

Published in final edited form as:

Hum Biol. 2012 February ; 84(1): 1–10. doi:10.3378/027.084.0105.

African Pygmies, what's behind a name?

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Keywords

African Pygmy; Genetic Diversity; Biological Anthropology; Cultural Anthropology; Pygmy stature; Linguistics; Evolution; Adaptation; Interdisciplinary Perspectives.

Numerous populations spread out across Central Africa have been named Pygmies by Western explorers, since the 19th century, in reference to the mythical Pygmy population from Homer (A people of short stature at war with migrating birds, *Iliad*, song 3, v. 1-6). For more than forty years, Pygmy populations have attracted the interest of biological anthropologists because they were seen as the lively example that the adaptation to the environment shapes the diversity of external physical or physiological characters (e.g. Froment 1993; Perry and Dominy 2009; Campbell and Tishkoff 2010).

Some biological anthropologists and geneticists wrongly perceived Central African Pygmies as a homogeneous group with similar cultural, morphological and biological features, and somewhat opposed to Non-Pygmy populations (often designated as “Bantu populations”, though they do not necessarily speak Bantu languages which Pygmy populations often speak). This view may be seen as the consequence of two misleading notions widespread in the Western culture. First, the prevalent historical use of the single exogenous term “Pygmy” to designate more than twenty human groups from the Congo Basin, *de facto* suggests that common historical, cultural, and even biological or morphological features are shared by Central African Pygmies. Second, Pygmy populations are often viewed as being exclusively forest hunter-gatherers, isolated from Non-Pygmy farmers, and living in the same way as ancestral human populations did before the Neolithic revolution.

Since the 1960's, such stereotypes have been repeatedly challenged by scientific research. For instance, cultural anthropologists observed that the various Pygmy populations do not share a common myth of origin. Most of them do not know each other and are unaware of a common designation as *Pygmies* from outsiders; in fact the various Aka, Baka, Bongo, Efé (...) Pygmy populations are not a federated group of populations (Bahuchet 1993; Hewlett 1996). Additionally, physical anthropologists have observed the wide diversity of average

height across African Pygmy populations and found no height discontinuity between Pygmies and Non-Pygmy—some neighbouring Non-Pygmy populations being also of short stature (Hiernaux 1974, Froment 1993). Finally, it has been highlighted that Pygmies are not exclusive hunter-gatherers, as they often practice fishing and agriculture (e.g. Bahuchet et al. 1989; Bahuchet 1992; Hewlett 1996) and, further challenging stereotypes, Pygmies are not isolated from neighbouring Non-Pygmy populations since these groups of populations have close socioeconomic relationships including intermarriages (e.g. Turnbull 1965; Kazadi 1981; Bahuchet and Guillaume 1982; Hewlett 1996; Joiris 2003).

The short stature of African Pygmies

The issues raised by the common view that Pygmies form a uniform group are best (but not only) exemplified by extensive research focusing on the short stature of these populations. Three “classical” hypotheses have been proposed to explain this phenotype: It could be an adaptation either to the hot and humid environment of the rainforest (Cavalli-Sforza 1986) or to the difficult mobility in a densely forested environment (Diamond 1991) or, finally, the outcome of the scarcity of food resources in the forest (Bailey et al. 1989). A fourth hypothesis has been recently proposed: The short stature of Pygmy populations could be an adaptation to the earlier onset of reproductive life in a context of high rates of mortality from parasitism and poor nutrition (Migliano et al. 2007).

While being relevant approaches to the understanding of Pygmy height, each one of these hypotheses fails explaining the variability of adult stature observed today within and among the various Central African Pygmy populations when considered separately. Nor can such theories account for the differential stature between specific Pygmy and neighbouring Non-Pygmy populations that live in comparable climatic, nutritional or parasitic environments (Froment 1993; Perry and Dominy 2009; Becker et al. 2010).

In fact, understanding the evolution of stature-differences across Central African populations requires a tremendous effort in gathering much more anthropometrical, physiological and demographic data than those currently available and previously used. More specifically, it is necessary to gather longitudinal data in the various populations designated as Pygmies instead of taking a single Pygmy group (e.g. the widely studied Aka from Central African Republic) as being representative of all Pygmies across Central Africa (Becker et al. 2010). With richer data taking into account cultural, environmental and morphological diversity of African Pygmies, anthropologists could better understand the respective roles of the climatic, environmental, and demographic forces that shaped the differential stature among and between the various Pygmy and Non-Pygmy populations from Central Africa.

Despite archaeological remains attesting the dense and continuous presence of *Homo sapiens* in the Congo Basin since at least 40,000 years (Cornelissen 2002), there is no evidence of an ancient *Homo sapiens* population of a particularly short stature having lived in Central Africa. Consequently, we do not know if Pygmy populations evolved towards shorter statures or if their Non-Pygmy neighbors evolved towards taller statures. To this end, knowing whether Central African Pygmy populations have an independent or a common origin is an essential starting point, which was somewhat overlooked by some biological

anthropologists. If Pygmy populations had independent origins, then their short stature could be the result of convergent evolution while, if they had a recent common origin, their short stature could have been inherited and the adaptation process (if any) would have occurred in a single ancestral population sometime in the past. If an accurate evolutionary framework and a more representative sampling methodology are to be developed concerning the evolution of Central African populations, it is appropriate for biological anthropologists and geneticists to consider the complexity and the ambiguities raised by the binary categorization of populations in Pygmies and Non-Pygmies in the multi-ethnic context of this region.

A glimpse into the evolutionary history of African Pygmies: A change of perspective

In the book “African Pygmies” (1986), Luigi Luca Cavalli-Sforza reviews the results of demographic, medical, genetic and anthropological researches initiated in 1966. According to this scholar, the Sua (or Mbuti) Pygmies from the Ituri forest would be directly descended from the ancestors of most—if not all—Pygmy groups, whereas the Aka from the Central African Republic would have undergone a high level of genetic admixture with Non-Pygmy neighbour populations. According to such results and while being unable to provide formal evidence, Cavalli-Sforza favoured the hypothesis of a common Pygmy origin with subsequent diversification, as opposed to the theory of Hiernaux (1974) of independent adaptations to the rainforest environment.

More than fifteen years after the publication of “African Pygmies”, the genetic admixture pattern initially found in the Aka Pygmies has been further analysed using sex-specific genetic markers (mitochondrial DNA and Y-chromosome polymorphisms) and signatures of sex-biased genetic admixture between Aka Pygmy groups and Non-Pygmies have been detected by Destro-Bisol et al. (2004b), in agreement with the ethnographical origins of sex-biased matrimonial regimes. The same research team further hypothesized a common origin of all Pygmy populations and suggested, on the basis of simulation approaches and on phylogenetic inferences, that a first separation between the ancestors of Pygmy and Non-Pygmy populations took place between 60,000 and 30,000 years ago and suggested a more recent divergence between the two Pygmy group of populations now living at the longitudinal extremes of Central Africa with a split occurring prior to 18,000 years ago (Destro-Bisol et al. 2004a; Batini et al. 2007). Such estimates were later confirmed by a phylogenetic approach using mitochondrial DNA sequences on a wider population set (Quintana-Murci et al. 2008). However, these studies could not formally test the common or independent origin of Central African Pygmies using a model based approach since they considered a very limited number of Pygmy population and/or only two non-recombining sex-specific loci. These limitations have since been overcome.

Indeed, starting with 2009, fundamental advances concerning the reconstruction of the history and diversity of Central African populations have been reached thanks to the high-resolution population sampling obtained by interdisciplinary teams of biological and cultural anthropologists. In this context, the population sampling strategy of Verdu et al. (2009) benefited from the numerous cultural criteria suggested by cultural anthropologists (e.g.

Bahuchet 1992; Hewlett 1996; Joiris 2003). Verdu et al. (2009) collected more than six hundred DNA samples from 9 Pygmy populations living in Cameroon and Gabon and from 12 Non-Pygmy neighboring populations with whom Pygmies maintain close socio-economic interactions. Their analysis enabled *i*) the quantification of the extent of autosomal neutral genetic diversity in Western Central African populations, *ii*) the investigation of the complex Pygmy/Non-Pygmy categorization from a genetic perspective and *iii*) the formal test of a common or independent origin of numerous Western Central African Pygmy populations through a model based approach.

Far from being a genetically homogeneous group of populations, the genetic diversity of Western Central Africans is mainly explained by considerable genetic distances between pairs of Pygmy populations, Non-Pygmy populations often being not significantly genetically different from each other (Fig. 1). This biological diversity echoed the large cultural diversity observed in the populations sampled and further challenged the common origin conveyed by the use of the blanket term *Pygmy*.

Interestingly, the linguistic diversity of Western Central African Pygmy and Non-Pygmy populations did not predict the genetic distances computed among pairs of populations and Non-Pygmy neighbors. While speaking closely related languages, they can be genetically very distant from each other (e.g. Baka Pygmies and Bangando Non-Pygmies, see figure 1). Differently, Non-Pygmy populations speaking languages belonging to different linguistic families have small, often not significant, genetic distances (see figure 1).

Furthermore, each Pygmy population had different levels of genetic admixture with its Non-Pygmy neighbors (Patin et al. 2009; Tishkoff et al. 2009; Verdu et al. 2009). These heterogeneous levels of asymmetrical gene flow from Non-Pygmies into Pygmies were found inversely related to the strength of socio-cultural barriers that impede intermarriages between each specific pair of neighboring communities (Verdu et al. 2009). These results illustrate how the diversity of genetic patterns across Pygmy populations are determined by specific socio-cultural factors, and show how the description of the biologic diversity of Central African Pygmies can be biased when only a few groups are analyzed.

Towards the quest of the genetic determination of the differential stature between Pygmies and Non-Pygmies, the work of Becker et al. (2011) is very promising. They have shown that Pygmy individuals that are more admixed with Non-Pygmy neighbors are also likely to be taller. By analyzing the patterns of genetic admixture across several Western Central African Pygmy populations, they demonstrated, though indirectly, that the differential stature phenotype observed between Pygmies and Non-Pygmies had a genetic basis.

Finally, using genome-wide autosomal microsatellites and Approximate Bayesian Computation (ABC) methods (Beaumont et al. 2002; Cornuet et al. 2008), Verdu et al. (2009) formally tested, for the first time, whether numerous Western Central African Pygmy populations shared a common or an independent origin, and estimated the divergence times between populations. Despite the wide genetic differentiation among Western Central African Pygmies, the most probable scenario appeared to be that of a very recent split of Western Central African Pygmies, about 3,000 years ago, from an ancestral Pygmy

population that diverged from Non-Pygmy lineages 50,000 to 90,000 years ago (Verdu et al. 2009). This latter estimate overlaps previous estimation based on simulation and phylogenetic approaches by Destro-Bisol (2004a; 2004b), Batini et al. (2007) and Quintana-Murci et al. (2008).

A similar model-based methodology was later extended to other Central African Pygmy groups, particularly in the East, using neutral autosomal sequences (Patin et al. 2009) and mitochondrial DNA (Batini et al. 2011). Results showed that Eastern and Western Central African Pygmy populations, today living several thousand kilometers apart, probably shared a common origin some 20,000 years ago, while the divergence between the ancestral Pygmy and Non-Pygmy populations occurred around 70,000 years ago. Both estimates show confidence intervals that are consistent with previous studies based on simulation, phylogenetic and model-based approaches (Destro-Bisol et al. 2004a,b, Batini et al. 2007, Quintana-Murci et al. 2008, Verdu et al. 2009).

The studies we mentioned so far addressed the diversity of Central African populations in the framework of the complex cultural categorization Pygmy/Non-Pygmy and shed light on the widely unknown evolutionary and adaptation history of Central African populations. We would like to stress here that this research was only made possible by a proficient collaboration between biologists, social anthropologists and linguists. Future multidisciplinary work will allow the careful reconstruction of the history of admixture between Pygmies and Non-Pygmies, as *we do not know* when and how the dynamic of intermarriages between Pygmies and Non-Pygmies has evolved through history. More specifically, we would like to assess whether genetic admixture patterns have changed over pre-colonial, colonial and post-colonial times, in order to understand how changes in the rates of gene flow may have influenced the biological and genetic adaptation processes of these populations.

Beyond Genetics

We have been asked to write this editorial summarizing on-going genetic research in Central Africa to supplement the article by Serge Bahuchet (Bahuchet 2011 - same issue) about the linguistic diversity of Pygmy populations and their Non-Pygmy neighbours. Throughout his paper, Serge Bahuchet outlines at least two important messages to biological anthropologists and human biologists, the importance of which goes beyond the specific field of studies on African Pygmies.

First, he notes that the questions asked by linguists are often complementary to those that are the focus of molecular anthropologists. Such questions highlight how important is the understanding of the social dimension in any anthropological inquiry. If biological anthropologists are interested in the identification of the genetic features distinguishing Pygmies from their neighbours, if they wish to reconstruct the population dynamics and the demographic processes accounting for the substantial genetic diversity between and within these two groups of populations, then the investigation of the cultural mechanisms accounting for the conservation of a significant cultural Pygmy specificity (as opposed to Non-Pygmies with whom they are socially and economically largely tied) has a topical

relevance. Bahuchet agrees that a better knowledge of the migratory flows of African Pygmies throughout Central Africa and since their early contacts with Non-Pygmies would certainly provide more reliable microevolutionary insights on the genetic side. This is why addressing the historical relationship between languages spoken by Pygmies and Non-Pygmies will provide hypothesis that may be test by a molecular approach.

Second, Bahuchet notes that even disciplines that are commonly perceived as distant from biological anthropology are worth exploring and merging with other lines of evidence. For instance, studying musical practices (e.g. Fürniss and Bahuchet 1995) across populations may provide important insights about past and present cultural contacts between populations. Such “alternative” approaches are essential for understanding the early contacts between Pygmies and Non-Pygmies in the absence, we stress it once more, of archaeological and demographic data for these populations.

Epilogue

By combining past and current knowledge regarding both evolutionary and cultural aspects, we have shown how the category “Pygmy” can be misleading when used to describe culturally, morphologically and biologically heterogeneous populations. However, when appropriately used, this same term can be successfully considered to address numerous questions of fundamental importance for the understanding of human evolution in Central Africa. Caution invoked here is not a secondary aspect: It is imperative that biological anthropologists do not omit to precisely define what they mean by *Pygmy*. As Serge Bahuchet convincingly explains, we should never forget that while “Pygmies” do not exist as a single homogeneous cultural group: Populations such as the Aka, Asua, Baka, Bongo, Efe, Kola, Koya, Sua, Twa etc. exist as communities of people having rich, complex and diverse cultures who are in contact with several neighbouring ethnic groups with equally rich, complex and diverse cultures. If such proviso does apply to all human populations, we note that “biological anthropologists” often tend to use misleading terminologies, as some past investigations of Central African Pygmy and Non-Pygmy populations have shown. Let us think about how many messages and inspirations these groups could give to us if we deconstructed more systematically the western prism by which we perceive them, and if we tried to embrace and correct more openly our lack of understanding of the complexity of the Central African pluriethnic context.

Acknowledgments

The authors would like to sincerely thank Dr. Franz Manni for his numerous advices and comments concerning this editorial. Paul Verdu wants to thank Evelyne Heyer and colleagues at the CNRS and the MNHN of Paris (UMR 7206 “Ecoanthropology and Ethnobiology”) for giving him the opportunity to work on Central African Pygmy populations between 2005 and 2008, a work which was supported by the ACI Prosodie. The current work is supported in part by the US National Institutes of Health grant RO1 GM081441.

Giovanni Destro Bisol is grateful to Gabriella Spedini for giving him the opportunity to study Pygmy populations from the Central African Republic and Cameroon. He was supported by grants from the University of Rome “La Sapienza”, the Ministero dell’Istruzione, dell’Università e della Ricerca and the Istituto Italiano di Antropologia.

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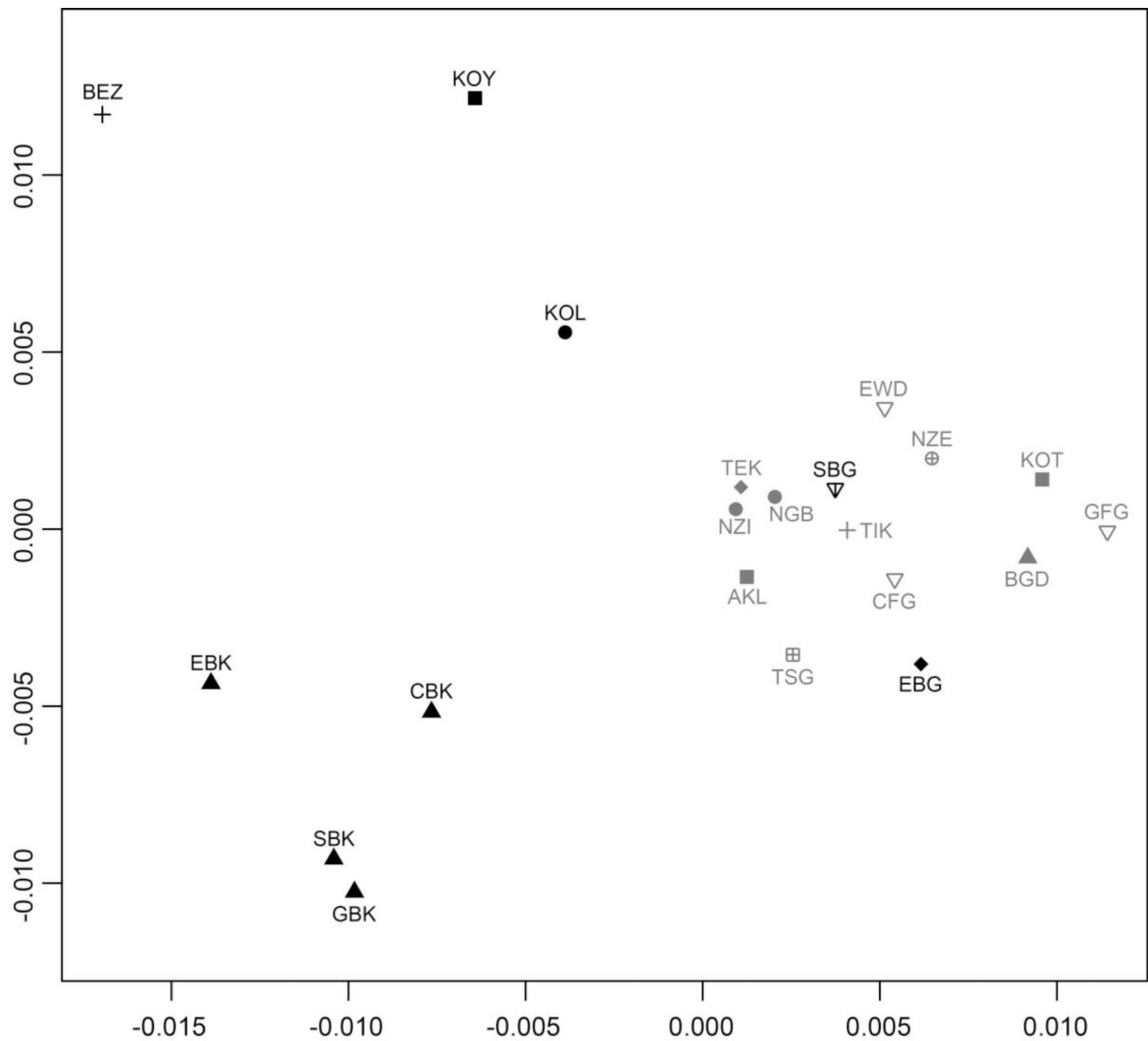


Figure 1. Multidimensional scaling representation of the pairwise genetic dissimilarities between Central African Pygmy and Non-Pygmy populations

Metric multidimensional scaling (MDS) plot based on pairwise population genetic dissimilarities (F_{ST} , Weir and Cockerham 1984) computed using 28 autosomal tetranucleotide microsatellite markers genotyped in 9 Pygmy and 12 Non-Pygmy neighboring populations (F_{ST} matrix previously published in Verdu et al. (2009)). Non-significant pairwise F_{ST} values based on permutation tests were set to 0 prior to computing the metric MDS (Verdu et al. 2009). To evaluate how accurately the two-dimensional MDS plot represented the pairwise population genetic dissimilarities, we computed the Spearman correlation between the Euclidian distances among pairs of populations on the MDS plot and the corresponding values of pairwise genetic F_{ST} . We obtained a Spearman's ρ equal to 0.84 (p -value $< 10^{-5}$). Furthermore, we found that the Euclidian distance calculated between any two populations on the MDS plot provided the corresponding F_{ST} value plus or minus 0.004 on average.

Pygmy populations are labeled in black as follows: BEZ = Bezan, central Cameroon; CBK = Baka, central-eastern Cameroon; EBG = Bongo, eastern Gabon; EBK = Baka, southeastern

Cameroon; GBK = Baka, northern Gabon; KOL = Kola, western Cameroon; KOY = Koya, northeastern Gabon; SBG = Bongo, southern Gabon; SBK = Baka, southern Cameroon. Non-Pygmy populations are labeled in grey as follows: AKL = Akele, eastern Gabon (Bongomo); BGD = Bangando, southeastern Cameroon; CFG = Fang, southern Cameroon; EWD = Ewondo, central Cameroon; GFG = Fang, northern Gabon; KOT = Kota, central Gabon; NGB = Ngumba, western Cameroon; NZE = Nzebi, southeastern Gabon; NZI = Nzime, central-eastern Cameroon; TEK = Teke, eastern Gabon; TIK = Tikar, central Cameroon; TSG = Tsogho, central Gabon.

The linguistic affiliation of samples is mainly based on (Greenberg 1966; Guthrie 1967) reads as follows: Adamawa-Ubanguiian family = (▲); Bantoid Non-Bantu family = (+); Bantu family: A.70 = (▽); A.80 = (●); B.20 = (■); B.30 = (⊞); B.30-B.50 = (▼); B.50 = (⊕); B.70 = (◆).