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The Late Peopling of Africa According to Craniometric Data. A Comparison of Genetic and Linguistic Models

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This paper shows the results of a multivariate study on a large craniometric database collected from literature to examine the late peopling of Africa. Our study includes cranial samples from terminal Pleistocene to Historic times, from most of the African continent. We discuss the implications of such findings with reference to the genetic/linguistic model.

The results show the primitive morphology of early *Homo sapiens* fossils from Middle Pleistocene and a possible continuity of this conservative pattern in some Late Paleolithic populations. The great diversity of the Pygmy populations across East and West Africa, which suggests different origins is also shown too. Finally, a late expansion of relatively homogenous Bantu-speaking populations is conjectured.

Key words: *Modern Homo sapiens, African continent, classic craniometrics, microevolution and migrations.*

A series of major craniological studies have been carried out on the people of Africa. However, explanations based on a raciological approach for the late peopling of the African continent, together with technical limitations in treating large quantities of data, have considerably confined the scope of such studies. Furthermore, the subsequent abandonment of the raciological paradigm has led to the rejection of large databases, which also contained valid measurements and insights.

The development of a new paradigm in physical anthropology, which encourages the analysis of population variability and the dynamics of change over time and space, has benefited from the development of new technologies which enable us to perform accurate multivariate calculations in the short term (*cf*. Howells, 1974; Keita, 2004; Pucciarelli, 2008). This has given rise to new hypotheses on the population dynamics of Africa over the last 10,000 years.

Additionally, the analysis of linguistic families in Africa has led to several models based on the possible migratory flows across the continent (Diamond & Bellwood, 2003; Holden, 2002). Genetics has also provided a large quantity of consistent data about the genetic diversity throughout the territory (Reed & Tishkoff, 2006). Interaction between these two disciplines has produced a general model of population movements over the past thousands of years in Africa.

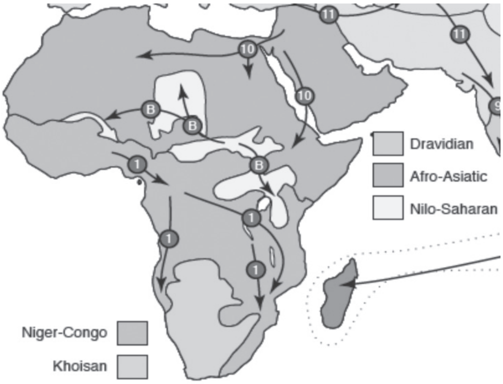

Figure 1. Linguistic families in Africa. (From Diamond and Bellwood, 2003).

TABLE 1 - Populations and bibliographical references.

POPULATION	REFERENCE
Fish Hoek	This study (*cast*)
Akoa from Cap Lopez	Marquer, 1972
Ba Binga from Binga	Marquer, 1972
Ba Binga from Bayanga	Marquer, 1972
Ba Binga from Bouetou	Marquer, 1972
Ba Binga from Zomie	Marquer, 1972
Ba Binga from Ouesso	Marquer, 1972
Ba Bongo from Franceville	Marquer, 1972
Ba Bongo from Zanaga	Marquer, 1972
Ba Bongo from Haut Ogooué	Marquer, 1972
Bushman A	Broom, 1923
Bushman Cape Colony	Broom, 1923
Bushman Kalahari	Broom, 1923
Bushman (Howells)	Howells, 1973
Dogon	Howells, 1973
Egypt	Howells, 1973
Herto	White, et al., 2003
Kef Oum Toviza	Balout y Briggs s/d
Korana	Broom, 1923
Mali	Oliver, 1989
Rabat	Odano and Riquet, 1978
Sahara	Chamla, s/d
Southeast Cameroon	Chamla, s/d
Taforalt	Odano and Riquet, 1978
Teita	Howells, 1973
Zulu	Howells, 1973
Eastern Pygmies	Beningthon and Peason, 1912
Nazlet Khater	Crevecoeur, 2006
Basuku	Ribot, 2003
Bahutu	Ribot, 2003
Eastern Africa	Ribot, 2003
Horn of Africa	Ribot, 2003

TABLE 1 - Populations and bibliographical references.

GOL	Glabello-occipital length
BNL	Basion-nasion length
BBH	Basion-bregma height
XCB	Maximum cranial breadth
ZYB	Zygomatic breadth
NLB	Nasal breadth
OBH	Orbit height
OBB	Orbit breadth

This paper demonstrates the results of a multivariate study on a large database collected from literature, including cranial samples (from populations, as well as isolated skulls), from the Terminal Pleistocene to Historic times (individual fossils from Middle Pleistocene, like Herto, Rabat and Kebibat, were included), from most of the African continent. We will discuss the implications of such findings with regard to the genetic/linguistic model.

Traditional craniometry has proved to be useful in the study of the biological diversity of human beings, as well as for the reconstruction of the history of migration and microevolutionary processes throughout the globe. We now propose its application as a research tool, given its primary importance in our discipline, to provide new insights into past and present human groups of a continent which represents the cradle of mankind.

We aim to test certain hypotheses about the possible origins of the earliest people in Africa, their evolution, and mutual relations.

An important aspect here is the arrival of human groups, who probably adapted to the semi-arid environment of Eastern and Southern Africa, the main forest ecosystems of Central and West Africa, the Mediterranean region, and the great deserts of Sahara and Sahel.

Studies on the morphological diversity of Africa generally accept that the Niger-Kordofanian family of languages, including Bantu languages, recently spread from the Central and Western parts of the continent. Such expansion would reflect a series of great migrations by groups transporting technological innovations, including metal working, farming, and cattle breeding. These people would have displaced other groups already settled in the continent, who apparently spoke several languages of the Khoisan family, some of which are still present in Southern Africa. Other groups, such as the Pygmies of Central Africa, would have lost their former language, adopting those of migrant shepherds and peasants, without mixing with them genetically (Cavalli-Sforza & Cavalli-Sforza, 1994). Moreover, the people of Northern and Eastern Africa would have been the result of interbreeding between natives and immigrants from Asia. A process which would have led to the presence of Afro-Asiatic languages in these areas. Finally, there is the Nilo-Saharan family of languages, which is present along the upper course of the Nile and Southern Sahara (Diamond & Bellwood, 2003).

Materials

Data for this study were extracted from the bibliographic references shown in Table 1. Since Howells' database (1973) has predominantly been used in recent studies, we have relied on it as a starting point for the selection of measurements employed. For other publications, we have used equivalent measurements to those referred to by Howell. This has significantly reduced the number of variables, but it has also added a great number of populations which reinforces the geographic representativeness of our material. The total number of applied measurements is eight (see Table 2).

Data have been used from a total of 1103 individuals, geographically distributed across the Northern, Eastern, Central, Western, and Southern parts of Africa. From a chronological point of view, the samples were divided into Paleolithic, Epipaleolithic, Neolithic, Recent, and Historic periods.

Methodology

Metric data from each skull were documented in an Excel database. We also recorded the geographic origin and the serial number of each skull. Whenever only the average was available for a population, we recorded this figure.

Individual skulls were also included in the samples because, in most cases, they represent periods at the end of Pleistocene and the beginning of Holocene, or otherwise poorly represented geographic areas.

Due to the fact that in many cases the ethnic origin was uncertain, we based the analysis on essentially geographic criteria, without taking into account any *a priori* conditions other than geography and chronology. Only for the interpretation of results, have we examined the linguistic, ethnic, and historical information available, to evaluate which hypothesis can best be applied in describing the causes for the distribution of certain traits in each region or period of time.

Contrary to other studies, our analyses were not divided into the traditional cranial regions (base, facial region and cerebral region) because this procedure isolates functional regions which are closely interrelated. Therefore, we have based our functional interpretation of skulls on Pucciarelli's proposal (2008): neurocranial components (anteroneural, midneural, posteroneural) and facial components (otic, optic, respiratory, masticatory, alveolar). It was not possible, however, to make a complete cranial-functional study because not all the required measurements were available.

In the case of data analysis, we have applied two multivariate procedures: Firstly, a cluster analysis for the construction of dendrograms according to UPGMA (Unweighted Pair-Group Method with Arithmetic Mean), which reflects possible phenetic or morphometric distances between subjects. This method could be used in the construction of phylogenies where the evolution rate was similar among cases, and provided the forma-

TABLE 2 - Craniological Measurements

Sheet1

PLACE	SOURCE	GOL	BNL	BBH	XCB	ZYB	NLB	OBH	OBB
Fish hoek	This study (cast)	198	88	103	148	130	25	31	40
Akoa du Cap Lopez	Marker, 1972	163	92	127	137	119	26	31	37
Ba Binga de Binga	Marker, 1972	170.9	98.9	128.4	128.4	126.8	28	33.4	28.6
Ba Binga de Bayanga	Marker, 1972	181	101	128	131	125	32	36	42
Ba Binga de Binga	Marker, 1972	169.9	96.4	123.4	125.4	122.4	27.4	31	37.4
Ba Binga de Bouetou	Marker, 1972	175.5	95.8	129.2	133.9	121.3	27.1	30.9	39.5
Ba Binga de Zomie	Marker, 1972	185	103	139	136	131	30	33	41
Ba Binga dOuesso	Marker, 1972	173	102	131	131	134	28	30	40
Ba Bongo de Franceville	Marker, 1972	173.3	96.6	127.9	128.2	124.2	26.6	34.3	37.6
Ba Bongo de Zanaga	Marker, 1972	172.9	96.2	126.6	123.3	123.8	26.6	33.2	35.9
Ba Bongo du Haut Ogooué	Marker, 1972	169.4	93.4	130.4	140	126.4	24.9	31.9	39.4
Bushman A	Broom, 1923	176.7	93.8	122.2	130.7	113.4	24.4	30.4	37.3
Bushman Cape Colony	Broom, 1923	182.5	96.4	125.9	137.9	121.9	25.3	29.9	39.1
Bushman Kalahari	Broom, 1923	176.4	90.6	120.8	131.1	120.3	25.1	30.9	37.9
Bushman Howells	Howells, 1973	174.6	92.9	120.8	130.5	119.4	26.4	30.8	38.3
Dogon	Howells, 1973	173.4	96.5	129.9	134.5	124.9	27.9	33.1	38.7
Egyot	Howells, 1973	180.6	98.7	130.6	137.3	124.5	24.3	32.8	38.6
Herto	White, et al., 2003	219.5	110	147	155	142	29	34	42
Kef Oum Toviza	Balout y Briggs S/F	200	117	143	148	140	27	31	42
Korana	Broom, 1923	188	100.3	130.8	130.8	127.1	26.8	32.2	39
Mali	Oliver, 1989	182.5	101.5	133.4	132.5	120.2	26.8	32.9	41.6
Rabat	Odano et Riquet, 1978	193	120	153	132	125	25	34.5	51
Sahara	Chamla, s/d	185.3	99	131	132.5	121.3	26.7	33.5	40.9
Sud Est du Cameroun	Chamla, s/d	181	107	142	138	135	28	34	36
Taforalt	Odano et Riquet, 1978	182.7	103	132.7	139.7	131.5	26.7	29.8	41.3
Teita	Howells, 1973	178.2	98.6	126.5	127.7	126.8	27.4	32.5	38.4
Zulu	Howells, 1973	182.2	99.7	131.2	132.9	126.5	28.2	33.3	39.8
Pygmées Orientaux	Beningthon y Peason, 1912	176.7	95.11	129.5	134.1	128.3	26.6	32.4	37.8
Nazlet Khater	Crevecoeur, 2006	187	106.5	132	136	148	27.21	36	4030
Basuku	Ribot, 2003	148.1	94.4	41.4	127	121.6	26.8	32.3	38
Bahutu	Ribot, 2003	181.5	95.2	124.6	132.4	128.2	26	32.3	39.4
Eastern Africa	Ribot, 2003	179.4	96.9	126.4	129.9	125.5	26.1	32.3	39
Horn of Africa	Ribot, 2003	177.7	96.7	130.6	131	122.7	24.1	32.3	38.8

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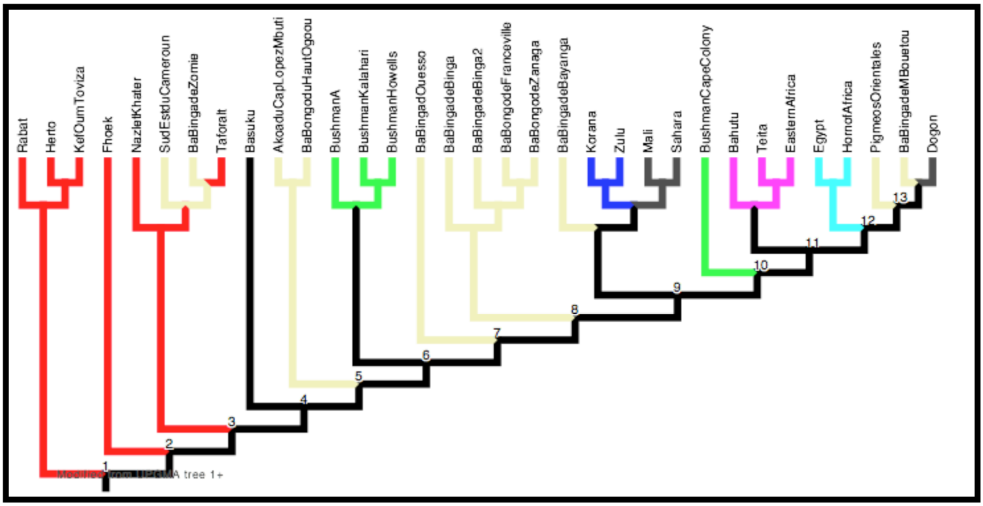

Figure 2. Dendrogram of Cranial Samples

tion of methodologically related groups. Here we used the program *Mesquite* (Maddison & Maddison, 2010) for the generation of dendrograms. Secondly, we carried out a Principal Components Analysis (PCA) by the covariance matrix, which uses an orthogonal transformation to convert a set of observations of possibly correlated variables into a set of values of uncorrelated variables, called principal components. This procedure enables the identification of variables (dimensions) with a greater loading of the generation of dendrogram clusters. We used the *Past (*Paleontological Statistics) program for the construction of plots and covariance tables.

Thus, specific variables, such as the length and breadth of skulls, could be individually compared and possible causes of similarities (common ancestry, physical activity, way of life, geographical location, etc.) evaluated.

The major limitation of the present study is the unequal sample size for each region, and the overrepresentation of certain regions, such as Northern and Southern Africa. In spite of this, we believe that the results provide a good starting point for the reconstruction of the continent's peopling and the formulation of new hypotheses.

Findings

We have made a dendrogram to illustrate the relationship between samples. This dendrogram contains 11 major branches. Generally, there is a tendency towards regional or geographic clustering of populations; however, a more detailed analysis of each segment is required to better understand the probable causes for each cluster.

The first three major branches in the dendrogram (Branches 1 2 & 3) correspond, almost entirely, to individuals or populations from the Middle Pleistocene, Upper Paleolithic and Early Holocene. Only two recent populations, both from Western Africa, have been integrated into the third branch, being near to the Paleolithic sample from Taforalt, Algeria. These populations are still too far away from the Neolithic and Historic samples, so they could not represent direct ancestors of any present human population. However, as we will see from the principal components analysis, the fossil from Fish Hoek may be more closely related to the Khoisan (Bushman) groups in South Africa, than to any other African people.

The cranium from Herto (Ethiopia), which is dated to 160,000 years ago, is included in the most remote branch, with the remains of Rabat, considered to be from the Middle Pleistocene. This cluster is at the root of the dendrogram, and suggests a historical and genetic continuity along the Pleistocene, from the earliest populations of *Homo sapiens* to the last groups of the Upper Paleolithic.

Branch 4 contains only one Bantu-speaking population, from Central Africa, and we cannot yet explain such isolation (perhaps it is related to the size of the sample).

Branch 5 contains two Pygmy groups, from Central-West and Central-East Africa, which moved apart from the rest of the Pygmy populations, reflecting the high diversity of these groups, perhaps inappropriately clustered under the same label of “Pygmies”, Vigilant et al., 1989, propose an early time for the separation of the Pygmy populations from East and West Africa of roughly 119,000 years ago, maybe reflected in the distances in Branch 5 and the rest of the Pygmy populations. On the other hand, recent studies propose a split scenario, about 18,000 years ago, separating East and West Pygmy populations (Anagnostou et al., 2010). This study may support the first hypothesis.

In Branch 6, we see a cluster of three Khoisan-speaking populations from Southern Africa, with the hunter-gatherer way of life, characteristic of the inner desert zones. Interestingly, the fourth population ascribed to these groups lies too far away, in a cluster assigned to groups with different origins (Branch 10, which we will discuss later). The next two Branches, 7 & 8, comprise clusters of groups characterized as Pygmies from Central and Western Africa only. These consist of very widespread Bantu-speaking populations, which apparently acquired these languages through an acculturation process following contact with other Bantu-speaking cattle breeders and farmer groups. Basically, their large morphologic homogeneity could be explained by the common origins of these people, prior to the expansion of the Niger-Congo language family, including the Bantu branch.

Branch 9 is divided into two large clusters: one includes a “Western Pygmy” population with two population groups speaking Bantu family languages (Korana and Zulu) in South Africa, and the other, two Niger-Congo language-speaking populations from Western Africa. This apparently confusing situation can probably be explained in two ways: 1) this reflects the same lifestyle as nomadic herders, or 2) this is in accordance with the hypothesis that the Bantu people of South Africa originated from a region between Central-Western Africa and South of the Sahara. A subsequent principal components analysis may support either one of these hypotheses.

The sample represented in Branch 10 was classified by Robert Broom as a “Bushman” group, despite living on the coast of the Cape region. Apparently, this ascription is inaccurate, and the skulls could possibly belong to another Bantu population, however the limited number of individuals may reduce the certainty of an analysis of this little know population.

Branch 11 clusters three Bantu-speaking groups from East Africa, all known to be archaeologically and ethnographically similar and probably recently derived from a common ancestral population.

Branch 12 clusters population groups from the Horn of Africa (Somalia) and Howells’ samples from dynastic Egypt. These groups seem to represent migrations of groups from the Middle East, who spoke languages of the Afro-Asiatic family (prior to the expansion of Islam) and mixed with the local African populations.

The last, Branch 13, includes populations from West Central Africa (Dogon from Mali and Babiga from Cameroon) which are not culturally related, clustered with the sample from Central-Eastern African Pygmies. This clustering seems to make little sense. However, it seems to justify the hypothesis that Western and Eastern Pygmies, despite having very ancient common ancestors, reached their cranial morphology separately, leading to similarities in height, through a process of convergent evolution caused by living in similar environments with an almost identical way of life, as genetic studies suggest.

The Dogon people, on the other hand, lived in close proximity with Pygmy groups in the South of Mali for centuries, until the expulsion of the Pygmies in the twelfth century. It is possible, therefore, that a certain degree of interbreeding took place, which might explain the morphological relations identified.

Principal Components Analysis

Principal Components Analysis (PCA) provides supplementary information on the morphological models of the populations studied and can yield a phenetic pattern recognition by projecting the cases onto the PC axes. Figure 3 shows the relationship between the first and second components, which account, as a whole, for 65.261% of the sample * variance. The symbol: ✸) refers to the Pygmy populations; ✸) refers to the Khoisan (Bushman) groups in South Africa; ✸) refers to the Dynastic Egypt and the Horn of Africa populations; ✸) refers to the people from Sahara and Mali (including the Dogon); ✸) refers to the Bantu-speaking populations in Eastern Africa, while) refers to Bantu people from Central Africa, and ✸) to the sample from Pleistocene Africa.

The most elongated ellipse corresponds to 93% of the Pygmy variability, while the oval group corresponds to the Bushman variability. As we can see, almost every African

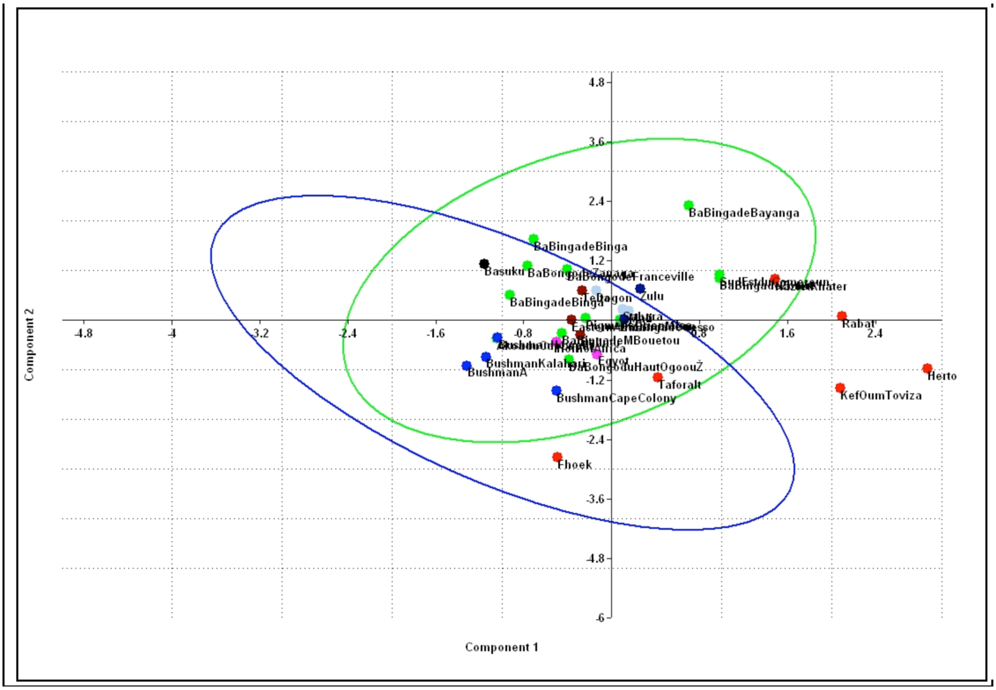

Figure 3. Representation of the First and Second Components in PCA (see text for interpretation).

population falls clearly within the two ellipses, which indicates that the variability of the continent, though significant, is within well-defined limits. The great exceptions here are the Paleolithic remains from the Pleistocene and the early Holocene, which fall outside the variability range or are too close to its limits.

Certainly, there is a tendency towards a "primitive" morphology across the continent, characterized by the large size of the cranium and an extreme anteroposterior length, when compared to shorter and more rounded forms.

The Fish Hoek skull is clustered almost exclusively with the samples from South Africa, which suggests that this fossil, dated at roughly 12,000 to 20,000 years ago, could represent an ancestral branch to the Khoisan people, even if it is at the limits of its variability.

If we were to draw a graph, with the loadings of each measurement comprised in the principal components, we would observe the following distribution pattern:

For Component 1 (Figure 4), every correlation is positive, which means that the skulls to the right of the graph are long (GOL), high (BNL, BBH), the facial region is broad (ZYB), and the orbits are broad (OBB). In comparison, the skulls to the left are short, low and with a narrow face. To sum up: big skulls fall to the right side of the graph.

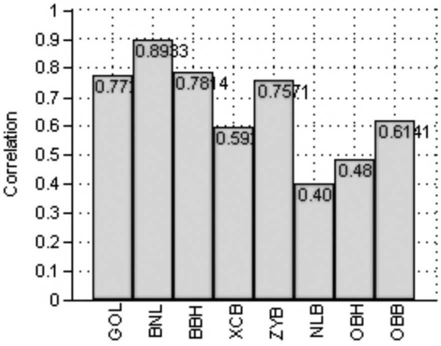

Figure 4. Analysis of Component 1.

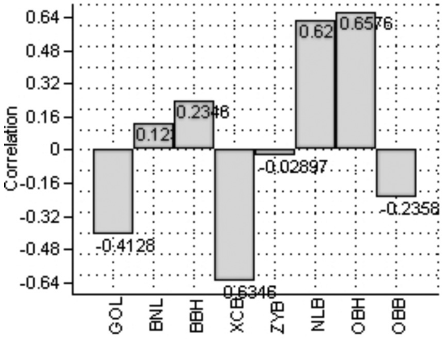

Figure 5. Analysis of Component 2.

The graphic of Component 2 (Figure 5) shows mixed correlations: for example, the skulls to the top of the graph are short (GOL), narrow (-XCB), with a broad nose (NLB), and high, narrow orbits (OBH », OBB); while the skulls to the bottom are round, broad, with a narrow nose, and low, broad orbits. In short, PC2 accounts for residual nasal and orbital height variation.

To summarize, therefore, the Pleistocene skulls from across Africa tend to be broad, long, with a broad face and broad, short orbits.

By contrast, the skulls of the Khoisan ("Bushman") population are relatively short, low, broad, narrow, with a comparatively intermediate nose.

Pygmies are characterized by great variability, but they usually have small-sized round skulls, and a balanced face. Their degree of dispersion, however, contradicts the findings of other studies, which have detected a strong homogeneity among Pygmy populations, even if these support the hypothesis that the typical features of these populations, including their short stature, took place after their geographical separation through convergent evolution. As is suggested by other more recent studies (Ramírez Rossi y Sardi, 2010; Anagnostou, 2010; Vigilant, 1989).

The Bantu-speaking populations are mostly at the center of the graph, which represents a common morphological tendency, but with a strong variability, whether they come from Southern, Eastern or Central Africa. This supports the idea of a common, more recent ancestor than that for the Pygmy and Khoisan groups, as well as a similar way of life founded on cattle breeding and farming, independent of their surrounding environment.

Conclusion

Although this comparative exercise is at an early stage, we would like to highlight how difficult it is to explain the morphological diversity of the African continent exclusively via one cause or simple set of variables, such as the expansion of the Bantu languages or the migration of people from one part of the continent to another or from abroad.

Microevolutionary processes, such as selection pressure, genetic drift or gene flow, have merged over time to produce the current distribution model observed in recent and modern populations. We need to create, however, larger databases, and to apply complex theoretical models, which incorporate geographic and historical variables, in order to fully understand the demographic history of this continent, together with its most ancient and enduring human populations in the world.

Note. Authors wish to express our gratefulness to the journal's reviewer for the useful observations to the manuscript.

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