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<RRH>Craniodental Morphometrics to Study Bonobo Divergence

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Evidence for Divergence in Populations of Bonobos (*Pan paniscus*) in the Lomami-Lualaba and Kasai-Sankuru Regions Based on Preliminary Analysis of Craniodental Metric Variation

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Abstract Historical climatic events and riverine barriers influence the distribution of primates. The River Congo exerts the most significant influence on primate distribution in equatorial Africa, but the extent to which the inner basin of the Congo provided a refuge against Plio-Pleistocene climatic fluctuation is poorly understood. In this study we use cranial and dental morphometrics to examine how riverine barriers affect population patterns in bonobos (*Pan paniscus*). Bonobos and chimpanzees (*Pan troglodytes*) are sister species and share the distinction of being the closest evolutionary relatives of humans, yet comparatively little is known about bonobo morphological diversity. We selected 55 adult bonobo crania with well-preserved postcanine dentitions and divided them into regions separated by the rivers Lukenie, Kasai, Lomami, and Lualaba. We found good discrimination among these regions in cranial and dental metrics, but whereas the discriminant functions from cranial metrics were statistically significant, the discriminant functions from dental metrics were not. Mean classification accuracy was 89% for craniometrics, and ranged between 72% and 93% for dental metrics. On average 84–97% of phenetic variation was encountered within regions. Our results mirror molecular studies in suggesting that bonobos are characterized by a long-term stable demographic history allowing strong gene flow between regions and precluding drift and population differentiation. There are some indications that the bonobos from the Lomami-Lualaba and the Kasai-Sankuru regions are divergent, but modest sample sizes do not allow us to be conclusive. We would welcome the opportunity to work with field researchers to augment our sample sizes and reanalyze our data.

Keywords Chimpanzee · Congo River · Craniometrics · Odontometrics · Vicariance biogeography

Introduction

Throughout their distribution primates are found clustered with other plant and animal species in discrete nonoverlapping biozones. In Africa Grubb (1982) has identified five such zones of species richness as centers of species endemism. The centers correspond with the large forest blocks of West Africa, West Central Africa, East Central Africa, East Africa, and South Central Africa. The biozones mark the presence of past refugia, with self-sustained and stable environments, where the biotic community was able to withstand the vicissitudes of Pleistocene climate in Africa (Diamond and Hamilton 1980; Haffer 1977, 1982; Kingdon 1971; Mayr and O'Hara 1986). According to the Pleistocene refuge theory (Haffer 1982), climatic extremes following from the glacial and interglacial cycles of the northern latitudes led to habitat fragmentation, vicariance or redistribution within fragmented habitats, dispersal into refugia, and extinctions. Protracted isolation within refugia and allopatry would have led to character divergence and high degrees of endemism. With climatic amelioration there would be secondary contact, following migration and dispersal, leading to increased genetic and phenotypic variation. This could result in the formation of new species and subspecies (Avice 2000; Endler 1977; Hewitt 2004).

Climatic factors and Pleistocene refugia can account for the demographic history and phylogeography of several African primates, including *Cercopithecus* (Hamilton 1988), *Papio* (Zinner *et al.* 2009, 2013), *Mandrillus* (Telfer *et al.* 2003), and the Hominidae (Anthony *et al.* 2007; Clifford *et al.* 2004; Jensen-Seaman and Kidd 2001; Morin *et al.* 1994). However, not all aspects of primate phylogeography can be accounted for by large Pleistocene refugia. The East Central Center, for example, seems to have had several interconnected centers that followed the tributaries of the Congo River, rather than one large core area (Colyn *et al.* 1991). There are other minor centers linked to the major ones, forming

peripheral Pleistocene refugia (Grubb 1982). In addition, factors such as vagility of primates, interspecific competition, and vegetational zones can affect distribution patterns (Oates 1988).

An alternative paradigm is the riverine barrier hypothesis (Ayers and Clutton-Brock 1992), which states that rivers found at the edge of the distribution of most primates promote allopatric speciation by preventing gene flow. Rivers border the distribution of primates in South America (Ayers and Clutton-Brock 1992), Asia (Meijaard and Groves 2006), Madagascar (Goodman and Ganzhorn 2004), and Africa (Harcourt and Wood 2012), providing tacit support for the hypothesis. Quantitative analysis of the extent to which they function as barriers to gene flow suggests that larger rivers are more effective than smaller ones, and on the whole rivers pose a greater barrier to smaller-bodied than larger-bodied primates (Ayers and Clutton-Brock 1992; Harcourt and Wood 2012).

The River Congo spans a distance of 3000 km in central Africa and exhibits the greatest overall impact on the distribution of primates in Africa in terms of the number of taxa confined to one bank of the river and not the other (Grubb 1990). A wide range of habitats, including savannah, tropical, and montane forests are found to the north of the river. Major and minor Pleistocene refugia, as well as rivers, influence the biogeography of primates along this bank (Ackermann and Bishop 2009; Anthony *et al.* 2007; Clifford *et al.* 2004; Jensen Seaman and Kidd 2001; Morin *et al.* 1994; Pilbrow, 2006; Telfer *et al.* 2003; Zinner *et al.* 2009, 2013). The inner Congo basin along the south of the river is covered for the most part by dense tropical rain forest. Kingdon (1989) and Maley (1996) have suggested that the levées and sump-lands of the inner basin of the Congo afforded a single long-term fluvial refuge and allowed the biotic community within it to survive several arid periods without fragmentation, vicariance, and secondary contact. The existence of a single fluvial refuge is debated for the Congo River region (Colyn *et al.* 1991). As reviewed in Fjeldså and

Lovett (1997), the role of environmental factors in maintaining biogeographical patterns cannot be ruled out for this region. However, the potential role of refugia versus riverine barriers in shaping the biogeography of primates south the Congo River has not been thoroughly tested.

Bonobos (*Pan paniscus*) make an excellent model for testing the role of the inner Congo basin in vicariance biogeography because bonobos are confined to tropical rain forests south of the river covering a distance *ca.* 900 km west to east (Kano 1992; Fig. 1). The river constitutes the most important barrier to the dispersal of bonobos, with populations on either side designated as species. Chimpanzees (*Pan troglodytes*) occur along the north of the river covering a wide distribution of >5000 km (Wolfheim, 1983) and occupy varied habitats of gallery and montane forests, savannah, and tropical lowland rain forests. Bonobos share the distinction with chimpanzees of being the closest living relatives of humans and both are equal contenders as models for reconstructing the behavior and morphology of human ancestors. Yet, chimpanzees, not bonobos, serve as the default model for early hominin behavior and morphology (McGrew 2010). This is mostly because chimpanzee populations have been studied at more than 40 localities across Africa (Wrangham *et al.* 1994). At least five of these localities have been monitored for decades and provide excellent information on variation in life history patterns, behavior, ecology, genetics, and morphology (Boesch and Boesch 2000; Goodall 1986; Nishida *et al.* 1990; Sugiyama 1984; Wrangham *et al.* 1992, 1996).

The vicariance biogeography of chimpanzees is fairly well established. Large, well-provenienced cranial and dental data sets provide support for geographically defined subspecies of *Pan troglodytes* separated by river barriers: *P. t. verus*, *P. t. troglodytes*, and *P. t. schweinfurthii* (Johanson, 1974; Pilbrow 2003, 2006, 2007; Shea and Coolidge 1988; Shea *et al.* 1993). The divergent status of *Pan troglodytes verus* is recognized through

morphometric and mitochondrial DNA (mtDNA) analyses (Braga 1998; Morin *et al.* 1994; Pilbrow 2003, 2006, 2007; Uchida 1996), suggesting that the Dahomey Gap of West Africa provides a biogeographic barrier, although a recent review suggests that rivers bordering the Dahomey Gap rather than the aridity of the Gap itself were most likely to be effective barriers (Harcourt and Wood 2012). There is also evidence for the distinction of chimpanzees from the Bamenda highlands of Nigeria (Groves 2001; Pilbrow 2006; *contra* Gonder *et al.* 2011), substantiating a claim that the Sanaga River forms a biogeographic barrier (Gonder *et al.* 1997; Oates *et al.* 2009). Further, there is craniometric evidence for an additional subspecies, *Pan troglodytes marungensis*, from the southeastern range of the East African chimpanzees (Groves 2005; Groves *et al.* 1992), along with evidence from mtDNA that chimpanzees in this region lived in and out of refugia (Goldberg 1998).

In contrast, relatively little is known about bonobo patterns of diversity (Boesch 2002; Stanford 1998). The Democratic Republic of Congo (DRC) has the highest ranking for endemism and species richness in primates in Africa, and *Pan paniscus* is identified as a top priority species for studying phylogenetic diversity (McGoogan *et al.* 2007). Bonobos are also listed as endangered in the IUCN Red List of Threatened Species (2012). They inhabit fairly inaccessible tropical forests along the south of the Congo River, making field studies in the wild difficult, and wars in the Democratic Republic of Congo in the mid-1990s forced researchers to abandon their study sites. Until recently only two study sites, Lomako and Wamba in the north of the DRC, provided information about behavioral and habitat diversity of bonobos in the wild (Furuichi and Thompson 2008). These sites are situated in close geographical proximity to each other and researchers reported similar findings of moist and swampy rain forest habitats, large group sizes, and female cohesiveness. A relatively new study site at Lukuru south of the Lukenie River is demonstrating variability in bonobo habitat and behavior (Myers Thompson 2001, 2002). A preliminary molar morphometric study

suggests that populations east of the Lomami and south of the Lukenie River regions could be divergent from other bonobo populations (Pilbrow 2006), but there is need for further study. Early studies of genetic variability, albeit from captive individuals of unknown geographic origin or individuals from a single wild locality, highlighted low levels of genetic diversity in bonobos compared to chimpanzees (Fischer *et al.* 2011; Gerloff *et al.* 1999; Hashimoto *et al.* 1996; Reinartz *et al.* 2000; Yu *et al.* 2003). More recent population genetic studies using a greater sampling of bonobos from across their distribution in the wild show significant differences among populations (Eriksson *et al.* 2004, 2006; Kawamoto *et al.* 2013).

We used cranial and dental metrics to study patterns of morphological variation in bonobos. We test the contention that the inner Congo basin provided a Pleistocene refuge in the face of habitat fragmentation against the hypothesis that the tributaries of the Congo act as barriers to gene flow and affect patterns of diversity in bonobos. We address the following questions: 1) Can bonobo populations separated by rivers be differentiated statistically using cranial and dental metrics? 2) What is the nature of morphometric variation within and among bonobo populations? 3) Do dental and cranial patterns of population structure correlate with each other and with patterns of population structure?

Methods

Bonobos are found in the DRC roughly between 4°S–2°N and 16°E–26°E, bounded by the Congo River to the west and north, the Kasai-Sankuru Rivers to the south, and the Lualaba River to the east (Fig. 1). Samples for our study came from localities throughout the range of bonobo distribution and were studied in the Koninklijk Museum voor Midden-Afrika, Belgium; the Natural History Museum, U.K. [formerly the British Museum Natural History)]; and the Museum of Comparative Zoology, Harvard University (Table I). Provenience

information from museum records was verified against the United States Official Standard Names Gazetteer (United States Geological Survey) and Davis and Missone (1964).

<Fig. 1 near here>

<Table I near here>

Throughout most of their range bonobos occupy dense tropical and swampy rain forests, although the southern range has bonobos adapted to mosaic forests with savannah environments (Myers Thompson 2001, 2002). Several major tributaries of the Congo River flow through this region and provide potential barriers for bonobo dispersal, because bonobos, like chimpanzees, cannot swim (McGrew 2010). To study the role of rivers in structuring bonobo craniodental variation we divided our samples into three populations with rivers serving as boundaries: between the rivers Congo and Lukenie, Lukenie and Kasai, and Lomami and Lualaba. The populations are described here as, respectively, the Lukenie, Kasai, and Lomami populations. The area between the Congo and Lukenie covers a substantial area with several major rivers flowing through, but small sample sizes prevented us from dividing this sample into smaller populations; moreover, previous research suggests that populations separated by rivers in this region show little genetic differentiation (Eriksson *et al.* 2004, 2006; Kawamoto *et al.* 2013). The population south of the Lukenie River was retained as a separate population despite small sample sizes because there is some indication that bonobos here are behaviorally and ecologically distinct (Myers Thompson 2001, 2002). Samples from the region between the Lomami and Lualaba Rivers formed a distinct study population because this region is known to harbor several endemic taxa (Colyn 1988; Colyn *et al.* 1991; Grubb 1990) and bonobos here were found to be distinct in odontometric and genetic structure (Eriksson *et al.* 2004; Kawamoto *et al.* 2013; Pilbrow 2006). Only adult individuals with permanent dentitions were used in the study. Table I shows the sample sizes with sex breakdown and localities included in each population.

Cranial measurements were taken by Colin Groves and have been described in several previous publications (Groves 1970; Groves *et al.* 1992; Shea *et al.* 1993). Twelve measurements on the cranium and three measurements on the mandible were included in the analysis. Dental measurements were taken on the occlusal surface of molars and have also been described thoroughly in prior publications (Pilbrow 2006, 2007, 2010). Molars are abbreviated throughout the text and in tables as upper (U) for maxillary molars; lower (L) for mandibular molars; and 1, 2, 3 for the mesial to distal position of the molar in the jaw. Thus, e.g., the mesial most maxillary molar is UM1. Eighteen measurements on the lower molars and 14 on the upper molars were included. The measurements are outlined in Table II, along with abbreviations used in the Electronic Supplementary Material. Separate analyses were carried out on cranial and mandibular metrics and on each of the molar teeth so as to maximize sample sizes. Male and female dental and cranial measurements did not differ in means and variances (ANOVA, $P < 0.05$) and were combined in all analyses (Electronic Supplementary Material).

<Table II near here>

Univariate one-way analysis of variance (ANOVA) with Tukey's *post hoc* comparisons ($P < 0.05$) were used to identify statistically significant variables separating groups. Discriminant function (canonical variates) analysis was used to test for multivariate separation among designated populations. The theoretical and methodological considerations underlying this analytical approach have been described previously (Albrecht 1978; Groves 1970, Groves *et al.* 1992). Briefly, multiple weighted metric variables are used to develop linear functions that discriminate among groups by maximizing intergroup variation while minimizing intragroup variation. The percentage accuracy of group allocation with cross validation was used to assess the strength of group separation. We used the discriminant functions in scatterplots to assess group separation visually. We used group centroids to

calculate Mahalanobis generalized squared distances (D^2), which provide an assessment of the phenetic distances between groups. We used F -statistics to assess the significance of the discriminant functions. The loadings of the variables on the discriminant functions helped to identify the variables responsible for group separation.

We calculated relative variation within and among bonobo populations using the phenotypic equivalence of Wright's (1951, 1969) F_{ST} . Under theoretical assumptions of random breeding or panmixia this formula calculates a fixation index (F) of genetic variation among subdivisions (S) of a population relative to variation within the total population (T). The relative proportion of intergroup to intragroup variation provides an indication of genetic discontinuity or differentiation among groups. High panmixia will result in low levels of variation among subdivisions, thus low F_{ST} values, and *vice versa*. Typically, selectively neutral genetic markers are used to estimate F_{ST} values and levels of divergence. When used with morphological data (for examples, see Leigh *et al.* 2003; Relethford and Blangero 1990; Relethford *et al.* 1997), the influence of heredity and environmental factors in the phenotypic manifestation of traits is taken into account. Thus, when calculated for morphological traits the F_{ST} is weighted by the heritability of the traits. Heritability estimates for cranial and dental measurements range from 0.5 to 0.7 (Cheverud 1981; Hlusko *et al.* 2002; Hunter 1990; Townsend and Brown 1978); thus we repeated each analysis using heritability estimates of 0.5 and 0.7. Population size provides important weighting in F_{ST} calculations because traits will reach fixation far quicker in small compared to large populations. Population size estimates are unavailable for the Lomami River bonobos, and density estimates from specific field sites in the Kasai and Lukenie regions (as defined here) have high variances attributed to methodological differences in density estimation, habitat variation, differences in hunting pressures, and warfare (Hart *et al.* 2008; Hashimoto and Furuichi 2002; Inogwabini *et al.* 2008; Mohnke and Fruth 2008; Reinartz *et al.* 2006). In the absence of accurate information

on population sizes the working hypothesis in this paper is that population sizes did not differ across study sites. To calculate F_{ST} we used RMET 5.0, a software program written by John Relethford (Relethford and Blangero 1990). The program corrects for bias introduced by small and unequal sample sizes by subtracting $1/2n_i$ from the i th diagonal of the R matrix for all values of i . If the bias-corrected estimate ends up being negative the r_{ii} value is set equal to zero and the bias corrected estimate is obtained as the weighted sum of the bias-corrected diagonals of the R matrix (Relethford *et al.* 1997). The program also provides a D^2 matrix, which provides the phenetic distances between the populations, and was used to compare the results with those obtained from discriminant analysis.

Results

In univariate comparisons (one-way ANOVA), only five molar dimensions on the upper second and lower third molars differed significantly among populations (Table III; see Electronic Supplementary Material for nonsignificant results). There were no interpopulation differences in dimensions of the first and third upper molars, or first and second lower molars. Tukey's *post hoc* comparisons with $P < 0.05$ indicate that on the UM2 the mesial cusps are closely spaced in the Lukenie bonobos compared to the Lomami bonobos, the mean length of the UM2 postparacrista is lower in the Kasai compared to the Lomami and Lukenie bonobos, and the buccal cusps on the UM2 are positioned more mesially in the Lomami bonobos compared to the Kasai bonobos. The mean length of the posthypoconid cristid on the LM3 of the Kasai bonobos is greater than in the Lomami bonobos, and the lingual cusps on the LM3 of the Lukenie bonobos are placed slightly more mesially than the buccal cusps compared to the Lomami bonobos. Three of the 15 craniomandibular metrics differed significantly among bonobo groups in one-way ANOVA (Table III). These show that in mean craniometrics the Lomami bonobos have a wider palate compared with the Lukenie

bonobos; the Lomami and Lukenie bonobos have wider jaws than the Kasai bonobos, and the height of the ascending ramus in the Lukenie and Lomami bonobos is greater than in the Kasai bonobos.

<Table III near here>

In multivariate discriminant analyses mean classification accuracy ranged from 72% to 93%, but cross-validation classification accuracy was poor, ranging from 32% to 61% (Table IV). None of the discriminant functions were significant in the dental analyses, but both discriminant functions were significant in the craniometric analysis (Wilks' lambda $P < 0.05$). The groups differ significantly ($P = 0.01$) in craniometrics based on the F -statistic for pairwise differences. Mahalanobis or generalized squared distances (Table V) for craniometrics show that the Kasai population is further away from the other two. A scatterplot (Fig. 2) shows that Kasai bonobos are differentiated from the Lukenie and Lomami bonobos on discriminant functions 1 and 2, while there is high overlap between samples from Lukenie and Lomami. Sample sizes for Kasai are comparatively small, however, and as such likely to violate the assumption of multivariate normality. This could potentially lead to type I errors in falsifying the assumption of equal covariance matrices across samples, and provide a false impression of discriminatory accuracy. The variables with high scores on the discriminant function are the same as those identified through the one-way ANOVA (Table III): height of ascending ramus and breadth of palate have high correlations with function 1, and mandibular bicondylar breadth correlates with function 2. Bigonial breadth and nasion-prosthion length have high correlations with function 2, although these variables do not help to differentiate bonobo groups in univariate comparisons.

<Tables IV and V near here>

<Fig. 2 near here>

On the whole, F_{ST} values for bonobo populations are low (Table VI). For dental metrics F_{ST} values range from 0.05 to 0.13 at heritability of 0.5, and from 0.03 to 0.09 at heritability of 0.7. For craniometrics, F_{ST} estimates range from 0.14 for heritability of 0.5 to 0.09 for heritability of 0.7. These suggest that 84–97% of variation in dental and cranial metrics in bonobos is found within the three main regions of the study, leaving only 3–14% occurring between them. Pairwise phenetic distances obtained from the R matrix show that in craniometrics the Kasai population is the most distinct; it is most strongly differentiated from the Lomami population, followed by the Lukenie population (Table VII). The distance matrices for UM1, UM2, LM1, LM2, and LM3 repeat this pattern and are documented in supplemental materials. Pairwise distances for the UM3 also show the Kasai population to be most strongly differentiated from the Lomami population, but the next strongest differentiation is between the Lomami and Lukenie populations. A sampling bias correction was applied, but even so, small sample sizes for the Kasai group need to be taken into account when interpreting these results. The pattern of pairwise distances is the same as that obtained from discriminant analysis (Table V), where only the craniometric distances between regions were statistically significant.

<Tables VI and VII near here>

Discussion

Three populations in this study demarcated by the rivers Lukenie, Lomami, Kasai, and Lualaba differ significantly in craniometrics. Classification accuracy with cross validation is high in multivariate analyses. Cranial dimensions relating to the width of the palate and jaw, and height of the jaw differed significantly among populations. All three populations were classified with high levels of accuracy using dental dimensions; however, the discriminant functions were not statistically significant. Cross validation of the classification accuracy was

high for LM2, but not for other molars. These results indicate that there is some evidence of geographical differentiation among bonobo populations, but the pattern is not strongly evident across all data sets. A lack of clear population structure could be because there is continuous gene flow between bonobo populations.

Two previous groups have researched the partitioning of variation in wild bonobos at a similarly wide scale. Drawing mtDNA samples from localities in the west, north, northeast, east, center, and south of the distribution of bonobos, Eriksson *et al.* (2004, 2006) and Kawamoto *et al.* (2013) found significant differences in mtDNA haplotypes among these regions. On the whole, however, their molecular phylogeny was haphazard with regard to geographic origin of haplotype, which is similar to the poor discrimination encountered in some data sets in our study.

The lack of clear population structure evidenced in our study is suggestive of a stable long-term demographic history within the Pleistocene refugium of the inner Congo. Most (84–97%) of the variation in craniometrics and dental metrics is encountered within regions, with only 3–14% among regions, suggesting close genetic contact among populations. Studies using mtDNA report similarly that 50–70% of variance in bonobos is encountered within regions, in keeping with a mating pattern of female migration from the natal group (Eriksson *et al.* 2004; Kawamoto *et al.* 2013). There was significant correlation between mtDNA genetic distances and geographical distances when measured circumventing river barriers in the Eriksson *et al.* (2004) study, thus providing support for the riverine barrier hypothesis for vicariance biogeography. The study by Kawamoto *et al.* (2013) found greater support for the Pleistocene refuge hypothesis. There is nonetheless some indication in both studies that the Lomami River marks a significant biogeographic barrier to bonobo dispersal. This fits with this region being a center of species endemism harboring several endemic primate taxa (Colyn 1988; Grubb 1990; Hart *et al.* 2012). In univariate statistics in our study

the Lomami bonobos are distinguishable from the Lukenie bonobos by having widely spaced mesial cusps on the UM2, and from the Kasai bonobos by a mesiobuccal taper to the UM2 and shorter postthypoconid cristid on the LM3 (Table III). They also have wider upper and lower jaws, and mandibles with taller ascending rami. Their dental distinction was not substantiated in multivariate analyses in our study, but craniometric analysis showed that the Lomami bonobos are significantly divergent, especially from the bonobos of the Kasai region. Given that our cranial and dental results do not corroborate each other strongly this conclusion bears further testing.

The most divergent population in our study was the Kasai bonobos, from the region between the Lukenie and Kasai Rivers. This group was most divergent from the Lomami group in univariate comparisons (Table III), Mahalanobis distances (Table V), and with craniometrics in pairwise phenetic distances (Table VII). Our results are in contrast somewhat with mtDNA results, which showed little differentiation between the central and southern populations separated by the Lukenie River (Eriksson *et al.* 2004). They are congruent with the divergent status of the Lukuru bonobos south of the Lukenie River as recognized from behavioral studies (Myers Thompson 2001, 2002). The Lukuru bonobos live in drier forests and savannah grassland environments, they consume foods with higher protein and lower sugar levels, and their group sizes are similar to those of bonobos from Wamba and Lomako despite sparser distribution of food resources (Myers Thompson 2002, 2003). We signal caution in interpreting our results, however, because only five individuals from this region are represented in our study even though we included all known museum specimens. To test these patterns of diversity further we would like to augment our sample sizes, perhaps through collaboration with field workers.

Incongruent results for dental and cranial metrics in the same individuals in our study have implications for understanding the phylogenetic value of cranial and dental morphology.

In particular, it is expected that aspects of cranial and dental morphology that are subject to nonselective evolutionary forces such as mutation, migration, and random genetic drift will provide a population structure reflective of phylogenetic history, whereas morphology affected by natural selection will explain the adaptive history of populations. Dental and cranial metrics provide good overall congruence with neutral genetic data in deciphering population structure and history in great apes (Groves 2001; Groves *et al.* 1992; Pilbrow 2006, 2007, 2010), but it is known that some morphological features have greater value for reconstructing phylogenetic population structure (von Cramon-Taubadel and Smith 2012) . Future studies, with increased sample sizes, would help tease apart those morphological features that have greater phylogenetic value by correlating dental and cranial matrices with matrices derived from neutral genetic loci. Similarly, future studies could test the role of geography and topography in influencing population structure by correlating phenetic distances with geographic distances. Such analyses were not possible with our data set owing to unequal sample sizes. We would welcome the opportunity to increase our sample size.

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1 **Table I** *Pan paniscus* cranial and dental samples used in this study, localities from which
2 they were obtained and the sex breakdown

Region and localities included	Male	Female
Between Rivers Congo and Lukenie	10	14
Ndjembe, L. of River Congo opposite Lisala, Lingomo, R. of River Lopori, Bongandanga, South Befale, Yahuma, Ikela, Basankusu, Djolu, Lukolela, Yokamba, Coquilhatville, Wamba, Dongo, Bolobo, Botanankasa, Inongo		
Between Rivers Lukenie and Kasai-Sankuru	1	4
Kasai, Dongo Oshwe, Djeka, Lubefu, Katako-kombe		
Between Rivers Lomami and Lualaba	11	15
Stanleyville, Ponthierville, Kisangani, Banalia, Bagwase, Batiasera, Yatolema, Batiamoyowa, Biondo, Babusoko		
Total	22	33

3

4

1 **Table II** Cranial and dental measurements taken in this study, and abbreviations used

Cranial measurements	Abbreviation
Prosthion-opisthocranium length	PR
Glabella-opisthocranium length	GL
Bieuryonic breadth	EU
Biorbital breadth	BI
Orbital breadth	ORB
Interorbital breadth	IO
Nasion-prosthion length	NP
Nasion-basion length	NB
Basion-bregma length	BA
Prosthion-staphylion length	PS
Length outside lateral incisor	IN
Palate breadth outside second molar	MO
Bigonial breadth	BG
Bicondylar breadth	CO
Condylion gonion height	CG
Dental measurements	
Mesiodistal length	MD
Buccolingual length at mesial cusps	BLMES
Buccolingual length at distal cusps	BLDIS
Distance between mesial cusp tips	L_MCU
Distance between distal cusp tips	L_DCU
Length of prearcuate crest	LPREP

Length of postparacrista	LPOST
Length of premetacrista (id)	LPREM
Length of postmetacrista (id)	LPOS1
Length of pre-entoconidcristid	LPENT
Length of postentoconidcristid	LPOEN
Length preprotocrista (id)	LPRE1
Length of postprotocrista (id)	LPOPR
Length of prehypocrista (id)	LPREH
Length of posthypocrista (id)	LPOS2
Length of prehypoconulidcristid	LPRHY
Length of posthypoconulidcristid	LPOHY
Position of mesiobuccal cusp	AN_BC
Position of hypoconid	AN_HY
Position of cristid obliqua	AN_CR

1

 For illustrations of these measurements see Shea et al. (1993) and Pilbrow (2006).

2

Table III Results of ANOVA showing dental and cranial variables that differ between bonobo populations

Trait	<i>F</i> (df)	SIG	Tukey HSD	<i>P</i> value
UM2 Distance between mesial cusp tips	<i>F</i> (2,40) = 3.51	0.04	Lomami mean 7.74 mm (SD 0.55) > Lukenie mean 7.30 mm (SD 0.39)	0.034
UM2 Length of postparacrista	<i>F</i> (2,40) = 5.25	0.01	Lukenie mean 3.00 mm (SD 0.39) and Lomami mean 2.97 mm (SD 0.39) > Kasai mean 2.39 mm (SD 0.22)	0.011, 0.011
UM2 Angle of mesiobuccal cusp	<i>F</i> (2,40) = 4.38	0.02	Lomami mean 100.05° (SD 4.84°) > Kasai mean 94.11° (SD 2.36°)	0.018
LM3 Length of posthypoconidcristid	<i>F</i> (2, 30) = 4.97	0.01	Kasai mean 1.90 mm (SD 0.60) > Lomami mean 1.17 mm (SD 0.35)	0.010
LM3 Angle of mesiolingual cusp	<i>F</i> (2,30) = 3.81	0.03	Lukenie mean 95.18° (SD 3.91°) > Lomami mean 90.04° (SD 6.10°)	0.027
Breadth of palate outside 2nd molar alveoli	<i>F</i> (2,46) = 4.03	0.02	Lomami mean 53.45 mm (SD 2.31) > Lukenie mean 51.63 mm (SD 2.72)	0.046
Bicondylar breadth of jaw	<i>F</i> (2,46) = 3.89	0.03	Lukenie mean 95.50 mm (SD 4.75) and Lomami mean 95.46 mm (SD 4.94) > Kasai mean 87.60 mm (SD 12.90)	0.027, 0.031
Height of ascending ramus	<i>F</i> (2,46) = 4.98	0.01	Lukenie mean 57.64 mm (SD 3.23) and Lomami mean 58.19 mm (SD 3.28) > Kasai mean 52.00 mm (SD 8.52)	0.017, 0.009

Only significant results are reported. Abbreviations: U (upper) refers to maxillary molar, L (lower) refers to mandibular molar; 1, 2, 3 refers to mesial to distal position of molar in the jaw.

Table IV Discriminant analysis classification accuracy with Wilk’s lambda significance for discriminant functions (DF)

	Lukenie (%)	Lomami (%)	Kasai (%)	Mean accuracy (%)	Cross- validation (%)	Wilks’ lambda for DF 1, 2	<i>P</i> value
UM1	57 (14)	94 (18)	100 (5)	84	46	0.29, 0.81	0.20, 0.95
UM2	71 (14)	79 (24)	100 (5)	83	37	0.41, 0.71	0.36, 0.56
UM3	67 (15)	85 (13)	100 (4)	84	41	0.26, 0.71	0.36, 0.85
LM1	69 (13)	68 (19)	80 (5)	72	32	0.35, 0.70	0.87, 0.94
LM2	93 (15)	83 (23)	75 (4)	84	60	0.19, 0.51	0.05, 0.26
LM3	86 (14)	93 (14)	100 (5)	93	33	0.15, 0.42	0.29, 0.34
CRANI	83 (24)	85 (24)	100 (5)	89	61	0.22, 0.49	0.00, 0.02
OMETR							
ICS							

Sample sizes are in parentheses.

Table V Generalized squared distances between bonobo populations using craniometrics

Population	Lukenie	Lomami	Kasai
Lukenie		4.97 (0.001)	4.97 (0.001)
Lomami	2.495		5.42 (0.001)
Kasai	6.571	7.419	

Generalized squared distances are shown below the diagonal with F statistic (P value) above the diagonal.

Table VI F_{ST} results at heritability of 0.5 and 0.7, with standard errors in parentheses

	Heritability 0.5 (SE)	Heritability 0.7 (SE)
UM1	0.07 (0.02)	0.04 (0.02)
UM2	0.06 (0.02)	0.03 (0.02)
UM3	0.08 (0.02)	0.05 (0.02)
LM1	0.05 (0.02)	0.03 (0.02)
LM2	0.13 (0.02)	0.09 (0.02)
LM3	0.13 (0.02)	0.08 (0.02)
Craniometrics	0.14 (0.02)	0.09 (0.02)

Population sizes for each analysis are the same as for discriminant analysis.

1 **Table VII** Pairwise D^2 matrix from craniometrics and UM3 (heritability 0.5)

	Lukenie	Lomami	Kasai
UM3			
Lukenie		0.085	0.100
Lomami	0.341		0.164
Kasai	0.103	0.515	
Craniometrics			
Lukenie		0.061	0.126
Lomami	0.323		0.137
Kasai	0.481	0.566	

2 Pairwise distances are shown below the diagonal, associated standard errors above the
3 diagonal.

4

Fig. 1 Map of the Democratic Republic of Congo with shaded region showing the distribution of bonobos. Rivers separating regional samples are labeled. Dots show regions where bonobo samples were collected.

- 1 **Fig. 2** Scatterplot showing spread of bonobo populations on discriminant functions 1 and 2
- 2 and percentage (%) of variance explained by the functions in craniometric analysis.

3

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