" is closely related to the emergence and diversification of various kinds of food production (horticulture, agriculture, herding). In fact, sedentism cannot be defined by a single aspect and a single geographical area in Africa, as food production is very diverse, as well as its emergence. More precisely, the archaeological traces appear not to be similar between Western, Central and Eastern Africa, as they probably reflect different environments (Cornevin 1993). In Eastern African savannas and North-Western Africa, grain crops and domesticated animals could have been revealed very early in time (around 6,000 B.C. at Nabta Playa), even before the Bantu-speakers expansion (Wendorf *et al.* 1984). In the forests of Western-Central Africa, artefacts, such as polished stone tools, grinding stones and palm oil nuts, were discovered at around the late first millennium B.C. In Cameroon (Obobogo) and Gabon (Okala), traces of village compounds with refuse pits, pottery, extensive domestic grinding equipment, animal husbandry and evidence of horticulture already appeared at around 1,500 B.C. (de Maret 1982, 1985; Clist 1987). These Later Stone Age-Iron Age sites are also very important for the archaeology of Western-Central Africa, as they can bring supporting evidence for the hypothesis of a linguistic "proto-Bantu cradle" in the Grassfields (Bastin *et al.* 1983).

Therefore, are Bantu-speaking populations synonymous to sedentism, as it is suggested with archaeological evidence? It is probably easier to answer this question for early “proto”-Bantu-speakers, previous to their subsequent expansion and diversification. Through the Holocene in sub-Saharan Africa, various groups of “cultures” have been characterized by a common range of functional activities (hunting, fishing and/or collecting). Their lithic assemblages or “techno-complex” differed mainly in the proportions of artefacts, although the latter belonged to the same general families (microlithism, macrolithism) (Holl 1993). According to Clist (1991), polished tools are an example of confusion with the word “bantu”: their presence is not strictly related to a period of sedentism. Polished tools appeared firstly since the Later Stone Age and before the Bantu-speakers expansion, and secondly, in different contexts localized south and north of the forest. In Western-Central Africa, the site of Shum Laka in the Grassfields (Cameroon) illustrates quite well the technological changes that occurred at around 3,000-1,000 B.C. (de Maret 1990). The presence of a macrolithic industry on basalt (hoes, picks) increased at the expense of a microlithic industry on quartz (Cornelissen 1997). This phenomenon could reflect a subsistence shift in Western-Central Africa, where horticultural practices using hoes and picks developed intensively, although always associated with hunting. Therefore, according to the evidence from stone tools, the early “proto”-Bantu-speakers were probably horticulturists (yam growers), but afterwards food production diversified into a variety of subsistence strategies that do not allow reference to a common or single “bantu” system of food production.

Although both the geographical origin and routes of the Bantu-speakers dispersal are still debated (Clark 1980; David 1982; Phillipson 1985; de Maret 1989; Muzzolini 1993; Vansina 1995), the common broad lines of consensus are as follows:

—the Bantu-speakers expansion was probably initiated by a population, who was not in equilibrium with its environment, and who was undergoing both food production shortages and increasing population density; these conditions could have occurred especially during a dry phase at around 2,000-1,000 B.C.;

—after a first differentiation and dispersal from a “proto-Bantu” centre in the Grassfields, there were several secondary centres of expansion, from which western and eastern streams moved south, followed by

fissioning within each main subdivision; different hypotheses about the earliest stream are still debated too;

—according to the various archaeological data discussed above, these “proto-Bantu” peoples living north of the forest, who expanded southward via clearings and river valleys, were village-dwellers; they cultivated yams and vegetable crops, using both axe/hoes and pottery, and they probably also raised sheep and goats;

—the first trajectory must have occurred mainly through the forest belt and/or along the latter; the two streams (western, eastern) of dispersal probably reflected two major ecological zones (forest, savanna); the expansion might also have been confronted by numerous ecological barriers (limit of summer rainfall, tsetse fly-infested areas), beyond which both cereal cultivation and cattle rearing that was adopted by Bantu-speakers agriculturists from pastoralists, could spread only into specific areas.

### Genetic data

Genetic data support large-scale population movements dated to the mid-Holocene period, not only on a worldwide scale, but also within sub-Saharan Africa (Semino *et al.* 1996). Both their approximate dating and analysis of diversity can provide information about the Bantu-speakers expansion.

First, based on a very high rate of mutation, the mitochondrial DNA has been exploited as a molecular clock by dating divergence events between closely related populations. In fact, its pattern of inheritance (passed on exclusively by females) is advantageous, as it mutates at a constant rate without undergoing recombinations. For example, mtDNAs from southeastern Africans of Mozambique having affinities with northern and southern populations showed that its major components (L2a) provided an age range of  $6,700 \pm 2,100$  years (Pereira *et al.* 2001). This result is more or less compatible with linguistic and archaeological data (Bastin *et al.* 1983; de Maret 1989) on the Bantu-speakers expansion, although slightly older and approximate.

Second, a large-scale dispersal of populations usually leaves genetic traces such as a loss in diversity in relation to a founder effect phenomenon. In fact, this genetic homogeneity has been frequently observed within Bantu-speaking sub-Saharan Africans (Excoffier *et al.* 1987; Cavalli-Sforza *et al.* 1994; Biondi *et al.* 1996; Spedini *et al.* 1999; Pereira *et al.* 2001). Both synthetic

and case studies including various genetic markers seem to agree broadly on this process of homogenization.

According to a large survey of various genetic polymorphisms including mainly classic markers, Cavalli-Sforza *et al.* (1994) showed that Bantu-speaking populations have high intra-population variation and low inter-population variation. Through a founder effect phenomenon, the dispersal probably produced an overall homogeneity within sub-Saharan Africa. This fact supports the hypothesis that Bantu-speaking people could be the outcome of the recent expansion of a relatively small group (Vansina 1995). Still analysing mainly classic genetic markers (ABO, JK, MNS, Rh, ACP1) but with a new sample, Biondi *et al.* (1996) also found a good correspondence between both geographical and linguistic differentiation of Bantu-speaking populations.

Other molecular approaches with new genetical markers reflecting this phenomenon have also been revealed, such as on the non-recombining portions of both mitochondrial DNA (Bandelt *et al.* 1995; Chen *et al.* 1995; Soodyall *et al.* 1996; Pereira *et al.* 2001) and Y-chromosome (Scozzari *et al.* 1994; Passarino *et al.* 1998; Underhill *et al.* 2001).

For example, concerning mitochondrial DNA, Bandelt *et al.* (1995), suggested that the high frequency of a subset of cluster L1a (that is defined by a 9-bp deletion at np 8272-8289) could correspond to the traces left by a major dispersal within the Bantu-speakers. Another possible mitochondrial marker for this expansion could have been found by Vigilant (1990) and Soodyall (1993) in a sequence motif of subset of L3b (np 16124-16223-16278). The latter was in fact widespread in both Western and Southern Africans, all belonging to the Niger-Congo linguistic group.

Other recent results on mtDNA that have been obtained by Pereira *et al.* (2001), are similar to all those just cited above, but they appeared to be more detailed. The sequences of haplogroups L3b and L3e1a and subsets of L1a and L2a could represent again the traces left by the Bantu-speakers dispersal, by showing affinities of Mozambican with other northern and southern Bantu-speakers.

Concerning Y-chromosome, the widespread distribution of a haplotype (group III) in sub-Saharan Africa could indicate the homogenizing effects of a founder effect phenomenon in relation to the Bantu-speakers dispersal (Underhill *et al.* 2001). This fact was also supported previously by the high frequency of a related sub-clade (RFLP 49f Ht4) (Seielstad *et al.* 1994; Hammer *et al.* 1997).

Genetic data are still accumulating, but all of them so far, still provide strong evidence for a founder effect phenomenon causing homogenization within Bantu-speakers.

### Various biological data

Palaeoanthropological evidence in Africa, especially in Western and Central Africa is very scarce and difficult to obtain. Therefore, in order to try to understand present sub-Saharan African diversity and infer past evolutionary processes, most studies in Biological Anthropology have focused on historical populations (Hiernaux 1976; Rightmire 1976; Froment 1992a; Irish 1997).

However, so far, Hiernaux (1976) and Rightmire (1976) are the only ones to have attempted to address the consequences of the Bantu-speakers expansion from a biological perspective. They viewed this dispersal not only as a simple linguistic and “cultural” homogenization, but they argued that various biological and ecological parameters were probably involved in this process. In fact, they considered that this complex phenomenon initially triggered by over-population and climate change, probably proceeded irregularly with advances and reverses, assimilating partially or completely native populations.

According to results suggesting a clinal variation within sub-Saharan Africa, Hiernaux (1968) viewed the Bantu-speakers expansion as a continuous wave, spread over time and space. The latter although involving several populations, resulted in a homogenization with differences left mainly due to selective pressures. The presence and conservation of low biological distances required three major conditions: a relatively recent common origin, little differences between habitats and absence of important admixture with genetically very different groups. Those parameters therefore produced a “homogenization” which could be however only “apparent”, as according to Hiernaux (1976), cases of convergent evolution due to strong selective pressure are common in equatorial forests, especially for the postcranial morphology (limb proportions). For example, Hiernaux and Froment (1976) observed a high correlation between nasal breadth and average rainfall. Narrow noses appear to work better as a humidifier for dry air, as it was already suggested by Davies (1932), Weiner (1954) and Thomson and Buxton (1923). From various field data, Hiernaux (1974) also noted that, nasal breadth is part of a series of morphological features reflecting “climatic”

adaptation to wet and dry areas along the Equator. For example, in wet tropical areas where nasal breadth tends to be larger, trunk length is also greater, limbs are shorter, and skull tends to be low and broad. In contrast, in dry hot conditions when nose tends to be narrower and higher, the trunk is shorter, the limbs are elongated and the skull also tends to be higher and narrower.

Rightmire (1976) in contrast to Hiernaux, did not reach any detailed conclusion on the nature of the Bantu-speakers dispersal as a phenomenon itself. The statistical distances he obtained from metric and non-metric data did not always support the previous picture. And according to the author, this fact could reflect different mechanisms specific to the underlying nature of discrete variants and/or the relatively small size of his sample under study ( $N = 130$ ).

According to the craniometric analyses of Froment (1992a, b, 1993, 1995, 1998), the broad southward cline of sub-Saharan Bantu-speaking groups showing low biological distances between each other and marked differences with KhoiSan (and sometimes Pygmies) could reflect two major microevolutionary processes: firstly a progressive homogenization due to population admixture through adoption of agriculture, and secondly a retention of early differentiation through isolation and retention of hunting-gathering. These phenomena related to changes in subsistence patterns probably occurred during the Bantu-speakers expansion and indirectly shaped the present biological diversity in sub-Saharan Africa. Therefore Froment's work provided indirect supporting evidence for the Bantu-speakers expansion, as the author noticed no marked differences within the Bantu-speaking populations. Similar observations were also obtained through the analysis of the frequencies of dental non-metric traits (Irish 1997).

### **Complexity of a biological model**

So far, studies, both based on Genetics and other related fields of Biological Anthropology are in agreement with Linguistics and Archaeology in also supporting the hypothesis, that all present Bantu-speaking populations are the outcome of the recent expansion of a small group. However, the biological consequences of the Bantu-speakers expansion appeared to be a complex phenomenon. They could be difficult to distinguish from many confounding factors such as possibly a few environmental factors (*e.g.*, climate) but more importantly other recent historical events also involving population admixture.

Environmental factors are in general not clearly observable. Various degrees of correlation have been observed between cranial traits and climatic variables (Beals 1974; Guglielmino-Matessi *et al.* 1979). However, skull morphology does not seem to follow undoubtedly the thermoregulatory principles such as Allen's and Bergmann's rules. In fact, the genetic stability (balance between plasticity and heritability) of morphological traits is not completely elucidated, as suggested previously by Hiernaux (1963). Vault shape (cephalic index) seems to have a higher heritability than the rest of the body (stature). Furthermore, according to Relethford (2002), the strong similarity between genetic and craniometric results suggested that global patterns of craniometric variation can be considered on average selectively neutral.

Most probably, various population admixture on a microscale could also have been superimposed on the phenomenon of homogenization, obscuring the founder effect phenomenon due to the large-scale dispersal of Bantu-speakers. For example, during the Bantu-speakers expansion, agriculturists admixed to some extent with hunter-gatherers and pastoralists within each region of sub-Saharan Africa. This phenomenon occurred at various degrees and between different and/or similar groups, as also suggested by genetic data (Cavalli-Sforza *et al.* 1994; Destro-Bisol *et al.* 2000). Furthermore, modern variation has been probably extensively affected by additional population movements and growth, especially during the last five hundred years.

Therefore, in this perspective, the present paper aims to study skull morphology as the outcome of a complex process of diversification where geography and history can interplay. Two questions are addressed here. Firstly, do an expanded corpus of data agree with previous craniometric work and/or provide additional information on the geographical differentiation of sub-Saharan Africans? And, secondly, despite other sources of variation, are there any traces left from the Bantu-speakers expansion within sub-Saharan Africa such as a founder effect phenomenon or homogenization?

## **MATERIALS AND METHODS**

### **Populations studied**

A total sample of 957 skulls corresponding to several modern African populations was available for study. It consisted of data which have been both compiled from the literature ( $N = 502$ ) and collected in several museums by the author ( $N = 455$ ). The appendix provides detailed



information (references, geographical and/or ethnic origin, linguistic affiliation, place of deposit) about the entire sample. However, 26% of the total sample was of unknown ethnic origin: the latter within each group (except from Pygmies and KhoiSan) was not always established, either by the publications or the museum archives.

In order to broadly perceive the origin of each sub-sample in terms of both geography and history, the whole sample has been subdivided into six groups (*table 1*): Western Africa (including Western-Central regions such as Cameroon and Nigeria), Central Africa (without Pygmies), Eastern Africa (excluding the Horn), Southern Africa (without KhoiSan), Pygmies and KhoiSan. The first six groups corresponded to approximate regions defined by physical geographical features or natural barriers that are observed all over the African continent. In fact, this broad inter-regional classification has already been used by other authors for ethnographical purposes (Giles *et al.* 1997). The last two groups such as the Pygmies and the KhoiSan were considered separately from the other groups, even if the Pygmies in particular have adopted Bantu-speaking languages. These two historic foraging groups represent in fact autochthonous populations, who were already settled in sub-Saharan Africa previous to the Bantu-speakers expansion, and according to previous data (Hiernaux 1976), they are still biologically very different from all other groups despite some possible admixture.

The most likely affiliation of each group to one of the four major families of languages (Niger-Kordofanian, Nilo-Saharan, Afro-Asiatic, KhoiSan) was also determined (Murdock 1959; Greenberg 1964). Within the Niger-Kordofanian family, several groups of the Niger-Congo branch were present such as the West Atlantic, the Mande, the Kwa and the Benue-Congo languages. The last ones are spoken mainly by Bantu-speaking populations, who represented 62% of the sample on an inter-regional level. However, this linguistic grouping provided only a very general picture of broad linguistic affiliations, as it also depended on the reliability of the museum records about the identity of each individual under study. In fact, 6% of the sample was of unknown linguistic affiliation (N = 55). It corresponded to a sub-sample of Ugandese dissected in hospitals and whose detailed origins have not been recorded (Górny 1957). As in Uganda, there is a very high diversity of both ethnic and linguistic groups, it was not possible to provide here further information apart from a very broad geographical origin.

The total sample (only adults) was composed of a very high percentage of males (50%) and females (44%), and only a small percentage of unknown sex (6%). For personal data, sex was assessed morphologically according to the methods used by Ferembach *et al.* (1980) on the skull. However, for compiled data, no information was available about the methods used for sex determination.

Groups under study	Total by region	Bantu-speakers	Non Bantu-speakers				Unknown linguistic origin	Females	Males	Unknown sex
			NK	NS	AA	K				
Western Africa	241	37	161	0	1	0	42	107	112	22
Central Africa	336	319	15	4	0	0	2	162	157	17
Eastern Africa	139	84	0	0	0	0	55	66	66	7
Southern Africa	134	134	0	0	0	0	0	36	96	2
Pygmies	21	21	0	0	0	0	0	10	4	7
KhoiSan	86	0	0	0	0	86	0	42	44	0
Total	957	595	260	4	1	86	109	423	479	55

Table 1—Sample sizes for inter-regional sub-Saharan African craniometric analyses. Linguistic groups: NK = Niger-Kordofanian sub-groups other than Benue-Congo or Bantu (West Atlantic, Kwa, Mande, Chadic, Central Sudanic, Adamawa Eastern), NS = Nilo-Saharan, AA = Afro-Asiatic; K = Khoisan.

Tabl. 1 - Taille des échantillons pour les analyses craniométriques de l'Afrique sub-saharienne au niveau inter-régional. Groupes linguistiques : NK = sous-groupes Niger-kordofaniens autres que Benue-Congo ou Bantu (Ouest-atlantique, Kwa, Mandé, Tchadique, Centre-soudanais, Adamawa-oriental), NS = Nilo-saharien, AA = Afro-asiatique ; K = KhoiSan.

## Methods

Nineteen metric traits of the skull, which have been previously standardized in the literature, were analysed (*table II*): fourteen variables for the cranium (three for the vault and eleven for the face) and five for the mandible. They have been already described in more detail in other works (Ribot 2002, 2003).

Statistical analyses were performed with SPSS software (version 11.5) and all graphs with SYSTAT (version 8.0).

All samples were checked for normality within each group or region, using stem-and-leaf displays, Q-Q plots and tables for testing and eliminating major skewness (Zar 1984). Therefore sixteen outliers were trimmed, and the final sample under study was only slightly reduced.

For analyses of variance and multivariate analyses, three data sets classified inter-regionally and of decreasing sample size were used such as: all available inter-regional groups, Bantu-speaking groups only without Pygmies, and non Bantu-speaking groups only (Niger-Kordofanian groups other than Benue-Congo, Nilo-Saharan, Afro-Asiatic, KhoiSan) with Pygmies (*table I*). However, before testing the two main questions initially addressed, three preliminary tests were also performed on the individual variables.

## Preliminary data analysis

A first preliminary study of inter-observer errors was undertaken, in order to evaluate the effects of possible error measurements in the entire sample. Only ten cranial measurements (GOL, XCB, BBH, BNL, BPL, NPH, ZYB, DKB, NLB, OBB) were recorded twice on a small sample of Teita originating from Kenya (N = 38), as they corresponded to those already measured by Kitson (1931) and by the author of the present paper. Paired t-tests were performed, as they assess the significance of a difference in means between two related samples (Sokal, Rohlf 1995). The results showed some significant differences between the duplicated data sets of the thirteen cranial measurements. However, the mean differences never ranged above 2 mm: between 0 and 1 mm for six variables (XCB, BPL, NPH, DKB, NLB, OBB), and between 1 and 2 mm for four variables (GOL, BBH, BNL, ZYB). These results showing no significant inter-observer error favoured the procedure of pooling both compiled and personal data together. This procedure was also carefully validated by checking in the literature the variable definitions with identical landmarks as we saw above (*table II*).

Broad anatomical location	Description of variable	Code of Shrubsall (1898)	Code of Shrubsall (1898)	Code used
Vault	maximum cranial length ( <i>glabella-opisthocranion</i> )	L	no.1	GOL*
	maximum cranial breadth (between parietals)	B	no.8	XCB*
	total vault height ( <i>basion-bregma</i> )	H'	no.17	BBH*
Face	facial length ( <i>basion-nasion</i> )	LB	no.5	BNL*
	facial length ( <i>basion-prosthion</i> )	GL	no.40	BPL*
	upper facial height ( <i>nasion-prosthion</i> )	G'H	no.48	NPH*
	bizygomatic breadth ( <i>zygion-zygion</i> )	J	no.45	ZYB*
	minimal frontal breadth (between <i>frontotemporalia</i> )	B'	no.9	WFB*
	biorbital breadth ( <i>ectoconchion-ectoconchion</i> )	-	no.44	EKB*
	bifrontal breadth (between <i>fronto-malare anterior</i> )	-	no.43	FMBlat
	interorbital breadth ( <i>dacryon-dacryon</i> )	DC	no.49a	DKB*
	maximum nasal breadth ( <i>alare-alare</i> )	NB	no.54	NLB*
	orbital breadth ( <i>ectoconchion-dacryon</i> )	O1'	no.51a	OBB*
orbital height (perpendicular to OBB)	O2	no.52	OBH*	
Mandible	bicondylar breadth (between lateral points of condyles)	W1	no.65	bb
	bigonial width ( <i>gonion-gonion</i> )	GoGo	no.66	bw
	symphyseal height ( <i>infradentale-gnathion</i> )	H1	no.69	sh
	minimal width of ascending ramus	rb'	no.71a	war
	mandibular angle	M<	no.79	ma

Table II—List of the metric variables under study for the skull. \*: Asterisk indicates measurement abbreviation from Howells (1989); other abbreviations were developed by present author for ease of study.

Tabl. II - Liste des variables métriques étudiées pour le crâne. \*: l'astérisque indique que l'abréviation de la mesure provient d'Howells (1989); les autres abréviations ont été faites par l'auteur pour la clarté de l'étude.

A second preliminary study was undertaken, in order to test cranial morphology in relation to differences reflecting sexual dimorphism. Although the latter are probably less marked than geographical (and/or ethnic) differences, they have to be taken into account and evaluated more precisely within each group of the whole inter-regional sample. Therefore mean differences for the nineteen metric traits were tested between male and female samples. As a minimal number of individuals ( $N \geq 15$ ) was needed within each group, the Pygmies could not be tested because of too small sample size. Most of the results were significant (at varying levels of probability): only 18 t-tests (over 94 in total) were not significant, especially for one variable (OBH) and one group (KhoiSan). Within most groups, the measurements under study except for a few cases were affected by sexual dimorphism at various degrees. Therefore, each individual variable was standardized into Z-scores for correcting for both size and sex while retaining intra-population variation (Howells 1973, 1989). In fact, this procedure allows to avoid biases not related to geographical (and/or ethnic) origin, as suggested by previous studies (Relethford, Harpending 1994; Stefan, Chapman 2003). Total sample size was in this manner increased, as samples were considered without reference to their sex after using this standard procedure.

A third preliminary study was undertaken, in order to determine the variables with the highest significance for

group mean differences using the three different inter-regional data sets cited above. Therefore an analysis of variance testing the equality of means amongst the groups under study was achieved on all variables. As a minimal number of individuals ( $N \geq 15$ ) was needed, the number of compared groups varied again (table III, V). When using all inter-regional groups (table III), the metric traits were all significantly different (at the highest level of probability except for variable Zwar). When using the Bantu-speaking groups only without Pygmies (table IV), most of them were also significant (at various levels of probability) except for one mandibular variable (Zbb). When using the non Bantu-speaking groups only with Pygmies (table V), most of tests were also significant (at various levels of probability) except for three variables (ZWFB, ZFMBlat, Zwar). Although the variables were ranked in a variable manner for their F-values and significance, five variables (ZBBH, ZBPL, ZNPH, ZZYB, ZNLB) were still in the first ten most highly significant ones for the three data sets. A vault variable (ZBBH) had the highest F-value, followed by the facial variables such as those related to prognathism (ZBPL) and both height (ZNPH) and breadth (ZZYB). Therefore, all variables were selected for the multivariate analyses, as all of them showed significant inter-regional differences for at least one data set.

Variables	N	F	Sig.	L.	Groups compared
ZGOL	919	42.36	***	NS	WA, CA, EA, SA, P, K
ZBBH	863	41.52	***	*	WA, CA, EA, SA, P, K
ZNPH	905	25.95	***	NS	WA, CA, EA, SA, P, K
ZBNL	916	24.69	***	NS	WA, CA, EA, SA, P, K
ZNLB	916	24.33	***	NS	WA, CA, EA, SA, P, K
ZOBH	914	21.82	***	NS	WA, CA, EA, SA, P, K
ZBPL	903	20.70	***	NS	WA, CA, EA, SA, P, K
ZFMBlat	467	19.91	***	**	WA, CA, EA, SA, K
ZDKB	862	19.55	***	NS	WA, CA, EA, SA, P, K
ZZYB	898	19.50	***	NS	WA, CA, EA, SA, P, K
ZEKB	696	15.60	***	**	WA, CA, EA, SA, P, K
Zsh	429	14.59	***	NS	WA, CA, EA, SA, K
ZOBB	862	14.21	***	**	WA, CA, EA, SA, P, K
ZWFB	918	11.71	***	**	WA, CA, EA, SA, P, K
Zbb	423	10.08	***	NS	WA, CA, EA, SA, K
Zbw	451	9.22	***	**	WA, CA, EA, SA, K
ZXCB	917	7.68	***	*	WA, CA, EA, SA, P, K
Zma	425	4.61	***	NS	WA, CA, EA, SA, K
Zwar	454	4.22	**	NS	WA, CA, EA, SA, K

Table III—One-way analyses of variance for testing inter-regional differences within modern sub-Saharan African groups.

Sig.: \*\* =  $P < 0.01$ ,  
 \*\*\* =  $P < 0.001$ . L.: Levene's test of homogeneity of variance. Groups compared: WA = Western Africa, CA = Central Africa, EA = Eastern Africa, SA = Southern Africa, P = Pygmies, K = KhoiSan.

Tabl. III - Analyses de la variance « One-way » pour tester les différences inter-régionales parmi les groupes contemporains de l'Afrique subsaharienne. Sig. : \*\* =  $P < 0.01$ , \*\*\* =  $P < 0.001$ . L. : test de Levene pour l'homogénéité de la variance.

Groupes comparés :  
 WA = Afrique occidentale,  
 CA = Afrique centrale, EA = Afrique orientale, SA = Afrique australe,  
 P = Pygmées, K = KhoiSan.

Variables	N	F	Sig.	L.	Groups compared
ZGOL	570	61.90	***	NS	WA, CA, EA, SA
ZFMBlat	350	34.18	***	**	CA, EA, SA
ZBBH	519	30.33	***	NS	WA, CA, EA, SA
ZNPB	565	26.03	***	NS	WA, CA, EA, SA
ZBNL	570	26.03	***	NS	WA, CA, EA, SA
ZZYB	562	22.22	***	**	WA, CA, EA, SA
ZEKB	390	18.87	***	NS	WA, CA, EA, SA
ZWFB	570	15.27	***	*	WA, CA, EA, SA
Zma	195	14.25	***	NS	WA, CA, SA
ZBPL	563	14.06	***	NS	WA, CA, EA, SA
ZNLB	570	14.01	***	NS	WA, CA, EA, SA
ZXCB	568	10.93	***	NS	WA, CA, EA, SA
ZDKB	571	10.54	***	NS	WA, CA, EA, SA
Zsh	191	9.95	***	NS	WA, CA, SA
ZOBB	570	8.45	***	*	WA, CA, EA, SA
Zwar	205	7.65	***	NS	WA, CA, SA
ZOBH	570	4.86	***	NS	WA, CA, EA, SA
Zbw	203	3.67	*	*	WA, CA, SA
Zbb	201	1.09	NS	NS	WA, CA, SA

Table IV—One-way analyses of variance for testing inter-regional differences within modern sub-Saharan African groups (Bantu-speakers only without Pygmies). Sig.: \*\* =  $P < 0.01$ , \*\*\* =  $P < 0.001$ .

L.: Levene's test of homogeneity of variance. Groups compared:

WA = Western Africa, CA = Central Africa, EA = Eastern Africa, SA = Southern Africa, K = KhoiSan.

Tabl. IV - Analyses de la variance « One-way » pour tester les différences inter-régionales parmi les groupes contemporains de l'Afrique sub-saharienne (seulement les Bantouphones excepté les Pygmées). Sig. : \*\* =  $P < 0.01$ , \*\*\* =  $P < 0.001$ .

L. : test de Levene pour l'homogénéité de la variance. Groupes comparés :

WA = Afrique occidentale, CA = Afrique centrale, EA = Afrique orientale, SA = Afrique australe, K = KhoiSan.

Variables	N	F	Sig.	L.	Groups compared
ZBBH	344	28.78	***	NS	WA, CA, EA, P, K
ZDKB	291	21.09	***	NS	WA, CA, P, K
ZNLB	346	20.76	***	NS	WA, CA, EA, P, K
Zsh	224	18.44	***	NS	WA, EA, K
ZOBB	292	18.24	***	NS	WA, CA, P, K
Zbw	234	17.99	***	NS	WA, EA, K
ZOBH	344	17.87	***	NS	WA, CA, EA, P, K
ZBPL	340	16.33	***	NS	WA, EA, P, K
ZNPB	340	14.06	***	NS	WA, CA, EA, P, K
Zbb	208	13.16	***	NS	WA, EA, K
ZZYB	336	10.67	***	NS	WA, CA, EA, P, K
ZBNL	346	10.54	***	NS	WA, CA, EA, P, K
ZEKB	306	9.07	***	NS	WA, CA, EA, P, K
ZGOL	349	6.25	***	NS	WA, CA, EA, P, K
ZXCB	349	5.59	***	*	WA, CA, EA, P, K
Zma	216	5.00	**	NS	WA, EA, K
ZWFB	348	1.72	NS	**	WA, CA, EA, P, K
ZFMBlat	120	0.63	NS	NS	WA, CA, K
Zwar	235	0.63	NS	NS	WA, EA, K

Table V—One-way analyses of variance for testing inter-regional differences within modern sub-Saharan African groups (non Bantu-speakers only with Pygmies). Sig.: \*\* =  $P < 0.01$ , \*\*\* =  $P < 0.001$ .

L.: Levene's test of homogeneity of variance. Groups compared: WA = Western Africa, CA = Central Africa, EA = Eastern Africa, SA = Southern Africa, P = Pygmies, K = KhoiSan.

Tabl. V - Analyses de la variance « One-way » pour tester les différences inter-régionales parmi les groupes contemporains de l'Afrique sub-saharienne (seulement les non-Bantouphones avec les Pygmées).

Sig. : \*\* =  $P < 0.01$ , \*\*\* =  $P < 0.001$ . L. : test de Levene pour l'homogénéité de la variance. Groupes comparés :

WA = Afrique occidentale, CA = Afrique centrale, EA = Afrique orientale, SA = Afrique australe, P = Pygmées, K = KhoiSan.

### Multivariate analysis

When all variables were considered, the initial entire data base possessed more than 95% missing data. This fact was the result of the state of preservation of specimens examined and lack of equivalent variables between both compiled and personal data. In order to reduce the percentage of missing data and maximize the completeness of the data set for subsequent multivariates, three groups of variables were analysed separately such as:

—for the cranium, twelve variables (ZGOL, ZXCB, ZBBH, ZBNL, ZBPL, ZNPH, ZZYB, ZWFB, ZDKB, ZNLB, ZOBB, ZOBH);

—for the face only, nine variables (ZBNL, ZBPL, ZNPH, ZZYB, ZWFB, ZDKB, ZNLB, ZOBB, ZOBH);

—and for the mandible only, five variables (Zbb, Zbw, Zsh, Zwar, Zma).

Although all traits showed significant differences amongst most of the groups under study, two of them (ZEKB, ZFMBlat) had to be removed due to excessive missing data. All these procedures resulted in both the reduction of missing data and increase of total sample. The number of individuals under study was 785 for the 12-variables analysis, 842 for the 9-variables analysis and 374 for the 5-variables analysis. Therefore, although the problem of missing data was not completely eliminated, the data set was increased. The data could also be analysed in a systematic manner testing the different parts of the skull through three series of variables.

In order firstly to re-evaluate the craniometric variation within sub-Saharan Africa, multiple discriminant function analyses were performed on the three series of variables selected above. As this kind of multivariate statistics maximize group differences, it also allowed us to determine the groups of variables with the best prediction for population differences on an inter-regional level. This procedure also provided a more complete assessment of the degree of overlap in the range of variation between the various groups. More precisely, it aimed to produce a linear combination of independent variables serving as a basis for classifying cases into one of the groups (SPSS Base 9.0 1999, Pietruszewsky 2000). Therefore the best discriminating variables were selected in a stepwise manner, using the Mahalanobis distance ( $D^2$ ) method, and prior probabilities were computed from group sizes. The jackknifing method, which is a common cross-validation procedure was also used (Hair *et al.* 1987). In fact, in order to avoid assignation on same

individuals causing distortion, cases were classified without using the misclassified individuals in computing the classification function. After this procedure, classification accuracy typically decreased but only slightly. A visual assessment of overall morphological relationships within and between groups was also provided. Seventy percent confidence ellipses were constructed around the centroid for the six groups under study. This method allowed us to evaluate the extent of overlapping variation between groups.

In order to test the second question about possible traces left from the Bantu-speakers expansion within sub-Saharan Africa such as a founder effect or homogenization process, similar multivariate statistics as described just above were performed again. However, in this case, smaller data sets were analysed, as they included either Bantu-speakers only without Pygmies, or non Bantu-speakers only with Pygmies. This procedure therefore allowed to see whether the levels of variation can change when using different inter-regional data sets.

### RESULTS

The total correct classification rates that were obtained from the nine multiple discriminant function analyses with crossvalidation are presented in table VI. The percentages of correct classifications were quite variable, as they ranged between 41% and 80.1%. The highest percentage was obtained for the 12-variables analysis (cranium) on non Bantu-speakers only (with Pygmies), and the lowest one for the 5-variables analysis (mandible) on all groups. Mandibular variables reflected quite low group differentiation, as the percentages could be below 50%. Furthermore, group differentiation was lower in the largest inter-regional data set (41%-54.4%) than in the two smaller ones (58.2%-80.1%). In addition, it was lower in Bantu-speakers (58.2%-71.4%) than in non Bantu-speakers (58.2%-80.1%). This fact suggested that, the latter reflected marked differences such as between Western Africa and KhoiSan, and that, Bantu-speakers groups were less differentiated between each other. However, this result could be partly due to the variable number of groups compared, as when using less groups, the percentage of correct classification tends to increase.

According to these results, the 12-variables (cranium) and 9-variables (face only) approaches were used preferentially for subsequent analyses. In fact, both a

relatively high amount of metric traits (at least nine) and the exclusion of mandibular variables tended to increase the group differentiation.

Table VII that summarizes more precisely the correct classification rates obtained for each group, suggested a high amount of overlapping variation present within the total sample. For example, the Pygmies had one of the lowest percentages (4.8%-38.1%), being misclassified most often with both Central Africa and Southern Africa that are mainly Bantu-speakers. These last two groups

were better classified with their corresponding region of origin (63.1%-91.2%) than Bantu-speaking Eastern Africa (11.1%-48.8%), which in turn was misclassified with Central Africa. When non Bantu-speaking groups only were analysed, the correct classification rate for Western Africa increased markedly, in comparison to other analyses that showed very low differentiation from other groups (5.6%-41.3%). Non Bantu-speaking Central Africa was also completely misclassified with non Bantu-speaking Western Africa.

Inter-regional data set	12-variables analysis (cranium)			9-variables analysis (face)			5-variables analysis (mandible)		
	N	groups no.	%	N	groups no.	%	N	groups no.	%
All groups	785	6	54.4	842	6	52.7	373	5	41.0
Bantu-speakers only without Pygmies	503	4	71.4	555	4	69.9	177	3	58.2
non Bantu-speakers only with Pygmies	282	4	80.1	287	4	72.8	191	4	58.6

*Table VI—Total correct classification rates in percentages (with crossvalidation) derived from multiple discriminant function analyses for testing inter-regional differences within sub-Saharan Africa.*

*Tabl. VI - Total des taux de classification correcte en pourcentages (avec « crossvalidation ») dérivés des analyses à fonctions discriminantes multiples pour tester les différences inter-régionales au sein de l'Afrique sub-saharienne.*

By group	All groups		Bantu-speakers only without Pygmies		non Bantu-speakers only with Pygmies	
	12-variables analysis	9-variables analysis	12-variables analysis	9-variables analysis	12-variables analysis	9-variables analysis
Western Africa	41.3	36.9	5.6	5.6	92.1	91.2
Central Africa	65.4	73.9	85.6	91.2	0	0
Eastern Africa	43.8	11.1	48.8	16	-	-
Southern Africa	63.1	64.1	75.4	71	-	-
Pygmies	23.8	14.3	-	-	38.1	4.8
KhoiSan	54.3	42	-	-	81.5	65.4

*Table VII—Correct classification rates in percentages (with crossvalidation) derived from multiple discriminant function analyses for each sub-Saharan African group.*

*Tabl. VII - Taux de classification correcte en pourcentages (avec « crossvalidation ») dérivés des analyses à fonctions discriminantes multiples pour chaque groupe de l'Afrique sub-saharienne.*

The plots representing the discriminant scores of the first two functions illustrate quite well all the facts cited above (*fig. 1, 2*). Group clustering increased markedly when only the reduced samples, especially non Bantu-speakers with Pygmies, were analysed. Eight variables (ZBBH, ZGOL, ZOBH, ZDKB, ZWFB, ZOBH, ZZYB, ZBPL) were often selected, as they presented the highest standardized discriminant function coefficients ( $\geq 0.5$ ). For all analyses especially using 12 variables (*fig. 1*), Western Africa and Central Africa clustered well together, and KhoiSan also fell quite apart.

In particular, when the full data set including all groups was analysed, most of the seventy percent confidence ellipses overlapped each other for at least 20% of their variation. The plots for both 12-variables (*fig. 1a*) and 9-variables (*fig. 2a*) analyses showed three clusters such as Southern Africa, KhoiSan, and Western Africa with Central Africa. The Pygmies fell between Southern Africa and the Western-Central Africa cluster, and Eastern Africa between the KhoiSan and the Western-Central Africa cluster. In figure 1a, function 1 accounted for 53.6% of the total variance and function 2 for 20.9%. Along function 1, the Western-Central Africa cluster had high long vault and wide orbits, and the KhoiSan low short vault and narrow orbits. The distinction of Eastern Africa from other groups appeared however more clearly along function 2, having one of the lowest vault height as the KhoiSan. In figure 2a, function 1 accounted for 54.9% of the total variance and function 2 for 24%. In comparison to previous plot, the positions of group centroids were more or less similar although slightly closer to each other such as for Southern Africa, KhoiSan and Pygmies. The overlapping variation in general was also higher. Western Africa and Central Africa were slightly more distant, but they clustered well with Eastern Africa. Along function 1, they showed that their orbits, interorbital and frontal breadths were all relatively much wider than the other extreme as the KhoiSan. Along function 2, the latter having narrow frontal and low orbits differentiated quite well from the other groups especially Western Africa, which was at the other end of the variation.

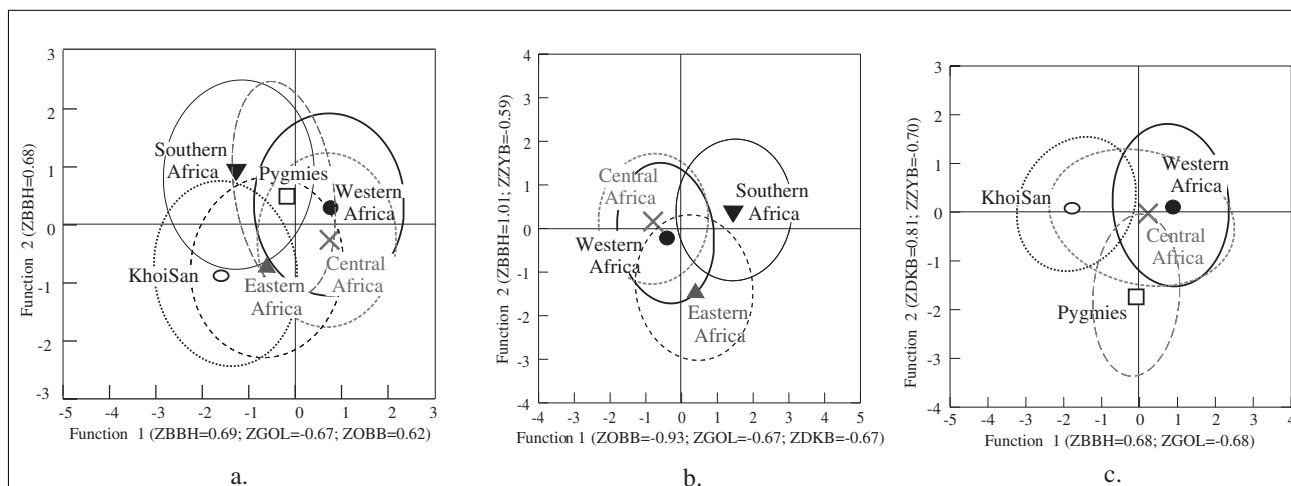
When Bantu-speakers only were analysed (*fig. 1b, 2b*), three other clusters appeared more clearly such as Southern Africa, Western Africa with Central Africa or Eastern Africa, and Eastern Africa or Central Africa. In figure 1b, function 1 accounted for 66.3% of the total variance and function 2 for 26.7%. Along function 1, the

morphological trends were similar to those identified in the previous analysis based on the cranium. Along function 2, two clusters were present such as Eastern Africa with low vault and narrow face and three other groups (Western Africa, Central Africa, Southern Africa) with moderately high vault and large face. In figure 2b, function 1 accounted for 79.2% of the total variance and function 2 for 15.6%. Along function 1, the morphological trends were similar to the previous analysis based on the cranium. Along function 2, the differentiation of the groups, especially in relation to both breadth and projection of the face was relatively low.

When non Bantu-speakers only were analysed (*fig. 1c, 2c*), the Pygmies and KhoiSan were well separated into two different clusters, and a third one corresponded to Western Africa (and Central Africa). The group clustering appeared more marked than in previous analyses, as the group centroids were positioned even more further apart, especially between Pygmies and all others. In figure 1c, function 1 accounted for 80.5% of the total variance and function 2 for 16%. Along function 1, the morphological trends were similar to those previously observed for the analyses based on the cranium. Along function 2, two clusters appeared to be quite marked such as the Pygmies with small interorbital breadth and narrow face, and the other groups with larger interorbital breadth and wide face. In figure 2c, function 1 accounted for 83.9% of the total variance and function 2 for 14.8%. Along function 1, the morphological trends were similar to previous analyses based on the cranium. Although the group differentiation was more visible along function 2, the two clusters were also more or less similar to those observed for the 12-variables analysis. However, the Pygmies were also differentiated here from the other groups by a lower facial prognathism.

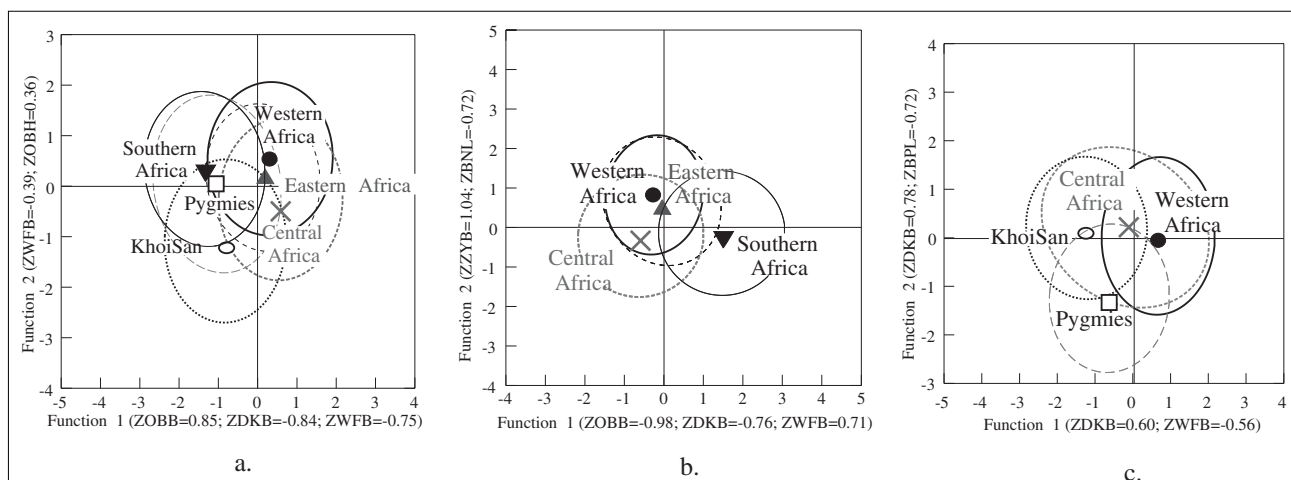
In summary, the morphological differences were most of the time reflected between two extremes with the following features such as: the KhoiSan with short low vault, low and narrow orbits and narrow frontal; and Western Africa with high long vault, high and wide orbits and broad frontal. The remaining groups were positioned between these two extremes, although varying and overlapping each other quite a lot. As group differentiation was very low for the analyses on the mandible, no morphological trend was determined in relation to the regional groupings and plots for the discriminant scores were therefore not presented.





**Fig. 1—Discriminant scores plots of modern sub-Saharan African populations for the 12-variables analysis (cranium).**  
70% confidence ellipses were drawn with their corresponding centroid.  
Highest standardized canonical discriminant function coefficients were put into brackets for each function.  
a—When analysing all groups, the first two functions account for 74.5% of the variance.  
b—When analysing Bantu-speakers only without Pygmies, the first two functions account for 93% of the variance.  
c—When analysing non Bantu-speakers only with Pygmies, the first two functions account for 96.5% of the variance.

**Fig. 1 - Graphiques des scores discriminants pour les analyses à 12 variables (crâne) sur les populations contemporaines de l'Afrique sub-saharienne.** Des ellipses à 70 % de la variation ont été représentées avec le centroïde correspondant. Les coefficients standardisés les plus élevés dérivés des fonctions discriminantes canoniques ont été mis entre parenthèses pour chaque fonction.  
a- Pour l'analyse incluant tous les groupes, les deux premières fonctions expriment 74,5 % de la variance.  
b- Pour l'analyse incluant seulement les Bantouphones sans les Pygmées, les deux premières fonctions expriment 93 % de la variance.  
c- Pour l'analyse incluant seulement les non-Bantouphones avec les Pygmées, les deux premières fonctions expriment 96,5 % de la variance.



**Fig. 2—Discriminant scores plots of modern sub-Saharan African populations for the 9-variables analysis (face).**  
70% confidence ellipses were drawn with their corresponding centroid.  
Highest standardized canonical discriminant function coefficients were put into brackets for each function.

a—When analysing all groups, the first two functions account for 90% of the variance.  
b—When analysing Bantu-speakers only without Pygmies, the first two functions account for 94.8% of the variance.  
c—When analysing non Bantu-speakers only with Pygmies, the first two functions account for 98.7% of the variance.

**Fig. 2 - Graphiques des scores discriminants pour les analyses à 9 variables (face) sur les populations contemporaines de l'Afrique sub-saharienne.** Des ellipses à 70 % de la variation ont été représentées avec le centroïde correspondant. Les coefficients standardisés les plus élevés dérivés des fonctions discriminantes canoniques ont été mis entre parenthèses pour chaque fonction.  
a- Pour l'analyse incluant tous les groupes, les deux premières fonctions expriment 90 % de la variance.  
b- Pour l'analyse incluant seulement les Bantouphones sans les Pygmées, les deux premières fonctions expriment 94,8 % de la variance.  
c- Pour l'analyse incluant seulement les non-Bantouphones avec les Pygmées, les deux premières fonctions expriment 98,7 % de la variance.



## DISCUSSION

Present results were in general difficult to compare with previous work, as nature and size of sample were very different as well as population subdivisions and methodological approach. For example, both Howells (1989) and Froment (1998) used “ethnic” affiliation as a framework for sample subdivisions. They also did not focus on the detailed results of classification rates obtained for each group from the multiple discriminant function analyses.

### **Re-evaluation of the craniomandibular variation in modern sub-Saharan Africa**

It was necessary to re-evaluate the craniomandibular variation in modern sub-Saharan Africa, as a much larger sample of African populations was used here in comparison to previous studies (Howells 1989; Froment 1998). Furthermore, at least eighty percent of the individual data were analysed together for the first time for both the cranium and the mandible (*Appendix*). Despite its heterogeneity, the sub-Saharan African sample under study was more representative of the geographical area than previous studies (Howells 1989; Froment, 1998). In comparison to Howells, the present study as well as Froment’s work had the advantage of being composed of far more known ethnic groups (at least 30 in total), which originated mainly from Western and Central Africa. In fact, Howells (1989) used only four ethnic groups for the whole African sub-continent. Therefore the size and nature of the sample under study provided various additional information.

Firstly, the results showed several aspects in agreement with previous work concerning the range of variation and affinities between groups.

The range of variation obtained through the multivariate with extremes such as the KhoiSan and other groups especially Western Africa, appeared to be similar to previous results (Howells 1989; Froment 1998). It often reflected size differences with the KhoiSan in the lowest values and the remaining groups in the higher values. In particular, these morphological trends in relation to facial features (orbits, frontal) showed similar geographical differences to those observed for vault breadth by Froment (1992b) within the African continent. This author identified Western Africans such as Cameroonians as having the broadest vault as it has been

observed here. Furthermore, in agreement with Howells (1989) and Froment (1998) again, but in contrast to the observations of Hiernaux (1974), the range of variation in sub-Saharan Africa was not continuous or clinal, as significant differences were still observed between the different regions. However, in agreement with all previous authors, inter-regional differences tended to increase, when they were analysed on a slightly smaller geographical scale (Bantu-speakers only without Pygmies). This fact supported again indirectly the presence of a higher amount of variation on an intra-regional scale rather than inter-regional one.

A very close affinity between Western Africa and Central Africa, which was nevertheless less marked when the face only was analysed, was also often observed. This fact was noted previously by Froment (1992b, 1998). It could be questioned therefore whether the morphological affinity between these two regions reflected a similar linguistic origin as well as geographical proximity: most of the populations analysed (at least 90%) in both Western Africa and Central Africa belonged to the Niger-Kordofanian linguistic family and were relatively close geographically. This supported the fact that morphology could agree with Linguistics, geography and Genetics, as it has been shown already previously (Cavalli-Sforza *et al.* 1994; Froment 1998). However, this observation was difficult to link with the Bantu-speakers expansion, as it concerned here a broader linguistic level.

In addition, although the “inter-ethnic” variation of the Pygmies was probably under-estimated, most of the latter despite their small sample size were often localized within or close to the variation of (Bantu-speaking) Central Africa. This fact also supported previous morphological observations as well as the hypothesis of a common origin for both Pygmies and Bantu-speakers, as it was proposed by Hiernaux (1976) and Froment (1993).

Secondly, in comparison to previous work, several new aspects have been also observed such as: a very high variability in the present sub-Saharan African sample, and a high group differentiation with both increasing number of variables and smaller data sets including different linguistic groups.

The total percentages of correct classifications obtained through the various multiple discriminant function analyses showed a very high variability in the morphology of all modern sub-Saharan Africans. The variation of each group always overlapped each other especially when the entire data set was used. The metric traits especially those related to the face appeared to be

more variable than previously thought (Howells 1989; Froment 1998). This was due most probably to the facts, that a larger data set was used, and that the analyses were based on individual data rather than group means. The plots obtained from the multivariate analyses had the advantage to suggest the rate of misclassifications between groups, which was often very high especially for Eastern Africa.

Group differentiation was the highest when using all twelve craniometric variables for both vault and face. It decreased slightly when using facial variables only, and markedly when using mandibular variables only. As the features selected for the mandible did not discriminate very well the groups even between the extremes of the variation (*e.g.*, KhoiSan, Western Africa), this fact could be explained by various reasons in relation to the methodology and/or evolutionary aspect of the mandible itself. Only a limited number of traits have been analysed here for the mandible, and they might have been not very representative of the complex morphology of the entire bone. In evolutionary terms, the mandible could also be shaped by different factors in comparison to the rest of the skull such as a lower heritability and/or possibly a higher biomechanical load (Carlson 1977, Van Gerven 1982). As morphological homogeneity, which was observed within all sub-Saharan African mandibles could reflect some of (or all) these factors cited above, it remained difficult to interpret mandibular results in relation to historical factors (Bantu-speakers expansion).

A high group differentiation, especially in smaller data sets (non Bantu-speakers) was also observed in the present sample. In general, subtle differences were found on an inter-regional level. Although group differentiation tends to increase with smaller sample size, it can also reflect the nature of the sample itself. Results also differed by number and type of variables suggesting differences between the various parts of the skull. Additional morphological differences were also localized geographically for two features such as: the height of vault, between Eastern Africans and Western Africans; and the orbital breadth, between Western Africans and Central Africans.

#### **Possible traces left from the Bantu-speakers expansion**

Two aspects derived from the present results on craniometry could support indirectly the hypothesis of

possible traces left from the Bantu-speakers expansion such as a homogenization process. They are related to the degree of group differentiation and the range of variation itself with some specific group affinities.

Firstly, group differentiation appeared to increase markedly and systematically when non Bantu-speakers only were analysed. This fact could support indirectly that there is less diversity (and rather homogeneous) within Bantu-speakers only, although group differentiation tends in general to increase with decreasing sample size.

Secondly, the range of variation itself within sub-Saharan Africa also supported the fact that not only geography but also history might have left traces. It was observed through present multivariates as well as previous work (Howells 1989; Lahr 1996; Froment 1998; Ribot 2002, 2003) that, as distance increases, differences increase. More precisely, this observation was suggested by the presence in the variation of two extremes, which corresponded to the geographically most distant groups (KhoiSan, Western Africa). However, as this is not applicable to the case of Southern Africa, which was often closer to Bantu-speaking Pygmies and Western Africa, it could support the hypothesis of a common origin for all these groups.

Furthermore, the overlapping variation observed between, for examples, Pygmies and Bantu-speaking groups, and KhoiSan and Southern Africa, could be also indirectly related to the Bantu-speakers expansion. As the latter was a large-scale phenomenon both geographically and chronologically, most probably interactions occurred and genes were exchanged between agriculturists and foraging groups in both Central Africa and Southern Africa (Morris 1992; Vansina 1995). Therefore, because of this intensive and long-term gene flow, the morphological features of the ancestral population of Bantu-speakers might have been completely “lost” or “diluted” in the modern variation.

However, other factors related not exclusively to the Bantu-speakers expansion could have been responsible for this variation. The overlapping ellipses drawn in the two figures were indicative of a certain amount of gene flow between all the groups. In particular, they could reflect very recent population admixtures that intensified inter-regionally especially during the last five centuries.

Not only gene flow might have been superimposed on the effects of the Bantu-speakers wave. But also other microevolutionary processes (*e.g.*, natural selection, genetic drift) could have both obscured and altered patterns of population history. Although the impact of

natural selection and genetic drift on skull morphology has not yet been clearly demonstrated especially on short time scales, it was not possible here to ignore them totally.

### CONCLUSION

In comparison to previous studies (Howells 1989; Froment 1998), information has been added here especially about sub-Saharan African diversity. A larger sample subdivided into several regions allowed us to specify the affinities of the groups between each other.

Morphological differences on an inter-regional level were identified in a more subtle manner than previously (Howells 1989; Froment 1998). And they supported indirectly the morphological similarities (present within Bantu-speakers), which could result from a large-scale dispersal. Both the degree and range of variation also indirectly supported this expansion: despite overlapping variation, slightly more homogeneity was observed within Bantu-speaking groups, who were positioned far away from the KhoiSan most of the time.

Additional information especially derived from the whole cranium, confirmed the similarity of Pygmies with Bantu-speaking groups, and Western Africa with Central Africa. It also supported the fact that the effects of both geography and history are difficult to distinguish from each other. Therefore it was difficult here to propose a microevolutionary model for explaining the biological effects of one historical event only, as the origins of morphological variation are very complex, especially within sub-Saharan Africa.

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## APPENDIX

Groups under study	Sources for metric data	Country	Region or city	Language	Ethnic origin	Place of deposit	Total Sample
Western Africa	Ribot 2002	Senegal	various	NK nc wa	various	FA	19
	Ribot 2002	Senegal	Diola	NK nc ma	Diola	CAD	2
	Ribot 2002	Senegal	Centre, Dakar	NK nc wa	griots Serer, Lebu	CAD	28
	Knip 1971; Ribot 2002	Mali	Nokara	NK nc ma	(Kurumba)	Grav	41
	Ribot 2002	Benin	Abome, Whydah	NK nc kw	various	AMNH	13
	Ribot 2002	Togo	various	NK nc kw	Yendi, Ewe	AMNH	11
	Ribot 2002	Ghana	various	NK nc kw	various (Ashanti)	AMNH	59
	Ribot 2002	Liberia	various	NK nc kw	unknown	AMNH	3
	Ribot 2002	Nigeria	Hausa region	AA cha	Haoussa	IRScNB	1
	Ribot 2002	Nigeria	Calabar, Atakpa	NK nc kw	various	AMNH	21
Ribot 2002	Cameroon	various	NK nc bc	various	AMNH	43	
Central Africa	Benington 1912	Gabon	N'Komi	NK nc bc	N'Komi	NHM	111
	Shrubsall 1898	Congo	Ubangui	NK nc bc	unknown	AM	2
	Ribot 2002	Congo	Alima N'Gunda	NK nc bc	Tegue	IRScNB	2
	Shrubsall 1898	DRC	Low Congo	NK nc bc	unknown	AM	1
	Benington 1912	DRC	Makunji	NK nc bc	Batetela	destroyed	49
	Ribot 2002	DRC	various	NK nc bc	various	IRScNB	44
	Ribot 2002	DRC	Feshi	NK nc bc	Basuku	IRScNB	126
	Ribot 2002	Angola	Loango	NK nc bc	unknown	IRScNB	1
Eastern Africa	Górny 1957	Uganda	hospitals?	unknown	unknown	W	55
	Ribot 2002	Rwanda	Kivu, Kibuye	NK nc bc	Tutsi	IRScNB	1
	Ribot 2002	Rwanda	Bugoye, Ruhengeri	NK nc bc	Bahutu	IRScNB	57
	Ribot 2002	Burundi	Bujumbura	NK nc bc	Murundi?	IRScNB	1
	Reinecke 1896	Kenya	various	NK nc bc	Pare, Shambaa	MM	1
	Kitson 1931; Ribot 2002	Kenya	Dabida	NK nc bc	Teita	Duckw	24
Southern Africa	Shrubsall 1898	Mozambique	various	NK nc bc	Wahenga, Urega	BM	17
	Shrubsall 1898	South Africa	Natal	NK nc bc	Xhosa, Zulu	BD	52
	Shrubsall 1898	South Africa	Cape	NK nc bc	Angoni	BM	5
	Morris 1992	South Africa	various	NK nc bc	Sotho, Tswana	Wits	60
Pygmies	Marquer 1972	Cameroon	south-east	NK nc bc	unknown	MNHN	1
	Marquer 1972	Gabon	(inland)	NK nc bc	Babongo	MNHN	9
	Marquer 1972	Congo	(central region)	NK nc bc	Babinga	MNHN	8
	Ribot 2002	DRC	Ituri	NK nc bc	Efe	MNHN	2
	Ribot 2002	DRC	unknown	NK nc bc	Twa?	IRScNB	1
KhoiSan	Shrubsall 1897	South Africa	various	K	various	various	42
	Morris 1992	South Africa	Riet River	K	KhoiSan	SA	34
	Ribot 2002	South Africa	various	K	various	AMNH	10

*Information about populations under study (N = 957).*

*Linguistic affiliations: AA = Afro-Asiatic including Chadic (cha); NK = Niger-Kordofanian including Niger-Congo (nc) that also includes West Atlantic (wa), Mandé (ma), Kwa (kw), Benue-Congo or Bantu (bc); K = KhoiSan.*

*Place of deposit: AM = Anatomy Museum, Cambridge; AMNH = American Museum of Natural History, New York; BD = Baranard Davis' Collection, United Kingdom; BM = British Museum, London; Duckw = Duckworth Laboratory, Cambridge; FA = Faculty of Anatomy, Dakar; Grav = Gravenzande Collection, Leiden; CAD = Cheikh Anta Diop Institute, Dakar; IRScNB = Royal Institute of Natural Sciences of Belgium, Brussels; NHM = Natural History Museum, London; MNHN = National Natural History Museum, Paris; MM = Munich Museum; SA = South African Museum, Cape Town; Wits = University of Witwatersrand, Johannesburg; W = Wrocław University.*

*Informations sur les populations étudiées (N = 957).*

*Affiliations linguistiques : AA = Afro-asiatique incluant Tchadique (cha) ; NK = Niger-kordofanien incluant Niger-congo (nc) qui inclut aussi Ouest atlantique (wa), Mandé (ma), Kwa (kw), Benue-congo ou Bantu (bc) ; K = KhoiSan.*

*Lieu de dépôt : AM = Musée d'Anatomie, Cambridge ; AMNH = Musée Américain d'Histoire Naturelle, New York ; BD = Collection de Baranard Davis, Angleterre ; BM = British Museum, Londres ; Duckw = Laboratoire de Duckworth, Cambridge ; FA = Faculté d'Anatomie, Dakar ; Grav = Collections de Gravenzande, Leiden ; CAD = Institut Cheikh Anta Diop, Dakar ; IRScNB = Institut Royal des Sciences Naturelles de Belgique, Bruxelles ; NHM = Musée d'Histoire Naturelle, Londres ; MNHN = Muséum National d'Histoire Naturelle, Paris ; MM = Musée de Munich ; SA = Musée Sud-Africain, Le Cap ; Wits = Université de Witwatersrand, Johannesburg ; W = Université de Wrocław.*