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# Phenotypic diversity and history of the Congo Basin populations: Equatorial Guinea, Bantu Speaking Central Africans and African Pygmies

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## ABSTRACT

**Background:** African Pygmy Populations (APP) are believed to be one of the first groups of the Congo Basin rainforest peoples to separate from the rest of modern humanity. The arrival of Bantu speaking agriculturalists from 5,000 BP led to the formation of a large number of ethnic complexes in Central Africa and the Atlantic coastal area, mainly due to a one-way flow of pygmy women. There are now only a few small contingents of African Pygmy population groups who are mixed or who have almost disappeared as a result of migratory flows from Cameroon.

**Aims:** We analysed the adult phenotypic diversity of 9 populations (17 groups of both sexes) of the Congo basin and Bioko Island, which were anthropometrically characterised in 1948. The phenotypic clusters that we detected, which we interpret as likely mixing of local Pygmy populations and Bantus, may be useful as references for future studies, particularly genetics.

**Subjects and methods:** The matrix of inter-distances between populations was generated, using the 21 variables, with the Euclidean distance between the mean vectors relating to the standardised variables. When the UPGMA (Unweighted Pair Group Method with Arithmetic Mean) was used separately in men and women, the phylogenetic trees showed a clear separation between populations.

**Results:** The body measurements that most effectively distinguished the groups are linear dimensions and the width of the hips and mean thoracic circumference. In this study, the cephalo-facial dimensions were of little value in identifying the groups.

**Conclusions:** The samples of Equatorial Guinea show a major inter-group overlap, and considerable intra-group variations. There are also notable differences amongst African Pygmy populations in terms of height, but not in body proportions.

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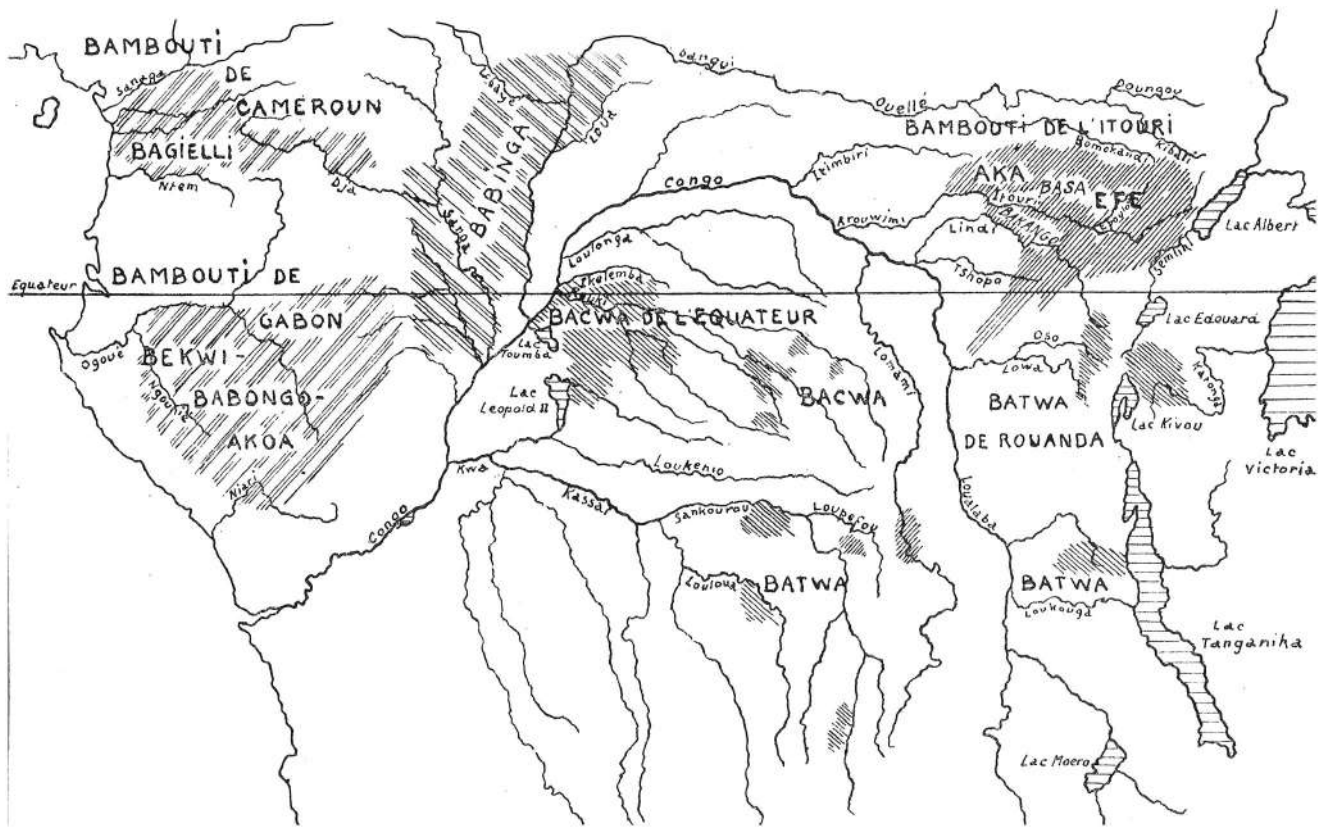
Equatorial Africa basin;  
humans and environment;  
somatology; meta-analysis

## Introduction

Africa is the most complex continent in terms of diversity and antiquity of human settlement. Nuclear DNA micro-satellite studies have shown that the African San, Biaka Pygmy and Bambuti Pygmy populations have the deepest coalescent times of the populations in the Human Genome Diversity Project (Sun et al. 2009; Bergström et al. 2020). Schebesta (1940) applied a simple and useful geographical division to distinguish between three geographical groups currently living in the rainforest: Eastern Pygmies (mainly Bambuti, from the Ituri, and Batwa), Central Pygmies (Bacwa and Babinga) and Western Pygmies (Schebesta 1940) (Figure 1). This subdivision is supported by Cavalli-Sforza et al. (1994, p. 177) who stated: "Many groups of Pygmies live in Central Africa, all of which have several characteristics in common. Small stature is the most important one ... In general, populations living in tropical forest are small the world round, in agreement with the idea the small stature represents an adaptation to warm and humid environments." Schebesta's

overall picture may act as a guide for geneticists who are currently collecting samples from the populations of the central and western areas of the Congo Basin, because it characterises the ethnic groups of African Pygmies that were probably isolated before the migrations of Bantu-speaking agriculturalists. Froment (2014) and Verdu (2014) provided an excellent summary of current human diversity in the areas we mention above. It is not unusual to see recent publications about the Biaka Pygmy ethnic groups or others from Central Africa that believe that their sample comes from Pygmy populations, when in fact the degree of mixture with Bantu speaking people remains untested.

In the area near the Atlantic coast, only a few groups of mixed Pygmy population groups are distinguishable at present, and they have almost disappeared as a result of migratory flows from Cameroon. Grollemund et al. (2015) stated that the Bantu expansions, that swept out of West Central Africa, began 5,000 years ago. This has been confirmed by recent genetic studies (Quintana-Murci et al. 2008; Verdu et al. 2009; Campbell and Tishkoff 2010; Jarvis et al. 2012;



**Figure 1.** Distribution of African Pygmy populations in about 1900. According to Schebesta (1940).

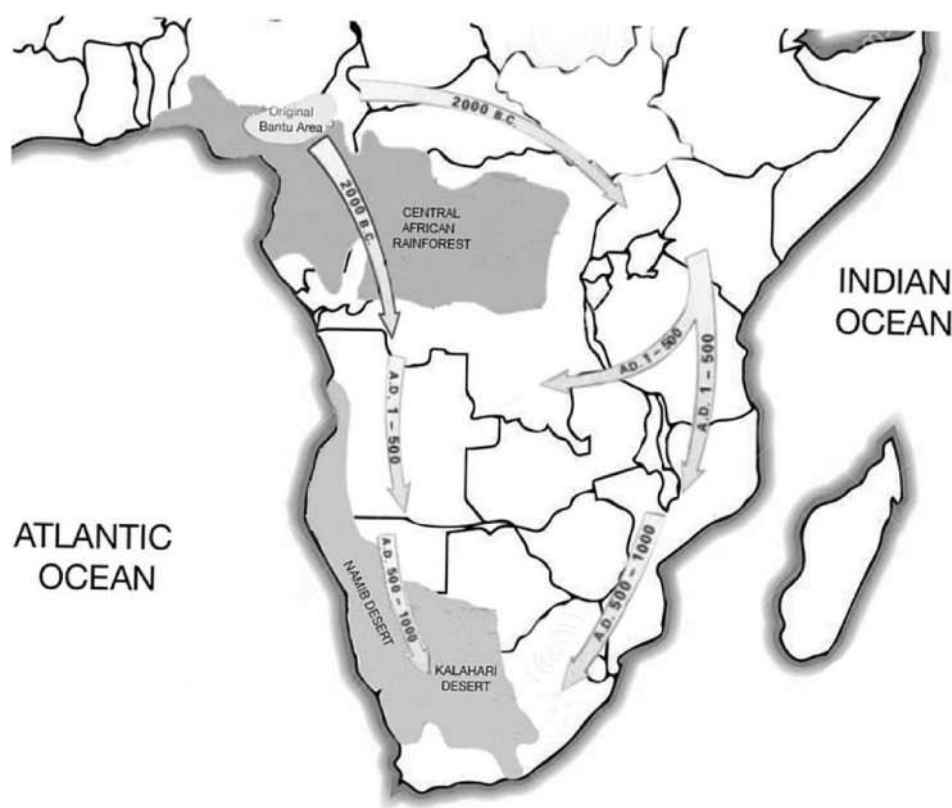
Bostoen et al. 2015; Gurdasani et al. 2015; Silva et al. 2015, Skoglund et al. 2017) (Figure 2).

There is practically no osteological pygmy fossil record to be found in the acid African soils, which dissolve the calcium phosphate in bone. A single skeleton, dated to 810 BP (1235 calibrated AD), from the rock shelter site of Matangai Turu Northwest in the Ituri Forest has been described, but the evidence available that might attribute it to a member of the Pygmy populations is inconclusive at best (Mercader et al. 2001). On the other hand, cranial differences between Eastern and Western Pygmy populations have been found in a sample of thirty-three skulls from African Pygmy populations preserved in European museums and collections (Ramirez-Rozzi and Sardi 2010). According to Cavalli-Sforza et al. (1994, p.180) the paucity of fossil records from dry areas supports the belief that Pygmy populations represent a long-term adaptation to the tropical forest (see also Froment (2014)).

In this context, the contribution of molecular genetics is decisive (Lopez et al. 2019, Patin and Quintana-Murci 2018, Bergström et al. 2020). The variation of mtDNA demonstrates that Western Pygmy populations show signs of a recent bottleneck 4,000–650 years ago, coinciding with the diffusion of the Bantu languages, while the Eastern pygmies appeared to have undergone an earlier reduction in population size (Batini et al. 2011). Phylogenetic analysis of the lineage L1c1a of mtDNA has shown that this clade is indigenous to Central Africa, with the most recent branches shared between Bantu agriculturalists and Pygmy populations (Quintana-Murci et al. 2008). There was an initial divergence of the ancestors of

contemporary Pygmy populations no later than 70,000 years ago (Jarvis et al. 2012; Verdu 2014), followed by a period of isolation between the two groups, with confirmation that there was a recent one-way maternal genetic flow of Pygmy populations towards the Bantu agriculturalists, which was remarked on by European colonisers.

Verdu et al. (2009) genotyped 604 individuals at 28 autosomal tetranucleotide microsatellite loci, in 12 non-pygmy and 9 neighbouring Pygmy populations from Western Central Africa. They found a recent common origin (~2,800 thousand years, kaBP) of all the Western Central African Pygmy populations, along with an older divergence (54,000 or 90,000 ka) between ancestral Pygmy and non-Pygmy populations. Some authors have proposed that, according to the mtDNA molecular clock, the inferred ancestors of modern Pygmy hunter-gatherers and Bantu-speaking agriculturalists could have diverged as long ago as 70 ka (Quintana-Murci et al. 2008), and that ancestral western and eastern Pygmy populations separated more than 18 ka, circa 62 ka according to Bergström et al. (2020). There was subsequent genetic differentiation among the Western Pygmy populations within the past 2800 years (Verdu et al. 2009), as we mentioned above. A recent study of the African L2 mitochondrial lineage shows that three moments of expansion from a Central African source were associated with L2: one migration at 70–50 ka into Eastern or Southern Africa, postglacial movements (15–10 ka) into Eastern Africa; and the southward Bantu Expansion in the last 5 ka (Silva et al. 2015) (see also Scally and Durbin (2012) for a comparative review of mutation rates of molecular clocks).



**Figure 2.** Routes of the Bantu expansions, as suggested by the genetic data, with direction arrows based on archaeological records (modified from Cavalli-Sforza et al. 1994).

There are few morphological studies available, since the French expeditions and those of other Central-European powers in the early 20th century used different measurement techniques. Froment (2014) provided a somatological summary, along with data about the palaeoanthropology and recent settlement in the Congo Basin and surrounding areas.

Shea and Bailey (1996) carried out an anthropometric study in a series of Efe pygmies that they compared with African non-pygmies. This article was a major advance, as it updated the study of the African Pygmy population phenotype. The authors calculated the allometry of the samples that were analysed and rejected the previous untested observations of the body proportions of the African Pygmy populations and other features, which had been interpreted by some as “ancient features” (see Lefrou 1943, p. 365; Marquer 1972, p. 112 and 115). The analyses by Shea and Bailey (1996) concluded that these supposed “primitive retentions” in African Pygmy populations should instead be considered as mere growth allometrics related to a rapid size decrease in these groups during the growth stage.

According to a little-known monograph by Gusinde (1948, p. 62), Pygmy populations with the smallest body size, the Mbuti people of the Ituri (plural Bambuti), in the north-eastern part of the basin of the river Congo, had an average stature of 144.03 cm in men (range of variation 126.8–159.7); and 137.04 cm in women (range of variation: 123.4–150.4). But the head, and to a lesser extent, the torso, are essentially of the same size as persons of average height (Froment 1993; Cavalli-Sforza et al. 1994).

Serological evidence has linked the low stature in African Pygmy populations to deficiencies in the growth hormone/insulin-like growth factor (Merimee et al. 1968, 1987, 1989, 1990). This line of research was brought up-to-date by Bozzola et al. (2009); Meazza et al. (2011); and Travaglino et al. (2011). More recently, Zoccolillo et al. (2020) identified novel genetic variants associated with short stature in a Baka Pygmy population. Reviews of the African Pygmy phenotype have been provided by Perry and Dominy (2009) and Campbell and Tishkoff (2010).

Using genoma-wide single-nucleotide polymorphism genotype data, Bamberg et al. (2013) found that short-stature populations (thought to be Asian Pygmy populations) in the Philippines and Papua New Guinea are more genetically similar to their neighbours than they are to each other and have undergone positive selection in different genes. These results show that the African Pygmy populations and Asian short-statured groups, which are geographically distant, have probably evolved towards a short stature independently. The authors also found that different genes associated with growth, thyroid function and sexual development, are under selection in these different short-statured groups.

Our study analysed the sexual and population variations of the somatometric and cephalo-facial variables taken from 17 samples in the Congo basin (Table 1). For some unknown reason Alcobe (1950) did not gather data about Combe women in the settlements on the coast of Equatorial Guinea, which explains why our study does not have a total of 18 samples (9 populations studied by sexes, with the Combe female population missing, since Alcobe did not collect their

**Table 1.** Number (*N*) of individuals analysed in this study.

	Male <i>N</i>	Female <i>N</i>
I. Bioko/Equatorial Guinea		
Pamue	115	110
Combe	115	–
Bubi	116	115
Total	346	225
II. Bantu-Speaking Central Africans		
Lese	36	39
Ndaka	54	16
Bali	22	26
Beyru	35	18
Total	147	246
III. Eastern Pygmies		
Efé	386	263
Aka	115	110
Total	501	373
Total	994	697

Three ethnic series are from Bioko/Equatorial Guinea (I), four belong to the Bantu-speaking Central Africans (II) and two to the Ituri (Eastern) Pygmies (III).

data in 1948). Our objective is to establish the phenotypic variations shown by these populations as a result of their respective evolutionary history. This study may help to define clearly demarcated population groups and so facilitate genetic studies within the scope of the African peoples.

### Study population

The basin of the Congo river, a huge geographical region shaped by the climate and the equatorial rainforest, is the backdrop to the major human migratory flows from the Atlantic coast that took place in the recent history of the area. The progressive desertification of the Sahara led to movements of peoples that extended from east to west all along the Sahel. One outcome was converging pressure from the region that is now Nigeria towards the rainforest from all around its perimeter, towards the south and east. Bantu speaking populations moved into the rainforest and created new multi-ethnic complexes. As we commented above, Grollemund et al. (2015) propose that the Bantu expansion extended from Central-West Africa about 5,000 years ago, bringing agriculture along the emerging savannah corridors (Figure 2).

The Pamue people studied here are part of the large ethnic group of the Fang that extends from Cameroon to Gabon, via Equatorial Guinea, along the area near the coast. All of Equatorial Guinea is covered by tropical rainforest that extends to the coast. The coast is inhabited by the Combe, another of the groups studied here. The Pamue and Combe did not originate in the area they inhabit but rather came from the north at an unknown date.

In the same way as the Bantu-speaking agriculturalists, who came to the southeast Congo basin from the Great Rift, the Pamue and the Combe received a one-way flow from Pygmy populations (Alcobe 1950; Alcobe and Panyella 1951). Prior to the expedition of Alcobe (1950), several French expeditions documented the populations of Cameroon and Gabon, although they used different anthropometric techniques from those of Alcobe (e.g. Cottés 1911–12; Dugast 1949; Vallois 1939, 1940, 1941, 1950). All the French colonial

bibliography makes constant reference to the introgression (marriage) from Pygmy Populations in the Bantu family clans and that they are patrilineal. Women from Pygmy populations were highly appreciated for their knowledge of medicinal plants. A sizeable number of the articles on molecular genetics that we cite also refer to this marriage pattern.

### Data collection and technique

Twenty-one somatometric variables were studied (Martin 1928). Use of the UPGMA (Unweighted Pair Group Method with Arithmetic Mean) showed the group structure. Combined analysis of the 21 samples was carried out using PCA (Principal Component Analysis) and Cluster analyses. The series relating to Spanish Guinea were gathered in 1948 by a scientific expedition of the Spanish National Research Council (Alcobe 1950; Alcobe and Panyella 1951) (unpublished data). Alcobe's data were collected in somatological sheets and photographs of 1,376 individuals who were adult natives of both sexes in the former Spanish colony of Spanish Guinea: the Bubi (Bioko Island), Pamue (central Guinea) and Combe (coastal) ethnic groups. We randomly selected a representative sample of 120 individuals from each series, approaching the sample size of the least represented series: 115 Pamue women (Table 1).

To contextualise our analysis of Alcobe's Guinean samples with their contemporaries in the Congo basin, we compared them to data collected from Pygmy populations and Bantu-Speaking Central African Groups studied by Gusinde (1948) (details shown in Table 2). We selected both sexes of the Efe and Aka ethnic groups respectively, from the Ituri pygmies, along with the 4 ethnic groups of the BSCA (Bantu-Speaking Central African) Groups: Lese, Ndaka, Bali and Beiru, separated by sex (Gusinde 1948).

For the data collection indicated above, Alcobe (1950) and Gusinde (1948), predated the Helsinki Declaration, and the contemporary standards for the protection of human subjects were not in place. In any case, our work has the consent of the Spanish Scientific Research Council (CSIC), which financed the Alcobe expedition in 1948, as well as the consent of the UB Bioethics Commission (University of Barcelona) and the Ethics Committee for Human Research (CEISH) of the UPV/EHU (University of the Basque Country), institutions to which the authors belong.

As we commented above, Schebesta (1940) showed the distribution of African Pygmy populations (Figure 1), which matches the reports of a number of scientific expeditions (Poutrin 1911–12; Schebesta and Lebzelter 1933; Pales 1938; Vallois 1940; Gusinde 1956). Gusinde (1948) also took measurements of men and women of the Bantu-Speaking Central African Groups of different linguistic groups that live within the equatorial rainforest, in the northeast region of the Republic of the Congo, near the capital Kisangani (old Stanleyville).

Both Gusinde and Alcobe were expert anthropologists and used the same measurement technique (Martin 1928; Martin and Saller 1962). In this study we selected 21

**Table 2.** Data sources of the collections studied in the present work.

Data source (see References)	Studied collections
Alcobe (1950)	1,376 individuals, adult natives of both sexes in the former Spanish colony of Spanish Guinea: the Bubi (Bioko Island), Pamue (central Guinea) and Combe (coastal) ethnic groups.
Gusinde (1948) (pages 206–214)	Ituri pygmy individuals: Efé and Basúa 386 men/263 women; Aka: 115 men/110 women; Beyru 13 men/9 women.
Gusinde (1948) (pages 350–357)	Bantu-Speakers Central African Groups (BSCA): Lese 36 men/39 women; Ndaka: 54 men/16 women; Bali: 22 men/29 women; Beyru 35 men/18 women.

variables (Table 3). These variables, taken in mm, are longitudinal and transverse measurements of the human body and head.

The standing individual's height was measured first. It was used as the reference for all other partial longitudinal measurements, such as arm and leg length, along with their respective segments. Next, the transverse diameters were taken (always in mm) of the width between the shoulders and the hips, respectively, as well as the thoracic circumference. This technique is reproduced and updated in the third volume of the famous manual by Martin and Saller (1962). Intra-observer error was negligible in our study. Admittedly, unlike osteological studies, the measurements may vary according to the pressure placed on the soft tissues of the human body, although Martin's anthropometric technique (1928) places the measurement points near the bone of a living individual. In our case both authors, Gusinde (1948) and Alcobe (1950), had considerable experience in anthropometry. We did not detect any major variations in the statistical normality tests of variables in Alcobe (1950). The values of the measurements in the work of Gusinde (1948) were as expected. In any case, since it was impossible to gain access to the individual data of Gusinde's series, we based our statistical analysis on the mean trends of the groups, thus minimising any potential observer error.

### Numerical processing

The variables analysed here are highly correlated. In such a context it is advisable to use the Mahalanobis  $D^2$  distance to shed more light on the underlying factors and identify and classify the differences between the populations (Mahalanobis 1936; Ghosh and Majumder 1993; Dasgupta 1995). This diversity measurement eliminates the effect of non-informative variables, redundant information and the effect of the unit of measurement. Unfortunately, Gusinde (1948) only provides the range of variation and the averages of the series of Pygmy populations and the Bantu-Speaking Central African groups. If the measurement values for each individual are not available, it is impossible to estimate the matrix of variances-covariances within populations, and replacing them with the matrix of variances-covariances between populations would be questionable when calculating the Mahalanobis  $D^2$  distance. With this limitation in

**Table 3.** Quantitative variables (body and head) analysed in this study.

Name of variables according to Martin-Saller technique (1962)	Name of variables in this study	Body
1	V1	height
23	V2	sitting height
6	V3	pubic height
45A	V4	arm length
47A	V5	humerus length
48A	V6	forearm length
13	V7	iliospinal height
53.1	V8	total leg length
55	V9	femur length
56	V10	lower leg height
17	V11	armspan
35	V12	biacromial breadth
40	V13	intercristal breadth
61	V14	middle thoracic perimeter
		Head
1	V15	maximun length
3	V16	maximun breadth
6	V17	bizygomatic breadth
8	V18	bigonial breadth
13	V29	nose breadth
21	V20	nose height
18	V21	facial height

mind, the Euclidean distance provides a sound approximation to the Mahalanobis  $D^2$  distance when it is applied to the informative variables (the non-informative variables have been eliminated). In addition, the variables under consideration have been previously standardised (the effect of the unit of measurement has been eliminated). In this context, the multicollinearity is in fact an implicit form of weighting.

The F test of multiple comparisons (one-way ANOVA) was used to identify and select the variables that provided significant differences between the populations (informative variables).

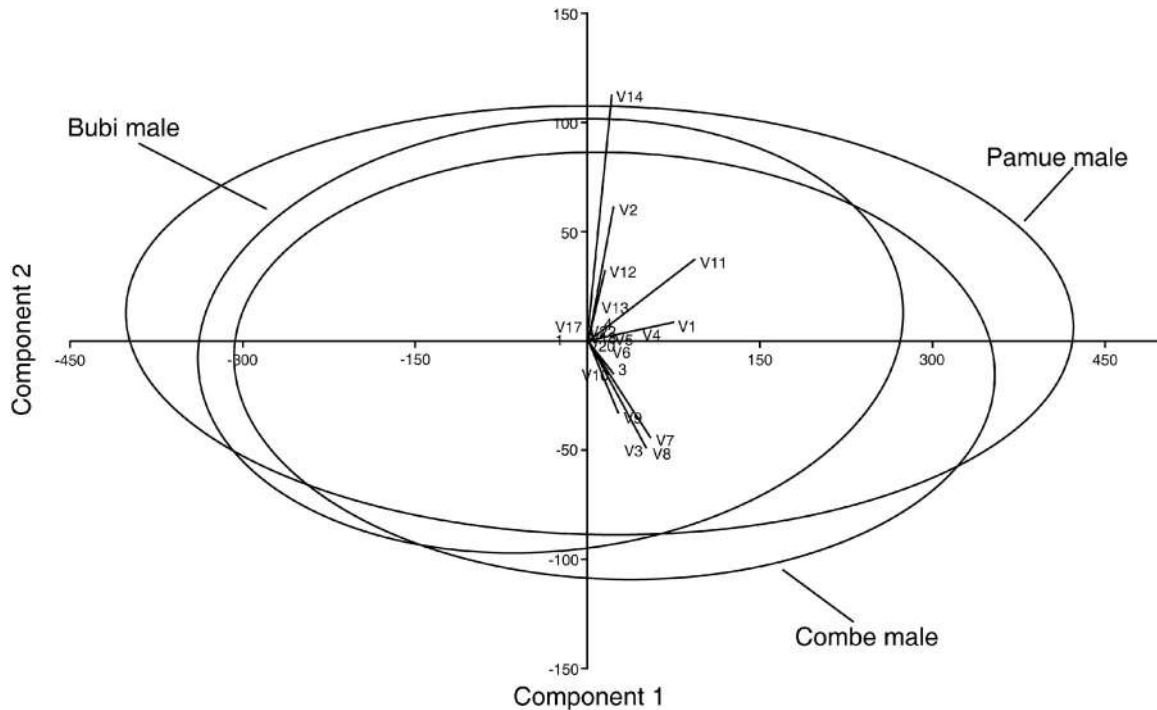
Bootstrap methods were used to computationally simulate 10,000 replicas for each sample scenario and the ratio was obtained between the observed range of variation ( $R = \max\{x_1, x_2, \dots, x_n\} - \min\{x_1, x_2, \dots, x_n\}$ ) and the standard deviation ( $s$ ), when this is unknown (details shown in Table 4). This approach provides results that are compatible with the ones described by Hozo et al. (2005) and Montgomery (2009). Student's t test (comparison of two populations) was used to contract the significance of the morphological variation between all the pairs of populations.

The values of the Fisher-Snedecor F test (multiple comparisons) and Student's t test (comparison of two populations) are affected by the size of the sample, which in the populations of our study is very unequal. To prevent this effect, the 95% confidence interval made it possible to calculate the overlap between populations in each variable. In particular, the percentage of overlap between the populations  $i$  and  $j$  was calculated as follows:

$$S(i, j) = \max \left\{ 0, \frac{\min\{\bar{x}_i + 1.96s_i, \bar{x}_j + 1.96s_j\} - \max\{\bar{x}_i - 1.96s_i, \bar{x}_j - 1.96s_j\}}{\max\{\bar{x}_i + 1.96s_i, \bar{x}_j + 1.96s_j\} - \min\{\bar{x}_i - 1.96s_i, \bar{x}_j - 1.96s_j\}} \right\} \cdot 100$$

**Table 4.** Ratio between standard deviation and range of variation in samples of size  $n$ .

$n$	16	18	22	26	35	36	39	54	110	115	263	386
$c = \bar{s}/\bar{R}$	0.2785	0.2705	0.2584	0.2495	0.2355	0.2342	0.2306	0.2179	0.1952	0.1939	0.1748	0.1668

**Figure 3.** Variance ellipses (95%) of the two First Principal Components (PCA) of Bubis, Combes and Pamues (men).

where  $(\bar{x}_i - 1.96s_i, \bar{x}_i + 1.96s_i)$  and  $(\bar{x}_j - 1.96s_j, \bar{x}_j + 1.96s_j)$  are the confidence intervals that characterise the populations (confidence 95%).

Using the above-mentioned informative variables, the Euclidean distance with standardised variables provided the matrix of inter-distances between populations and the representation of a phylogenetic tree showed the group structure. The UPGMA (Unweighted Pair Group Method with Arithmetic Mean) was used in the classification and, to reduce subjectivity in choosing the number of groups, the  $\Delta$ TESS statistics were used for being the most effective maximising cut-off level (Hartigan 1985), Pseudo-F (Calinski and Harabasz 1974) and Silhouette (Rousseeuw 1987). The classification obtained, labelled G1, G2, G3, was contrasted with the outcome from applying the k-means non-hierarchical clustering method. Furthermore, the geometrical representation in 2D space was obtained using the PCA (Principal Component Analysis) method to see the differences and explain the morphological variation. The ethnicities and groups obtained in the classification were shown together in this smaller space. The classification and graphic representation in a 2D space took the form of three scenarios: a) male variation; b) female variation; and c) joint variation, considering each ethnic group and sex as a differentiated population.

The values of the statistics (TESS, Pseudo-F and Silhouette) were obtained with the Ginkgo program (Bouxin 2005) and were confirmed by using the k-means clustering and R fviz-cluster functions. The geometric representations in phylogenetic tree and PCA were obtained with the Ginkgo program. The variation ellipses with a confidence of 95% of

the available information of all the individuals that made up the population samples (Figures 3 and 4) were obtained with PAST (Paleontological statistics software package v. 3.25, Hammer et al 2001). With information that was limited to descriptive values (mean and variance) and a highly reduced size of sample per group (Figures 8–11), the variation ellipses contain all the group populations and were built to follow the directions of the axes (principal and secondary). Finally, we used Statgraphics Centurion v18 to run the hypothesis tests and to generate the 1,000 replicas per experimental condition in the bootstrap simulation.

## Results

### Factor analysis of the Equatorial Guinea and Bioko Island series

We have drawn three main conclusions from the factor analysis (PCA) of the five samples from Equatorial Guinea and Bioko. Firstly, there is an evident intra-group overlap along with a major intra-group variability in the male series (Figure 3). Second, the main source of variation of the first component is associated with height, armspan and other longitudinal dimensions of the human body in both sexes. The diversity in the second component is mainly associated with the middle thoracic circumference. The same results are found in the female series (included in Figure 4). Third, the cephalo-facial variables appear in the other principal components, and their statistical weight is low in the overall analysis.

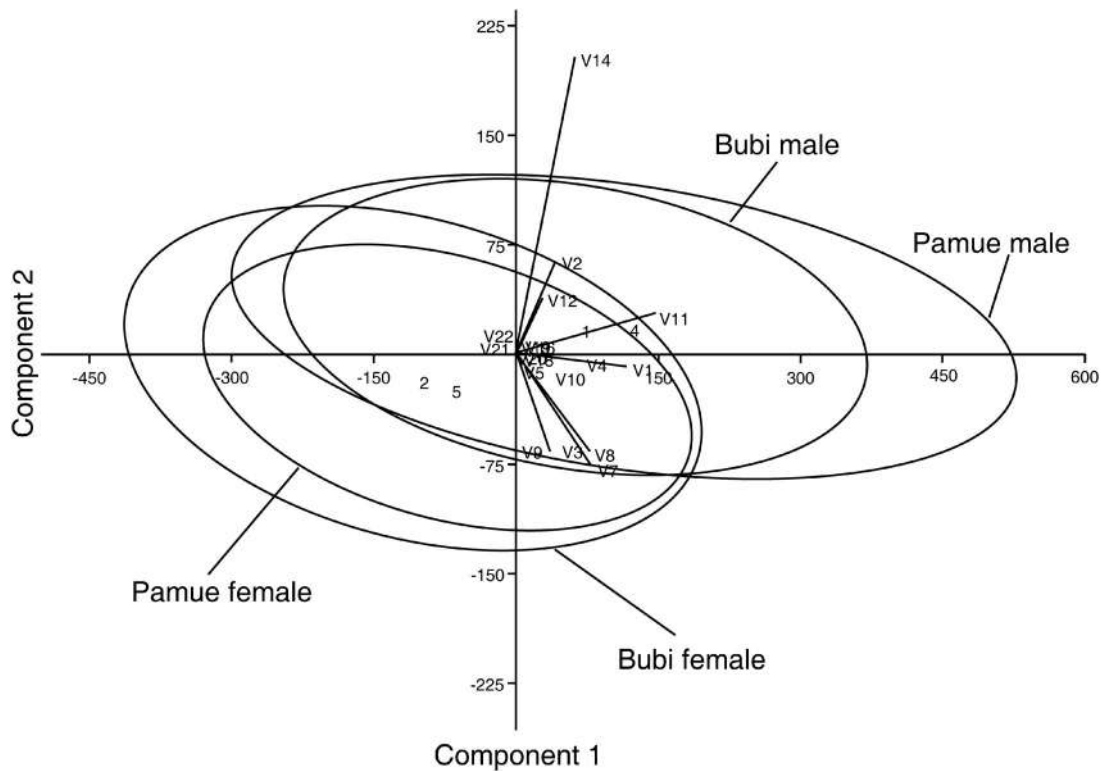


Figure 4. Sexual dimorphism amongst Bubi and Pamue. Variance ellipses (95%) of the two First Principal Components (PCA).

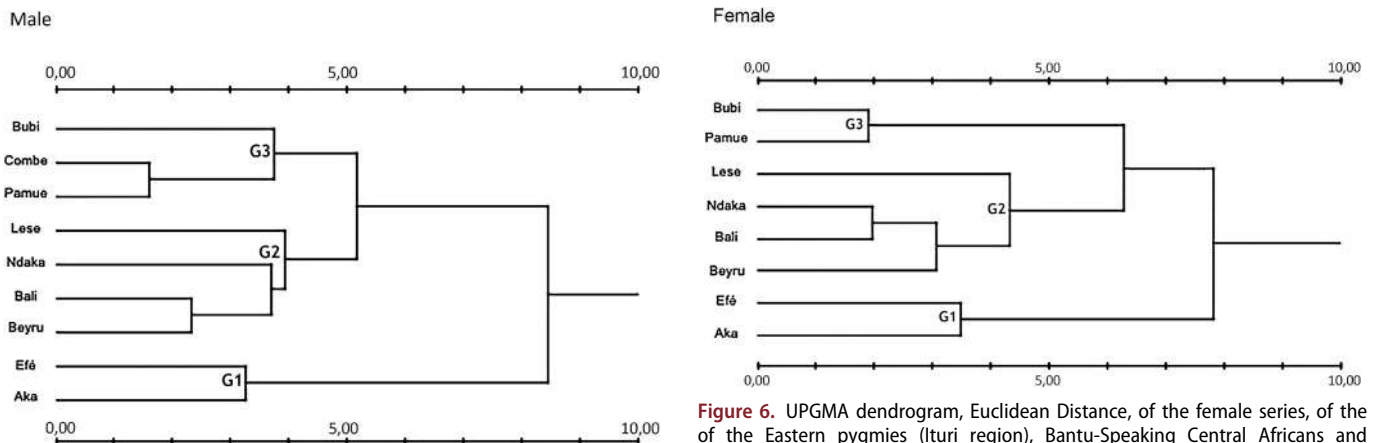


Figure 5. UPGMA dendrogram, Euclidean Distance, of the male series of the Eastern pygmies (Ituri region), Bantu-Speaking Central Africans and Bioko/Guinean groups. Note that the labels G1, G2, G3 are the groupings detected by our mathematical analysis, described in the Numerical Processing section, and that these are highly consistent with the initial assignment of ethnic groups with geographic and linguistic criteria.

Figure 6. UPGMA dendrogram, Euclidean Distance, of the female series, of the of the Eastern pygmies (Ituri region), Bantu-Speaking Central Africans and Bioko/Guinean groups. Note that the labels G1, G2, G3 are the groupings detected by our mathematical analysis, described in the Numerical Processing section, and that these are highly consistent with the initial assignment of ethnic groups with geographic and linguistic criteria.

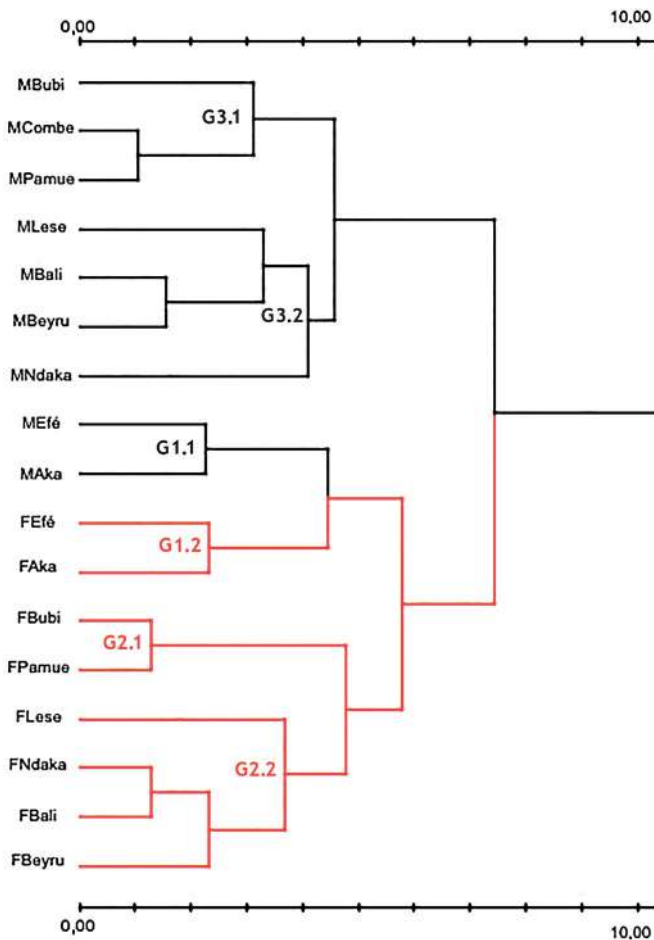
Given that the variables with most statistical weight in the Guinean series are height and the longitudinal segments of the body, we compared them with those of the Western Pygmy populations. Gusinde (1948) found no differences in the body proportions of the Efe Pygmy populations of the Ituri. Table 5 shows that neither are there any differences in the group of series from Bioko and Equatorial Guinea of the Efe African pygmies of the Ituri. It is impossible to calculate the allometric processes undergone by these populations during their growth and development as Gusinde (1948) did not study them in age and gender groups, he only studied

adults. From the data in Table 5, made with the data from Gusinde (1948) and ours from Bioko/Guinea, it is concluded that the interpretations of Marquer (1972) are incorrect and that Shea and Bailey (1996) were right.

### F test, UPGMA and cluster analysis

The multiple comparison F test showed significant differences in all the variables. In women, the Fexp statistics varied between 6.09 (bigonial width/breadth) and 400.45 (V2, bust height) and in all the cases, the *p* values were lower than  $6.4464 \cdot 10^{-7}$ . In men, the Fexp statistics varied between 11.02

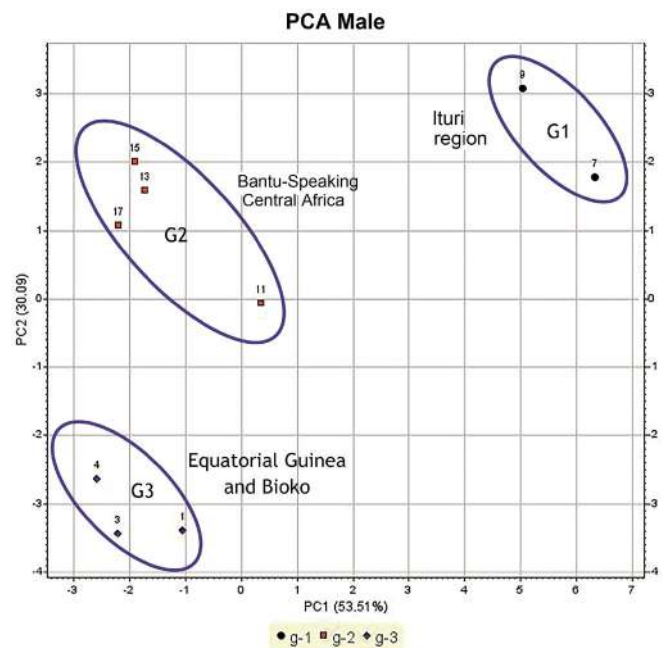




**Figure 7.** UPGMA dendrogram, Euclidean Distance, of the male and female series, of the Eastern pygmies (Ituri region), Bantu-Speaking Central Africans and Bioko/Guinean groups. The 17 series (Combe women were not measured) are distributed into the following: a) Pygmies (men G1.1 and women G1.2); b) other women, divided into two sub-groups (Bioko/Guinea G2.1 and Bantu-Speaking Central Africa G2.2, in red); and c) other men, also divided into two sub-groups (Bioko/Guinea G3.1 and Bantu-Speaking Central Africa G3.2). Note that the labels G1, G2, G3 are the groupings detected by our mathematical analysis, described in the Numerical Processing section, and that these are highly consistent with the initial assignment of ethnic groups with geographic and linguistic criteria.

(width of nose/nose breadth) and 631.68 (sitting height) and in all the cases, the  $p$  values were less than  $5.5951 \cdot 10^{-15}$ . For this reason, all the variables observed were maintained in the study.

The matrix of inter-distances between populations was generated by using the 21 variables, with the Euclidean distance between the means vectors relating to the standardised variables. Based on this matrix of inter-distances, the representations in phylogenetic trees, using the UPGMA separately in men and women (Figures 5 and 6) showed a clear separation between the Pygmy populations and the subdivision of the other populations, which are subdivided into two different groups (the Bantu-Speaking Central African groups and Bioko/Guinea). The results after separating sexes match the joint analysis of both sexes (Figure 7), in which each ethnic group and sex are considered as a different population (in total 17). In this case, the distribution in three and five groups is justified by the maximisation of the  $\Delta$ TESS, Pseudo-F and Silhouette statistics in the scenarios



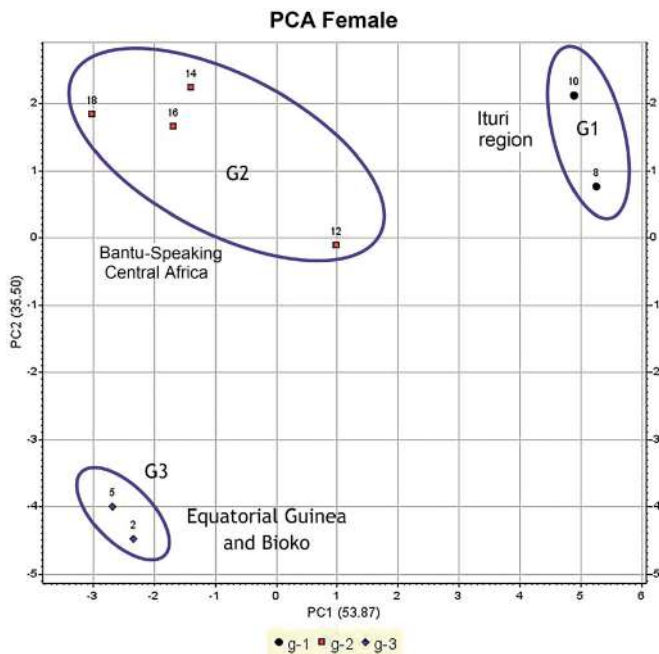
**Figure 8.** Male variation of the Eastern pygmies (Ituri region) (G1), Bantu-Speaking Central Africa (G2) and Bioko/Guinea (G3) groups, in the two First Components of a PCA.

that were studied (men and women separately, men and women jointly). Furthermore, the hierarchical classifications obtained with the UPGMA also match the classifications obtained with the k-means non-hierarchical clustering method.

The geometric representation of the populations with the PCA method (Principal Component Analysis), with Varimax rotation of the components, was limited to two components (principal axes).

### Male PCA analysis and overlapping variables

Analysis of the first two principal PCA components of males provided a representation that explains 83.6% of the variation (Figure 8). The first principal component (horizontal axis) is related to the variables that explain the longitudinal (V1, V3-V10) and cross-sectional dimensions of the body (V11-V14), except for the sitting height (V2), all with a negative sign: the populations of the largest size are located on the left of the graph and the smallest ones on the right. The correlation between the variables that identify the axis is very high (0.90), with the exception of intercrestal breadth. The Bantu-Speaking Central African groups, partially mixed with the African Pygmy Populations, are scattered between African pygmies and Guineans, who are widely separated by height and build (see Hiernaux 1975; Cavalli-Sforza et al. 1994, p. 183). For all the variables, the averages of each of the variables of the Pygmy populations are less than those observed in the Bantu-Speaking Central African groups. In turn, these averages are slightly lower than those observed in Guineans, with the exception of the males of the Lese group, located more to the right of Figure 8, who are smaller.



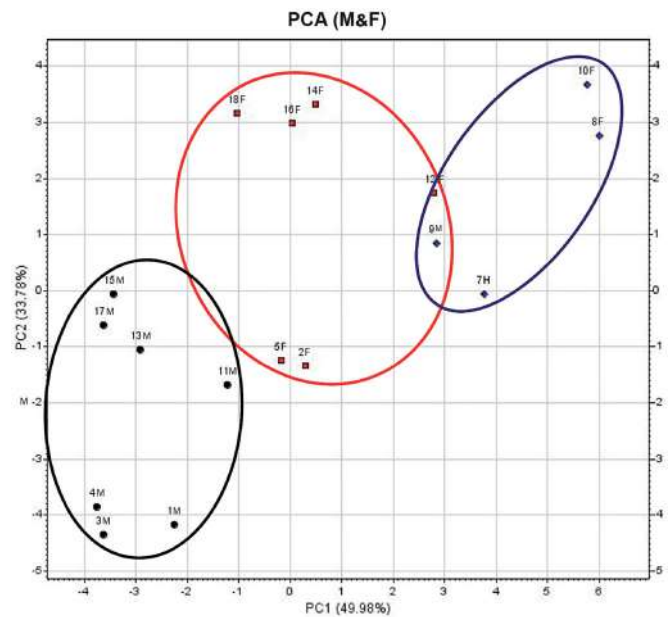
**Figure 9.** Female variation of the Eastern pygmies (Ituri region) (G1), Bantu-Speaking Central African (G2) and Bioko/Guinea (G3) groups, in the two first components of a PCA.

In lengthwise measurements (V1, V3-V10), the intra-group overlap is very high (83.83%, African Pygmy populations; 78.55%, the Bantu-Speaking Central Africa groups; 85.06%, Guineans), 72.72% between the BSCA groups and Guineans, in contrast to that of each group and the African Pygmy populations (17.61%, between the BSCA groups and Pygmy populations; 10.19%, between Guineans and APP).

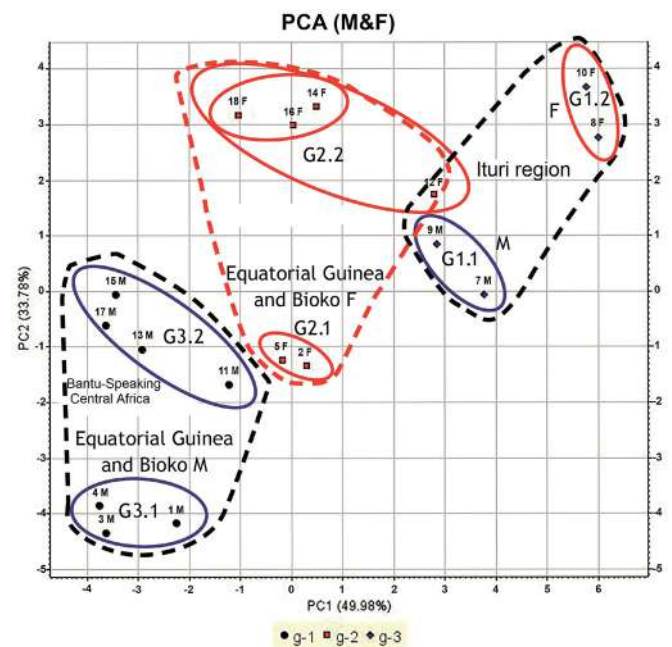
In the cross-sectional measurements (V11-V14), the average intra-group overlap is very high (75.83%, African Pygmy populations; 76.65%, the BSCA groups; 86.89%, Guineans), as it is between populations of the BSCA groups and Guineans (64.92%). As with the longitudinal measurements, the overlap of the BSCA and Guinean groups is less with regard to Pygmy populations (36.25%, between the BSCA groups and APP; 36.25%, between Guineans and Pygmy populations). For armspan and biacromial breadth the order described above is conserved for the longitudinal measurements (African Pygmy populations/BSCA groups/Guineans). For intercrestal breadth and middle thoracic circumference, the mean values of the BSCA groups are higher than the ones observed in the other two groups. Furthermore, the Guineans have narrower hips (intercrestal breath).

On the other hand, the biacromial width breadth of the males of the Lese ethnic group explains the high overlap (79.54%) with the African Pygmy groups and the closer proximity between them. The overlap of the Lese with the Pygmy populations in the intercrestal breadth is 76.37%, which is greater than that of the Lese with Guineans (89.72%). The overlap of the average thoracic circumference is 55.48% with Pygmy populations and 87.80% with Guineans.

The second principal component (vertical axis) is associated with bust height, the dimensions of the head (V15-V20)



**Figure 10.** Variation of the 17 series, male and female, of the Eastern pygmies (Ituri region) (right), Bantu-Speaking Central African (center in red) and Bioko/Guinea (left) groups, in the two first components of a PCA.



**Figure 11.** Proposed interpretation of the variation of the 17 series, male and female, of the Eastern pygmies (Ituri region) (G1), Bantu-Speaking Central Africa (G2) and Bioko/Guinea (G3) groups, in the two first components of a PCA. Identification of groups: 1) Bubi M; 2) Bubi F; 3) Combe M; 4) Pamue M; 5) Pamue F; 7) Efe M; 8) Efe F; 9) Aka M; 10) Aka F; 11) Lese M; 12) Lese F; 13) Ndaka M; 14) Ndaka F; 15) Bali M; 16) Bali F; 17) Beyru M; 18) Beyru F. Note that the variance in the first two axes of this PCA is not 100%, as it is in the UPGMA trees (Figures 5 and 6).

and the intercrestal breadth, all with a negative sign. The populations with larger body size are located at the bottom of the graph while the ones with smallest body size are at the top. The correlations between the variables that identify the vertical axis are less than the ones observed in the horizontal axis, with the exception of the variable intercrestal breadth, whose average Pearson correlation is 0.38. In this

**Table 5.** Body proportions in the series Bioko Island / Equatorial Guinea (present study) and the Efé pygmies from the Ituri region (Gusinde 1948). (Percentages with respect to height).

		Bubi Male	Bubi Female	Pamue Male	Pamue Female	Combe Male	Efe Male	Efe Female
height	V1	100%	100%	100%	100%	100%	100%	100%
pubic height	V3	52,6	52,3	52,3	51,8	52,8	50,8	50,4
arm length	V4	46,5	46,0	46,6	46,0	46,8	45,4	44,7
humerus length	V5	19,2	19,1	19,4	19,2	19,4	19,4	19,5
forearm length	V6	16,0	15,8	16,2	16,0	16,4	15,0	14,6
total leg length	V8	54,7	54,6	54,5	54,1	54,9	53,3	52,9
femur length	V9	27,8	28,6	27,6	27,8	28,2	27,2	26,9
lower leg height	V10	23,5	23,0	23,5	23,2	23,4	22,4	22,1
biacromial breadth	V12	22,6	22,0	22,3	21,9	22,4	21,6	21,3
intercrestal breadth	V13	15,0	16,1	15,2	15,7	15,0	16,5	17,5

second component, the results indicate that the males from the Pygmy populations have the smallest body size, the BSCA groups are intermediate (very close to the Guineans, with the exception of the males of the Lese ethnic group), and the Guineans are large. In the variables V2, V16 and V20, the averages of the Pygmy populations are very similar to those of the BSCA groups and less than those of the Guineans. The average intra-group overlap is very high (95.47%, Pygmy populations; 80.79%, BSCA; 89.20%, Guineans); it is high between the Pygmy populations and the BSCA groups (70.12%), much lower between the BSCA groups and Guineans (38.45%) and is even less so between Pygmy populations and Guineans (26.71%).

The second principal component indicates a different placing of males of the Lese ethnic group, whose overlap is lower with Pygmy populations (−6.81%) and greater with Guineans (+15.13%). In the variables V15 and V17 (length of cranium and width), both averages in Pygmy populations are less than those of the BSCA groups and these in turn are less than the ones observed in Guineans. The respective average overlaps are very high, both within the groups (93.69%, Pygmy populations; 77.74%, the BSCA groups; 89.74%, Guineans), and between groups (77.69% between Pygmy populations and the BSCA groups; 81.52% between the BSCA groups and Guineans; 63.30% between Pygmy populations and Guineans). Finally, there are small differences in the averages of the variables mandibular bigonial breadth and width of nose, where the average intra-group overlap is 82.92% and the average inter-group overlap is 80.04%.

After combining indicators, and in accordance with the results obtained in the overlap of the variables, differences have been observed in the nasal index (V19/V20: 1.02, Pygmy populations; 0.98, the BSCA groups; 0.83, Guineans). No differences were detected in the cephalic index (V16/V15: 0.78, Pygmy populations; 0.77, the BSCA groups; 0.78, Guineans), or in the gonio-zygomatic index (V18/V17: 0.75, Pygmy populations; 0.76, the BSCA groups; 0.73: Guineans). The Pygmy populations (G1) and Guineans (G3) are located at opposite ends (G1: top right hand quadrant; G3: bottom left hand quadrant) and the BSCA groups (G2) share a position in the first component with the Guineans and also share one in the second component with the Pygmy populations.

### Female PCA analysis and overlapping variables

The PCA analysis of the women in the first two principal components explains 89.4% of the variation (Figure 9). The variables that explain the axes are the same as the ones for the men, with some differences relating to correlations. In the horizontal axis, the average correlation between the explanatory variables is slightly lower than the one obtained in men (with the exception of intercrestal breadth, width of the pelvis, whose mean correlation is 0.85); and higher in the vertical axis, with the exception of intercrestal breadth, as in the men, whose mean correlation is 0.51. The overlap in longitudinal measurements (V1, V3-V10) is similar to that obtained in men (81.08%, Pygmy populations; 64.03%, the BSCA groups; 85.54%, Guineans; 19.17% between Pygmy populations and the BSCA groups; 8.97% between Pygmy populations and Guineans; 64.00% between the BSCA groups and Guineans).

The most important difference was seen in the populations of the BSCA groups and their relationship with the Pygmy populations. In particular, the BSCA groups are less compact because the males of the Lese ethnic group have an overlap much higher than the one in their group (33.09%, +88.85%). The overlap in cross-sectional measurements (V11-V14) in women is also similar to that obtained in men and the Lese ethnic group follows the layout described in the longitudinal measurements (68.34%, Pygmy populations; 76.64%, the BSCA groups; 90.38%, Guineans; 42.89% between Pygmy populations and the BSCA groups; 44.75% between Pygmy populations and the BSCA groups; 59.65% between the BSCA groups and Guineans; 63.07% (+50.88%) between Pygmy populations and males of the Lese ethnic group). In the variables V2, V15-V17 and V20 the averages of the measurements in Pygmy populations are very similar to those observed in the BSCA groups and less than in the Guineans. In line with this similarity, the overlap between Pygmy populations and the BSCA groups (79.88%) is very high in comparison to the other groups (35.40% between Pygmy populations and Guineans; 42.44% between the BSCA groups and Guineans). As regards the nasal variables, the behaviour is similar to that seen in men (V19/V20: 1.00, Pygmy populations; 0.95, the BSCA groups; 0.79, Guineans).

The interpretation and relative position of the populations in the graph are similar to that described in men, although the rotation of the axis of the ellipse of the BSCA groups (G2) towards the Pygmy populations (G1) provides closer proximity between Lese and Pygmy populations of women.

Finally, there is also greater sexual dimorphism in the Pamue than amongst the Bubi (Figure 4).

### PCA analysis of all the combined series

The PCA analysis of the first two components of the 17 series, with the male and female series regarded as independent populations, explains 83.8% of the variation (Figures 10 and 11). The differences in body size place the Pygmy populations (G1.1 and G1.2) and other men (Guineans G3.1 and the BSCA groups G3.2) at opposite ends; the other women,

not from Pygmy populations, are in an intermediate position (Guineans G2.1 and the BSCA groups G2.2). The differences between men and women of each group are detected in the two principal components, where the gradients of magnitude are similar and go in the same direction. The results match the ones separately described for men and women and confirm the Pygmy populations influence on Lese women (12F in [Figures 8 and 9](#)). Gusinde (1948, p. 361) took photographs of this body similarity between the Lese and the Bambuti.

## Discussion

There is evident inter-group overlap between the Bioko/Equatorial Guinea series along with the major intra-group variability in both sexes, both in size and in body shape. There is also greater sexual dimorphism in the Pamue than amongst the Bubi ([Figure 4](#)), which is not attributable to an admixture with Biaka Pygmy women. Pamue women have significantly higher averages for stature, arms and legs than Bubi women. The most likely reason for this difference is the high values of arms and legs of Pamue men.

The body proportions of our series (in percentages) are the same as the other groups that were studied (see [Table 5](#)), including the African pygmies, contrary to the findings of Lefrou (1943, p. 365; Marquer 1972, p. 112 and 115). We do not think it is necessary for the purpose of our study to calculate the isometrics and allometry as processes that determine the size and shape of the biological species. Allometry should be understood in present day humans as products of growth and development that are the outcome of gene expression and regulation, nutrition, disease and cultural factors. All this taken together is what is reflected in the adult phenotype. Indeed, the seminal work by Shea and Bailey (1996) on this topic in the African Pygmy populations was essential in refuting the points of view held by Lefrou (1943, p. 365) and Marquer (1972, p. 112 and 115). During the growth of an organism, with isometry = 1, the ratio between two body variables can be  $b > 1$  (positive allometry) or  $b < 1$  (negative allometry). In the human species, both cases of allometry can occur, depending on the observed variables, but these never change their trend (or are positive or negative), because they have been fixed on the genetic program of our species; therefore it can be applied to human fossil remains (Bolter and Cameron 2020). Although the value of allometry will always vary due to the influence of the environment, it will never change its mathematical sign (either positive or negative). In our study, the body proportions of the five groups of Bioko and Equatorial Guinea were not statistically different from the BSCA Groups or the African Pygmy populations studied by Gusinde ([Table 5](#)). Each one of the 17 groups analysed may have had different allometric trajectories during their respective growth and development processes; but the body proportions in the adult do not significantly differ, which tends to confirm Shea and Bailey's conclusion (1996) that there is no difference in the allometric growth of African Pygmy populations distinct from other

human groups, except their rapid size decrease during the growth stage.

We used the Euclidean distance as the best possible approximation to the Mahalanobis distance in our case ([Figures 5–7](#)). This procedure replaces the magnitude in mm with the variation in sigma units (standard deviation) for each group, although it conserves the original correlations. In our analysis, the body differences between Pygmy populations and non-Pygmy populations are evident, in size and shape. In our study, the three groups are well separated by the first component of the PCA, the second separates the BSCA groups of the Bioko/Guinea.

As regards the phylogeny of the populations studied here; in other words, the history of the population and its biodynamics, most of the molecular markers of current human biological diversity have an African origin. Progressive desertification commenced in the Sahara region 10,000 years ago after the last ice age and has continued to the present (Kindong 1993, p. 160). Despite this, the African population increased and spread across the continent (Cavalli-Sforza et al. 1994, p. 161; Bostoen et al. 2015). Microsatellites are accurate molecular clocks, and Sun et al. (2009), after analysing data from 783 microsatellite loci in human populations and 292 loci in chimpanzee populations, confirmed that there was a significant gap between Africans and non-Africans. The San, Biaka Pygmy, and Mbuti Pygmy African populations have the deepest coalescent times of the populations in the Human Genome Diversity Project. Therefore, these populations are key factors in the reconstruction of prehistoric African human lineages, whose dates of difference have already been extensively stated in the Introduction. As Cavalli-Sforza et al. (1994, p. 194) pointed out for different reasons, Khoisan and African Pygmy populations are phylogenetic outliers with respect to the rest of the African lineages. The most recent study published (Bergström et al 2020) proposes the splits between the two central African rainforest hunter-gatherer groups, the Mbuti and the Biaka, at ~62 ka; between the Mbuti and the West African Yoruba at ~69 ka; between the Yoruba and the southern African San at ~126 ka; and between the San and both the Biaka and the Mbuti at ~110 ka. Non-Africans have separation midpoints from the Yoruba at ~76 ka, from the Biaka at ~96 ka, from the Mbuti at ~123 ka, and, representing the deepest split in the dataset, from the San at ~162 ka. In sum, the genetic markers of the African Pygmy populations in particular not only reveal positive selection against infectious diseases but also, according to other markers, reveal a separation time of no less than 70,000 years compared to other humans. The available genetic data may not have been based on totally isolated populations, such as the groups of the Ituri region. That is why we consider Schebesta's map to be especially instructive ([Figure 1](#)) along with the geographic division into three groups of African Pygmy populations: Eastern (mainly Bambuti from the Ituri and Batwa), Central (Bacwa and Babinga) and Western Pygmies (Bambutu from Cameroon and Gabon, respectively), that existed in the early part of the 20th century and was witnessed by a number of expeditions (Poutrin, 1911–1912;

Schebesta and Lebzelter 1933; Pales 1938; Vallois 1940; Gusinde 1956). The mtDNA is especially useful in this evolutionary scenario, but the markers of Chromosome Y, as well as the micro-satellites of the other nuclear genomes of the central and western Pygmy populations, may reveal the genetic recombination of their mixing with Bantu who reached the Congo basin over the centuries.

On the other hand, the comparison of the phenotypes in this study is relevant because natural and sexual selection operates on them, and therefore reflect their past, which of course is greatly influenced by gene recombination and expression, and by environmental influences, particularly during the periods of growth and development, before the adult phase.

The powerful statistical tools used here show us that although there are evident differences in body size between Pygmy populations and Guineans, by groups and sexes; the BSCA Groups occupy an intermediate position. They also show that genetic samples should be gathered and adequately analysed to better understand this past phase in the evolution of African populations. One important feature is that neither this study nor the one carried out by Gusinde (1948) found significant differences in body proportions of the African pygmies, or between sexes, or in the comparison with our Guinean series.

The first principal component of the PCA of the male series (Figure 8) with standardised variables shows the major body differences highlighted by the longitudinal dimensions of the body and, indirectly, in the variables of intercrestal width/breadth and average thoracic circumference, respectively, inasmuch as the taller bodies are also broader. The vertical axis, or second principal component, is influenced above all by the variables of bust height and the nose, as well as by the intercrestal width/breadth and maximum breadth of the head, respectively. Guinean groups have very narrow hips (intercrestal width/breadth), while Pygmy populations are notable for having a nose that is as wide as it is high, in the shape of an equilateral triangle (see Lefrou 1943; Gusinde 1948, p. 207, 209 and 351–357). The above results appear in the same way when using standardised variables and Euclidean variables in millimetres.

The relative position of the BSCA Groups and the differential overlaps with the other groups (depending on the variables) are an indicator of the biological distance amongst Pygmy populations and Guineans. The geographical proximity explains the relation of the BSCA Groups and Pygmy populations and the possible common similarity with the Sudanese explains the ancestral relationship of the BSCA Groups and Guineans.

The coordinates axis (PCA) of the female series (Figure 9) is the same as the male one. The main difference is that the largest axis of the ellipse of the BSCA Groups rotates, with reference to the male ones, towards the ellipse containing Pygmy populations, which may be a result of (amongst other factors) the gene flow caused by the exogamy of female pygmies, so often commented on by researchers and eye witnesses (Cottes 1911–1912; Dugast 1949; Vallois 1939, 1940, 1941, 1950), which in this case are the women of the

Lese ethnic group (Gusinde 1948; Terashima 1987, Vallois 1950; Alcobe and Panyella 1951; Cavalli-Sforza et al. 1994; Jarvis et al. 2012). Alternatively, the position of Lese women in the PCAs cluster (point 12F in the Figures 10 and 11) could be influenced by recent Efe migrants, in the sample studied by Gusinde in 1948. In sum, joining both sexes in PCA analysis of the 17 samples (Figure 11) of Bioko/Guinea, the BSCA Groups and Pygmy populations, increases heterogeneity, which can be seen in the reduced Pearson's correlation coefficient with regard to the sex-specific analyses. Even so, the results are consistent, and the above-mentioned features are repeated for each sex: predominance of longitudinal body dimensions in the first component; repetition in the second component of the significant weight of the intercrestal width/breadth, of the bust and nose heights, and of the head values (length and width/breadth) and of the bizygomatic breadth. These results were already described in the comments on the female series.

The cephalo-facial variables, studied in such great detail by anthropometry in the early 20th century, were of little value in identifying and classifying groups. The measurements of the head are less indicative than the longitudinal and cross-sectional ones of the trunk and limbs. This assertion does not invalidate the conclusions of Ramirez-Rozzi and Sardi (2010) regarding the crania and those of other Africans from European museums and collections. For example, measurements of the nose differ greatly in a living individual from those taken of his cranium. Both Schebesta (1940) and Gusinde (1948) include photographs where one can see noses that are as high as they are broad (see Lefrou G 1943; Gusinde M 1948 p. 207, 209 and 351–357). However, the studies by these authors only use the dimensions of the cranium, while this article brings together the dimensions of the head and face and integrates them with the rest of the body.

The cluster analysis and the results of the UPGMA dendrograms (100% of variation) showed a picture that perfectly matched the one obtained with the PCA mentioned previously.

## Conclusions

This study provides useful somatometric information about the human phenotype of the populations of the Sahel and Equatorial Guinea in relation to the phenotype of the Ituri Pygmies and other peoples in the central area of the Congo Basin. No differences were found when comparing the body proportions of these groups, which may indicate that such populations came from the same ancestral tree, regardless of when they separated geographically. This data appears to confirm the notion that the short stature among Pygmy populations is an outcome of adaptive processes in the intricate African rainforest, as proposed by Merimee et al. 1968, Zoccolillo et al. (2020) and other authors cited at the start of this article.

The anthropometry of the populations of Bioko Island and Equatorial Guinea on adults in 1948 has revealed the tremendous intragroup variation that exists in each sex. The sexual differences are expressed in stature, and in the width of

shoulders and hips. We detected no signs whatsoever that would enable us to relate the phenotypical variation found with the potential presence of women from Pygmy populations amongst the Pamue and Combe of Equatorial Guinea. The cephalo-facial variables are of little relevance in our study in comparison to the rest of the body.

The new techniques applied in our analysis provide sufficient statistical robustness to the results obtained in the comparisons of the populations of Bioko/Guinea with the Bantu-speaking peoples of Central Africa and the Aka and Efe eastern Pygmy populations.

Our results contribute to a better understanding of the human phenotype: predominance of longitudinal dimensions, and secondarily of transversal dimensions. There are obvious sex differences in size in the shoulder and pelvic girdles. The head appears in our results as of minor importance, so it should be studied separately either in metric or facial recognition studies.

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## Disclosure statement

The authors report no conflict of interest

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