Variation in the nasal cavity of baboon hybrids with implications for late Pleistocene hominins

Kaleigh Anne Eichel^{1,*} and Rebecca Rogers Ackermann²

¹ Department of Anthropology, University of Waterloo, 200 University Ave W, Waterloo, Ontario N2L 3G1, Canada

² Department of Archaeology, University of Cape Town, Rondebosch 7701, South Africa

*Corresponding author:

E-mail address: keichel@uwaterloo.ca (K.A. Eichel)

Keywords: Hybridization, *Papio cynocephalus*, *Papio Anubis*, Neanderthals, Modern humans

Abstract

Hybridization is increasingly proving to be an important force shaping human evolution. Comparisons of both ancient and modern genomes have provided support for a complex evolutionary scenario over the past million years, with evidence for multiple incidents of gene exchange. However, to date, genetic evidence is still limited in its ability to pinpoint the precise time and place of ancient admixture. For that we must rely on evidence of admixture from the skeleton. The research presented here builds on previous work on the crania of baboon hybrids, focusing on the nasal cavity of olive baboons, yellow baboons, and first generation (F_1) hybrids. The nasal cavity is a particularly important anatomical region for study, given the clear differentiation of this feature in Neanderthals relative to their contemporaries, and therefore it is a feature that will likely differ in a distinctive manner in hybrids of these taxa. Metric data consist of 45 linear, area, and volume measurements taken from CT scans of known-pedigree baboon crania. Results indicate that there is clear evidence for differences among the nasal cavities of the parental taxa and their F_1 hybrids, including a greater degree of sexual dimorphism in the hybrids. There is also some evidence for transgressive phenotypes in individual F_1 animals. The greatest amount of shape variation occurs in the anterior bony cavity, the choana, and the mid-nasopharynx. Extrapolating our results to the fossil record, we would expect F_1 hybrid fossils to have larger nasal cavities, on average, than either parental taxon, with overall nasal cavity shape showing the most profound changes in regions that are distinct between the parental taxa (e.g., anterior nasal cavity). We also expect size and shape differences to be more pronounced in male F_1 hybrids than in females. Because of pronounced anterior nasal cavity differences between Neanderthals and their contemporaries, we suggest that this model might be effective for examining the fossil record of late Pleistocene contact.

Introduction

Genetic studies estimate that the Neanderthal lineage and the *Homo sapiens* lineage separated from each other between 270,000 and 690,000 years ago (Krings et al., 1997; Green et al., 2008, 2010; Endicott et al., 2010), enough time for these lineages to develop distinct morphologies through adaptation and genetic drift. Fossil, archaeological, and genetic evidence suggests that they may have come back into contact with each other in multiple geographic regions, with recent genetic studies indicating that during these periods of contact, admixture occurred between these taxa (Green et al., 2010; Prüfer et al., 2014; Hu et al., 2014; Fu et al., 2014, 2015). These periods of contact and potential admixture are estimated to have occurred conservatively between 37,000–86,000 years ago, resulting in Europeans with Neanderthal ancestry (more likely 47–65kya; Sankararaman et al., 2012), and between 48,000–80,000 years ago in the Near East (Cartmill and Smith, 2009). In Siberia, the level of Neanderthal admixture in a 45,000-year-old modern human suggested a probable mating period of between 50,000 and 60,000 years (Fu et al., 2014), however, admixture occurred as recently as ~40,000 years ago in Romania (Fu et al., 2015). Taken together, these studies suggest that gene flow between these taxa likely occurred multiple times across time and space, although the details of where, when, and how often this occurred are not well understood. Prior to this genetic evidence, the suggestion that Neanderthals interbred with *H. sapiens* during the movement of the latter into Eurasia had been proposed based on skeletal data alone (see Wolpoff et al., 2004; Smith et al., 2005; Cartmill and Smith, 2009), though there was considerable debate around this hypothesis (Stringer and Andrews, 1988; Stringer, 2008; Tattersall and Schwartz, 2008).

Several authors have proposed that specific skeletal specimens may be Neanderthal x *Homo sapiens* hybrids (e.g., Bräuer, 1981: Hahnöfersand; Duarte et al., 1999: Lagar Velho 1; Wolpoff et al., 2001: Mladeč [5, 6]; Rougier et al., 2007: Peștera cu Oase 2; Soficaru et al., 2007: Cioclovina 1; Ackermann, 2010: Skhul [IV, V], Qafzeh [6, 8, 9, 11]; Condemi et al., 2013: Mezzena). For example, Skhul IV and Skhul V, commonly considered modern *Homo sapiens* among current scholars, display features indicating underlying developmental instability that may indicate admixture (Ackermann, 2010). Marked dental crowding (Qafzeh 6, 8, 9), tooth rotation (Qafzeh 11), and reduced (Amud 1) or enlarged (Peștera cu Oase 2) dentition may also indicate hybridization-induced developmental instability (Ackermann, 2010). Duarte et al. (1999) argued that Lagar Velho 1, an Upper Paleolithic juvenile, was descended from a hybridized population, citing the juxtaposition of Neanderthal and *H. sapiens* traits. Similarly, Soficaru et al. (2007) suggested that Cioclovina 1 is a hybrid due to a mosaic pattern of *H. sapiens* neurocranial features with Neanderthal superior nuchal morphology. However, none of these specimens have been widely accepted as hybrids, and indeed such interpretations have been repeatedly disputed (e.g., Tattersall and Schwartz, 1999; Harvati

et al., 2007; Stringer, 2008) or dismissed as inconclusive (Klein, 2003). However, recent analysis indicates that the ~40,000-year-old modern human Peștera cu Oase 1, an individual that along with Peștera cu Oase 2 shows some Neanderthal traits (Rougier et al., 2007; Trinkaus, 2013), is a hybrid, with admixture having occurred a mere four to six generations prior (Fu et al., 2015).

One impediment to drawing firm conclusions about whether fossil individuals are, or are not, hybrids is that our current understanding of how hybridization manifests in the skeleton is still limited (see discussion in Ackermann, 2010). Most conceptions of hybrid morphology (see e.g., Duarte et al., 1999; Tattersall and Schwartz, 1999; Wolpoff et al., 2001; Harvati et al., 2007; Soficaru et al., 2007) are based on a “mosaic” of skeletal features, with hybrids having some features of one parental taxon and some of the other. However, studies of hybridization in primates have shown that hybrids can have a range of phenotypes, some hybrids being “intermediate” in morphology, but others having features observed along a gradient, such as stocky to gracile build (Alberts and Altmann, 2001; Arnold and Meyer, 2006; Harvati et al., 2007). Still other researchers propose that hybrids would most frequently have features more of one or the other parental species, thus making hybridization invisible (cryptic hybrids), concealed in the morphological diversity of the parental species (Jiggins and Mallet, 2000). Although a wide range of skeletal variation may be expected in a multigenerational recombinant hybrid zone, it is less clear where individual hybrids of given pedigree (e.g., F_1 , B_1 , etc.) lie on this spectrum. Without pedigree or genetic evidence, we cannot determine conclusively if a particular suite of phenotypic traits consistently indicate membership to one taxon or hybrid group, a problem encountered when examining Neanderthal and their contemporary *H. sapiens* skeletons. Nor is it clear whether it might be possible to detect hybridization within more specific regions of the phenotype (e.g., nasal region, orbits), or whether it is necessary to identify hybrids based on a more widespread evaluation of phenotypes.

Gene flow can have different effects on regions of the genome, depending on the degree of differentiation of the hybridizing lineages for regions of interest (Key, 1968; Harrison, 1986; Wu, 2001). Where two taxa are very similar genetically, as is the case with Neanderthals and their contemporaries, but have a subset of genes that differ substantially, our expectation is that hybridization will affect the regions of the genome that differ most profoundly while having a more limited effect on the rest of the genome. When considering the phenotype, and assuming that the traits of interest have genetic underpinnings where traits differ substantially, hybridization might be expected to have a greater effect on those traits that differ between parental groups as opposed to those traits that are shared. Although this remains to be demonstrated, this suggests that the effects of hybridization may be more localized, and

that we should look closely at regions of the skeleton where there are known, substantial differences between the parent taxa, in order to further understand the nature of these effects.

The nasal region may be one such area of interest for understanding the localized effects hybridization. The Neanderthal nasal area is remarkably different from the nasal area of their Pleistocene contemporaries, as well as extant humans, making this region one that has received considerable attention in studies of recent human evolution. It has long been recognized that the Neanderthal nasal aperture is wider or has a larger area compared to extant and/or Pleistocene *H. sapiens* (Sollas, 1908; Dean et al., 1998; Franciscus, 1999; Márquez et al., 2014), suggesting that the nasal cavities of Neanderthals and *H. sapiens* are also different. Although the nasal cavity is only occasionally preserved in fossil hominins, the unique Neanderthal morphology has been analyzed in a number of Neanderthals with complete or nearly complete nasal cavities: La Ferrassie 1, La Chapelle-aux-Saints, Forbes' Quarry Neanderthal FQ1, Shanidar 1, Saccopastore 1, Engis 2, Pech de l'Azé, Roc de Marsal, St. Césaire, Sima de los Huesos (see Schwartz and Tattersall, 1996; Franciscus, 1999; Friess et al., 2002; Bruner and Manzi, 2008; Schwartz et al., 2008; Arsuaga et al., 2014; Márquez et al., 2014). In particular, the Neanderthal nasal cavity features a bilevel internal nasal floor (Franciscus, 2003; Wu et al., 2012), triangular fossa intranasalis (Franciscus, 1999, 2003), vertically oriented conchal crest with medial projection (Schwartz and Tattersall, 1996; Schwartz et al., 2008; Márquez et al., 2014), and prenasal fossa with secondary internal crest (Márquez et al., 2014), though many of these features may not be as unique as previously believed (Franciscus, 1999; Bruner and Manzi, 2008; Wu et al., 2012).

Here, we analyze the nasal cavity of baboon skeletal remains (*Papio anubis* [olive baboon], *P. cynocephalus* [yellow baboon], and their first generation [F₁] hybrids) as an analogue for understanding the effects of hybridization on this anatomical region in hybridizing hominins. Our proximate goal is to understand the nature of size and shape alterations in the nasal cavity of F₁ hybrids; our ultimate goal is to increase our ability to detect phenotypic signatures of hybridization in the fossil record (discussed in Ackermann et al., 2010). Because shape alterations in the nasal cavity can have a dramatic effect on fitness, understanding these alterations could also provide some insight into the fitness of hybrids.

Previous work on this baboon collection focused on metric and nonmetric variation of the skulls of these hybrids relative to their parental taxa (Ackermann et al., 2006, 2014). Ackermann et al. (2006, 2014) found that hybrids are more variable than their parental taxa and display transgressive phenotypes including the presence of novel dental and sutural variants. Of particular interest to this study, the snout of male hybrids showed some indication of increased size and “boxiness” (Ackermann et al 2006), though it was not characterized or quantified

beyond this observation. Therefore, we expect comparable metric and nonmetric variation in the nasal cavity of the F₁ hybrids studied here. However, the morphology of internal structures in hybrids may have a different response to hybridization than the external skeletal morphology (Bastir and Rosas, 2013; Ito et al., 2015). In particular, this response may be lessened due to stabilizing selective pressures acting on the posterior nasal cavity to maintain the critical functionality of vision, respiration, and basal cranium structure.

Materials and methods

Our sample derives from a collection of known-pedigree baboon skulls; this sample has been described elsewhere (Ackermann et al., 2006, 2014). We focus on the hybrid morphology of the nasal cavity. The nasal cavity consists of two areas in a dry specimen: the bony cavity and the nasopharynx (Fig. 1). The bony cavity is defined as the anterior portion below the anterosuperior margin of the nasals to the posterior margin of the hard palate, or the posterior opening called the choana. Posterior to the choana is the nasopharynx (Jones, 2001; Mlynski et al., 2001; Noback et al., 2011). In this study, we examined the nasal cavities of olive baboons ($n = 79$), yellow baboons ($n = 5$), and first generation hybrids (F₁; $n = 54$). This represents a subset of the total available dataset in the collection.

Metric data are represented by 45 measurements of the nasal cavity, and include measures of total volume and total length, as well as area and linear distances taken at five slices along the length of the nasal cavity (Table 1). These data were collected from computed tomography (CT) scans. The five coronal slices were chosen at comparable locations that can be identified across primates (Fig. 1d). The first slice was taken at the rhinion, referred to as the anterior bony cavity. The second slice was taken halfway between the rhinion and the choana, referred to as the mid-bony cavity. The third slice was taken at the choana. The fourth slice was taken halfway between the choana and the posterior nasopharynx, referred to as the mid-nasopharynx. The fifth slice is defined as the location at which the orbital canals open to the nasopharynx. The first three slices define the bony cavity, while the last three slices define the nasopharynx, providing morphometric data throughout the whole nasal cavity.

Before proceeding with our analyses, we first tested for differences in sexual dimorphism in parental and hybrid groups. The trait mean values and standard deviations for the olive, yellow, and F₁ baboons, separated by sex, are given in Table 2. A Wilk's Λ multivariate analysis of variance (MANOVA) including all traits indicated statistically significant morphological differences between the sexes ($\alpha = 0.05$, d.f. = 44, $\chi^2 = 0.237$, $p < 0.005$). Univariate student t -tests were used to assess sexual dimorphism within taxa, at the Bonferroni corrected α -value of $\alpha = 0.0011$, indicating that 20 (44%) of the measurements are significantly larger in male versus female olive baboons, and 32 (71%) are significantly larger in F₁ hybrid males versus females. Although not significance tested,

40 (89%) of the traits are also larger in the (single) male versus female yellow baboons (i.e., the single male value lies outside of and above the 95% confidence interval for the female yellow baboons).

Because sexual dimorphism was found to be significant, metric analyses were performed in two ways. First, all traits were corrected to the female mean prior to metric analyses (adjusted male value = original male value + [female mean – male mean]) in order to reduce the potentially confounding effect of sexual dimorphism (see Cheverud et al., 1993; Kohn et al., 2001; Ackermann et al., 2006). Multivariate and univariate tests were then used to examine differences between the hybrids and parental taxa. Our quantitative genetic expectation for metric traits of hybrids, assuming no dominance, is that they should be intermediate to the parental values (Falconer and Mackay, 1996; Lynch and Walsh, 1998). We therefore focus on determining which hybrid traits deviate from this expectation by exhibiting heterosis—or hybrid vigor—here identified as hybrid trait means that exceed both parent mean values. Hybrid vigor primarily affects body size (and size-related shape), and therefore, data are analyzed in raw, unscaled form. Shape is analyzed by comparing how traits were altered in the hybrids relative to each other, thereby affecting the shape of the region. Because of the small sample size for yellow baboons, comparisons to the pooled yellow baboons were supplemented by a bootstrap test of significance. For each measurement and comparison, the yellow baboon mean was assessed against the distribution of sample means ($n = 5$; 1000 repeats), calculated for both the olive baboon and hybrid datasets. Values were considered significantly different when they fall outside of 95% of the distribution values.

Second, males and females are considered separately, without size adjustment, in order to examine whether hybridization affects the sexes differently. For the females, multivariate and univariate tests were then used to examine differences between the two parental taxa and the F_1 hybrids. For the males, these tests are limited to the olive baboons and F_1 hybrids, due to statistical limitations of comparing groups to the single male yellow baboon. In addition, we also used Welch's t -tests to examine differences in sexual dimorphism between olive baboons and F_1 hybrids, in order to determine whether sexual dimorphism is expressed more strongly in parental taxa or F_1 hybrids.

To further characterize size and shape differences among these groups, principal components analyses (PCA) were performed on the 31 linear distances described in Table 1. Canonical discriminant analyses (CDA) were also performed for these same 31 traits in order to maximize the differences between groups. These analyses were performed on both sexual dimorphism corrected and uncorrected data.

Given the high frequency of nonmetric traits previously identified in baboon hybrids (Ackermann et al., 2006, 2014), we also evaluated nonmetric traits here. During the segmentation process, as well as on the dry skulls

where possible, nonmetric variants were visually identified in the nasal cavity. Identified traits include: tooth roots that enter the nasal cavity, ectopic teeth in the nasal cavity, deviated septum, divided greater palatine canals, relative size of the lateral recess, the attachment of the inferior nasal conchae at the choana, and the presence of the alae of the vomer in the mid-nasopharynx. Each specimen was then re-examined for this suite of traits and scored for the presence, absence, and, where appropriate, expression of these traits (see descriptions of these traits and scores in Table 3). A Fisher's Exact test was used to test whether hybrids are significantly different from parental taxa in frequency or expression of the seven nonmetric traits.

Results

Quantitative differences among parental taxa and their hybrids, pooled for sex, are significant (Wilk's Λ MANOVA; $\alpha = 0.05$, $df = 88$; $\chi^2 = 1.509$), indicating measurable differences in size and shape of the nasal cavity among groups. Univariate ANOVA tests found significant differences among the three groups at $\alpha = 0.05$ for 21 (47%) of the traits, and 5 (11%) of the traits are significant at the Bonferroni corrected value of $\alpha = 0.0011$ (Table 2). In the majority of these cases, the F_1 hybrid mean values exceed those of both parental taxa. The traits were then analyzed using the Dunnett's C post-hoc test, which has a lower significance threshold, identifying 3 (7%) traits that are significantly different between the groups (Table 2). F_1 hybrids are significantly wider than both parental taxa at the nasal crest and in the inferior meatus of the anterior bony cavity, indicating size heterosis. F_1 hybrids also have a greater height to width ratio at the mid-nasopharynx relative to olive baboons (but were smaller than yellow baboons). For the bootstrapped tests of significance performed on the pooled samples, the yellow baboon mean falls outside of the 95% confidence interval based on the olive baboons for all 45 traits. Similarly, the yellow baboon mean falls outside of the 95% confidence interval based on the hybrid baboons for 43 traits, and within the hybrid baboon 95% confidence interval for the height at nasal crest in the mid-bony cavity and height of right inferior concha in the mid-bony cavity. These results from the bootstrapped tests support the results above indicating distinctiveness of the three taxa, despite small sample sizes for the yellow baboons.

When considering the sexes separately, univariate analyses of variance (ANOVA) and Dunnett's C post-hoc tests indicate significant ($p < 0.05$) differences between 19 (42%) of the traits for the three groups of females, and independent samples student t -tests indicate significant differences between 16 (36%) of the traits for male olive baboons and male hybrid baboons (Table 2). The male yellow baboon value falls outside the confidence interval for 12 (27%) of the traits for male olive baboons and in 1 (2%) of the traits for male hybrid baboons (Table 2).

The lower percentage of significant differences between the F_1 hybrids and parental taxa when the sexes are pooled can be explained by the opposing ways in which each sex responds to hybridization. Female hybrids showed narrower inferior measurements (1Wim, 3Wnc, 4Wim, 5Wim) compared to the females in the parental taxa, while male hybrids showed wider inferior measurements (1Wnc, 1Wim, 1Wic, 1Wmm, 5Wlr) compared to the males in the parental taxa. The opposite responses cancel out when the sexes are pooled in univariate testing. Figure 2 visually summarizes these statistics by highlighting the significant measurements, color-coded by the group with the largest measurement for that variable.

Welch's t -test determined that olive baboons and F_1 hybrid baboons differed in the degree of sexual dimorphism for 17 (38%) traits, with 15 of these indicating greater sexual dimorphism in hybrids (Vol, 1A, 3A, BCL, NCL, 1Hnc, 1Hicr, 1Hicl, 1Wic, 1Wm, 3Hnc, 3Wic, 4Wim, 4Wav, 5Wlr), one displaying greater dimorphism in olive baboons (2R), and one indicating different patterns of dimorphism in the two groups (4Himav; olive baboon males are larger than olive baboon females, female hybrids are larger than hybrid males).

Principal component plots for comparisons between all three taxa are shown in Figure 3. For the uncorrected data (Fig. 3a, b), PC1-PC3 cumulatively explain 67.5% of the variation in the data. The primary pattern observed in these plots is the separation of males and females on PC1, indicating that this component reflects sexual dimorphism as described in the metric analyses above. Separation along PC1 is driven by the width of the nasal cavity at the anterior bony cavity, width of the middle meatus at the choana, and width at the alae of the vomer in the mid-nasopharynx (all three become larger toward the left). Separation along PC2 is driven by the width at the alae of the vomer in the mid-nasopharynx (becoming larger toward the bottom of the graph), and the height of the artificial inferior margin to the alae of the vomer in the mid-nasopharynx (becoming larger toward the top of the graph). The separation along PC3 is driven by the width at the nasal crest at the anterior bony cavity (becoming larger toward the top of the graph). No other clear differentiation occurs among groups. For the corrected data (Fig. 3c, d), PC1-PC3 cumulatively explain 46.9% of the variation in the data. The same four variables drive the separation in the corrected PC1-PC3. The traits driving the separation of specimens along the principle components are consistent with the traits found to be significantly different between groups. Although no clear patterns of group separation are detected in these plots, the individuals that clearly fall outside of the tight cluster are all hybrids, providing some evidence for transgressive segregation.

Canonical discriminant plots for comparisons between all three taxa are shown in Figure 4. Only the first two discriminant functions are presented here, as combined they explain >90% of the variation in the data. In the

uncorrected data (Fig. 4a), once again males and females are separated along the first discriminant function. Unlike the PCA analyses, taxon-specific differences appear to be present along the second discriminant function, with the F₁ hybrids of both sexes occupying a position between the parental taxa. This is further emphasized in the corrected data (Fig. 4b), which shows distinct but somewhat overlapping ranges for all three taxa. The first discriminant function is strongly influenced by a combination of the width of the middle meatus at the anterior bony cavity (loading: -3.26), the width of the inferior margin in the mid-nasopharynx (-2.99), the height of the right inferior nasal conchae at the anterior bony cavity (2.25), the width of the lateral recess at the posterior nasopharynx (-2.03), the height from the nasal crest at the mid-bony cavity (1.90), and the height of the left inferior nasal concha at the mid-bony cavity (-1.78). The second discriminant function is influenced by the height of the right inferior nasal concha at the choana (-3.59) and the height of the right inferior nasal concha at the mid-bony cavity (1.87). Interestingly, when uncorrected data for males and females are plotted separately, male parental taxa and hybrids are more clearly differentiated from each other than female parental taxa and hybrids (Fig. 4c, d), suggesting that the effects of hybridization are more pronounced in males (see also Ackermann et al., 2006, 2014).

Results of the nonmetric tests are given in Table 4. Results indicate that hybrids and purebreds do not differ significantly in the frequency or expression of any nonmetric traits. This pattern also holds when males and females are considered separately.

Discussion

Although traditionally researchers have downplayed the role of hybridization in animal evolution, research over the last decade has shown that hybridization can act as a creative evolutionary force, and in certain circumstances can be advantageous. Hybrids often display a greater range of genotypic and phenotypic variation relative to purebreds, displaying characteristics outside of the range of parental variation, a phenomenon called transgressive segregation (Seehausen, 2004). Transgressive segregation is fairly common in hybrids; a survey showed that 45 of 58 (78%) studies of hybridization in wild animals demonstrated transgressive segregation based on an evaluation of 650 phenotypic traits (Rieseberg et al., 1999). Charpentier et al. (2012) also observed transgressive segregation and greater genetic diversity in wild olive and yellow baboon hybrids. Increased variation can lead to an adaptive advantage in hybrids relative to purebreds because it becomes more likely that one of the many hybrid phenotypes will be beneficial and selected for in novel environments (Seehausen, 2004; Nolte and Tautz, 2010). Hybrids may also have a competitive advantage due to preferential mate selection if a hybrid phenotype can survive better in an altered environment, such as might be the case with observed higher probability of mating success in

male hybrids that appear more like olive baboons in a hybrid zone with purebred olive baboon males, yellow baboon males, and yellow-like baboon hybrids (Charpentier et al., 2012; Tung et al., 2012). Taken to the extreme conclusion, higher fitness in hybrids can lead to the production of a new subspecies, or even a new species.

Previous research on the baboon collection studied here indicated that there were significant differences between hybrids and the purebreds for external skull measurements (Ackermann et al., 2006, 2014). The results presented here are consistent with these studies, indicating that F₁ hybrid baboons can be differentiated from their parental taxa on the basis of the size and shape of their nasal cavities, and provide further evidence that hybridization in the fossil record can be identified on the basis of the phenotype (Ackermann, 2010). As indicated in the PCA results, there is also some evidence for individual hybrids that are transgressive relative to their parental taxa, as seen in the skulls of other primate hybrids (e.g., marmosets [Fuzessy et al., 2014], gorillas [Ackermann and Bishop, 2010]). The F₁ hybrids are also more dimorphic than at least one of the parental taxa (olive baboons), a phenomenon which appears to be driven by increased size, as well as shape divergence, in the nasal cavities of the males. This is consistent with the previously observed large facial size and “boxiness” in the snout of male hybrids in this collection (Ackermann et al., 2006). However, unlike previous studies (e.g., Ackermann et al., 2006, 2014), F₁ hybrids do not appear to have a greater frequency of nonmetric traits in the nasal cavity relative to parental taxa, providing no clear nonmetric evidence for developmental instability in the nasal region in the face of hybridization. It may be that the nasal cavity is more functionally constrained than other aspects of the cranium and is therefore less amenable to trait variants. Or it may be that the differences seen in parental traits are not sufficient to produce developmental instability on re-merger (i.e., when genes from both parental genotypes attempt to regulate the same region in an individual). Regardless, it suggests that the nonmetric traits observed here in the nasal cavity, unlike externally observable dental and sutural variants, are not good indicators of hybridization in the fossil record.

With regards to characterizing these shape differences, this study illustrates that first generation baboon hybrids differ from parental groups, but that this difference is not uniform across the nasal cavity. The areas of most dynamic change in the hybrid baboons were the anterior bony cavity, the choana, and the mid-nasopharynx. The anterior region of the hybrids, at the rhinion, exhibited greater inferior width relative to the parental taxa. Both male and female hybrids showed overall size increases in this region, while female hybrids also show shape change in the inferior meatus of the anterior bony cavity. The region from the choana through the mid-nasopharynx exhibited many size and shape differences, and appears to be an area strongly affected by hybridization, with different responses (both size increase and decrease) at different height and width measurements. Interestingly, male and female F₁ hybrids show a different phenotypic response to hybridization, with males becoming wider inferiorly and

females becoming narrower, relative to parental taxa. The differences in this area are so great that the PCAs were primarily differentiating the individual specimens through measurements of the nasopharynx width in conjunction with the anterior bony cavity. The area that did not differ between any of the taxa was the middle bony cavity of the anterior region, suggesting that this region might be functionally conserved or similar due to shared ancestry. The posterior nasopharynx also shows minimal differences between the taxa, with only the width of the lateral recess larger in hybrids. Taken together, these results indicate that the regions of greatest change in the skeletal nasal cavity of hybrids are ones that also differ in the parental animals, while other undifferentiated regions remain unchanged. Hybridization also appears to affect the sexes in different ways. However, we advise caution here because of small sample sizes. We also cannot predict the effects this might have on function, as functional interpretations of morphological differences in hybrids must take into account soft tissue anatomy, which the skeletal elements examined here cannot demonstrate (Márquez et al., 2014).

Our ultimate goal in undertaking this research is to provide further understanding of the phenotypic effects of hybridization with an eye towards interrogating the fossil record of human evolution, and Late Pleistocene evolution in particular. The Neanderthal nasal cavity has been of particular interest in studies of human evolution because it is recognizably different from what is seen in their contemporaries and in modern peoples. If we extrapolate our findings to the hominin situation, we would expect F_1 hybrid fossils to have larger nasal cavities, on average, than either parental taxon, with overall shape that differs most profoundly in regions that themselves differ among the parental lineages. If the baboon is an accurate model of hominin hybridization, the most pronounced size and shape change should occur in the anterior bony cavity, as well as certain deep regions (choana, mid-nasopharynx). We would also expect that these effects—and especially size increase—would be more pronounced in males than in females. The fact that the parental differences are quite pronounced in the anterior nasal cavity of the baboons in particular, which is also observed in the literature describing differences between Neanderthals and extant *H. sapiens* and Pleistocene *H. sapiens* for this region (Sollas, 1908; Schwartz and Tattersall, 1996; Franciscus, 1999; Friess et al., 2002; Bruner and Manzi, 2008; Schwartz et al., 2008; Márquez et al., 2014), suggests that this model might be effective for interrogating the fossil record for this time period.

However, it is important to note that the hominin and baboon nasal cavity are not strictly analogous. Most obviously, hominins and baboons have very different faces, with the latter strongly affected by overall tooth size creating a dog-like snout and strong sexual dimorphism. There are also differences in anatomy of the internal nasal cavity between baboons and hominins. In particular, the maxillary sinuses that interact with the nasal cavity cannot

be analyzed in the baboon model because baboons, unlike Neanderthals and *H. sapiens*, do not have maxillary sinuses.

This study also suggests that identification of F₁ hybrids, or at least some F₁ hybrids, might be best accomplished by identifying individuals that display transgressive segregation. This was also the case for studies of nonmetric traits in these baboon hybrids (Ackermann et al., 2006, 2014). Such individuals lie on the edges (or beyond) of population variance of either parental taxon. As seen here, transgressive segregation might be visible when taking into account all measurements of the nasal cavity, or certain individual traits. A comparable study of Paleolithic hominins would compare individual specimen morphology to the morphology of parental taxa (in this case Neanderthals and *H. sapiens*); if a specimen falls near the edges of the variation of both parental samples, it ought to be further studied as a potential hybrid. The problem with this suggestion, of course, is that it presumes we know which specimens are “purebred” in the first place, which we do not know. Additionally, our study at this point is only applicable to F₁ hybrids; we are not in a position to evaluate later generations, including humans living today with Neanderthal ancestry.

Nonetheless, as a general model, the presence of increased size and possibly size dimorphism in the nasal cavity of hybrid baboons, as well as general shape changes and evidence for individual transgressive phenotypes, are consistent with what has been observed in other studies of the primate hybrid phenotype (Ackermann et al., 2006, 2014; Ackermann and Bishop., 2010; Fuzessy et al., 2014). If we use these guidelines to consider individual fossils, we can eliminate those that do not clearly fit this pattern and identify some that might. When doing this, again it is important to remember that we cannot make an assumption that any specimens during the time of purported Neanderthal-human hybridization are “pure” and, therefore, that their character states are representative of those “pure” species. For example, we know that some early modern humans have large nasal dimensions; although this has been interpreted as plesiomorphic, it could also be the result of hybridization. In this context, all we can conservatively predict is that early modern humans that have hybridized with Neanderthals (and vice versa) will be on the big-nosed (or at least medium-nosed) end of the spectrum of total variation. As one example, early *H. sapiens* specimens from Skhul and Qafzeh have large noses, with wide nasal breadths not that different from Neanderthals. Some of these specimens also show evidence for underlying developmental instability (Ackermann, 2010), shown to be an indicator of hybridization in baboons and other mammals through the production of transgressive traits (Ackermann et al., 2006, 2010, 2014). At least some of these specimens, therefore, may indeed be hybrids. However, since the Skhul and Qafzeh samples, dated to 80–120 kya (Franciscus and Holliday, 2013), precede the Neanderthals found in that region after 70 kya by a substantial amount of time, it is not clear who the other parent

taxon would be. Similarly, very large (and large-nosed) Neanderthal specimens such as Amud 1, which also has an atypical dentition (Ackermann, 2010), are consistent with our emerging model of hybrid morphology. On the other hand, Neanderthal and early *H. sapiens* specimens that do not demonstrate relatively large nasal cavity size, shape change, and/or transgressive traits do not fit our general predictions for being first generation hybrids.

Finally, although limited to one region of the phenotype, this study nevertheless confirms our expectations that where two taxa have diverged fairly recently and therefore are very similar genetically (Newman et al., 2004; Zinner et al., 2009), but have a subset of phenotypic traits that differ substantially, hybridization between these taxa has a significant effect on those traits that are most divergent while having little effect on the rest of the phenotype. It also shows that the effects of hybridization in a single isolated (but distinctive) region of the phenotype can be substantial. This provides a framework for further examinations aimed at identifying hybridization in the fossil record.

Acknowledgments

We are indebted to Jim Cheverud, Jessica Joganic, and Jeff Rogers for collecting and curating this remarkable baboon sample. We would like to thank them, as well as Joan Richtsmeier, for access to the scans and collection. Additionally, KE would like to thank her Masters committee for their support during the collection and analysis of these data: Maria Liston, Nancy Barrickman, and Fred Smith. KE would also like to thank Nathan Holton, Todd Yokley, Jim Ahern, Justin Eichel, and Matt Ingnot for theoretical discussion and technical assistance. This work was supported by funding from the Department of Anthropology at the University of Waterloo, the Natural Sciences and Engineering Research Council of Canada (NSERC), the National Research Foundation of South Africa, and the DST/NRF Centre of Excellence in Palaeosciences (COE-Pal). Funding for scanning the baboon skulls came from the Human Origins (HOMINID) grant (NSF BCS-0725068). The establishment, maintenance, and biological characterization of the pedigreed baboon colonies at the Southwest National Primate Research Center, Texas Biomedical Research Institute (SNPRC/Texas Biomed) has been supported in large part by grants to SNPRC/Texas Biomed Investigators by the Office of Infrastructure Programs, National Institutes of Health (P51 RR013986, P01 HL028972, C06 RR0114578). This manuscript was not prepared in collaboration with investigators at the SNPRC/Texas Biomed and does not necessarily reflect the opinions, views, or conclusions of SNPRC/Texas Biomed investigators.

References

- Ackermann, R.R., 2010. Phenotypic traits of primate hybrids: recognizing admixture in the fossil record. *Evol. Anthropol.* 19, 258–270.
- Ackermann, R.R., Bishop, J.M., 2010. Morphological and molecular evidence reveals recent hybridization between gorilla taxa. *Evolution* 64, 271–290.
- Ackermann, R.R., Rogers, J., Cheverud, J., 2006. Identifying the morphological signatures of hybridization in primate and human evolution. *J. Hum. Evol.* 51, 632–645.
- Ackermann, R.R., Brink, J.S., Vrahimis, S., Klerk, B.D., 2010. Hybrid wildebeest (*Artiodactyla: Bovidae*) provide further evidence for shared signatures of admixture in mammalian crania. *S. Afr. J. Sci.* 106, 1–4.
- Ackermann, R.R., Schroeder, L., Rogers, J., Cheverud, J.M., 2014. Further evidence for phenotypic signatures of hybridization in descendant baboon populations. *J. Hum. Evol.* 76, 54–62.
- Alberts, S.C., Altmann, J., 2001. Immigration and hybridization patterns of yellow and anubis baboons in and around Amboseli, Kenya. *Am. J. Primatol.* 53, 139–154.
- Arnold, M.L., Meyer, A., 2006. Natural hybridization in primates: one evolutionary mechanism. *Zool.* 109, 261–276.
- Arsuaga, J.L., Martínez, I., Arnold, L.J., Aranburu, A., Gracia-Téllez, A., Sharp, W.D., Qam, R.M., Falguères, C., Pantoja-Pérez, A., Bischoff, J., Poza-Rey, E., Parés, J.M., Carretero, T.M., Demuro, M., Lorenzo, C., Sala, N., Martínón-Torres, M., García, N., Alcázar de Velasco, A., Cuenca-Bescós, G., Gómez-Olivencia, A., Moreno, D., Pablos, A., Shen, C.-C., Rodríguez, L., Ortega, A.I., García, R., Bonmatí, A., Bermúdez de Casto, J.M., Carbonell, E., 2014. Neandertal roots: Cranial and chronological evidence from Sima de los Huesos. *Science* 344, 1358–1363.
- Bastir, M., Rosas, A., 2013. Cranial airways and the integration between the inner and outer facial skeleton in humans. *Am. J. Phys. Anthropol.* 152, 287–293.
- Bräuer, G., 1981. New evidence on the transitional period between Neanderthal and modern man. *J. Hum. Evol.* 10, 467–474.
- Bruner, E., Manzi, G., 2006. Saccopastore 1: the earliest neanderthal? A new look at an old cranium. In: Harvati, K., Harrison, T. (Eds.), *Neanderthals revisited: New approaches and perspectives*. Springer, New York, pp. 23–36.
- Cartmill, M., Smith, F.H., 2009. *The Human Lineage*. Vol. 2. John Wiley and Sons, New York.
- Charpentier, M.J.E., Fontaine, M.C., Cherel, E., Renoult, J.P., Jenkins, T., Benoit, L., Barthes, N., Alberts, S.C., Tung, J., 2012. Genetic structure in a dynamic baboon hybrid zone corroborates behavioural observations in a hybrid population. *Mol. Ecol.* 21, 715–731.

- Cheverud, J.M., Jacobs, S.C., Moore, A.J., 1993. Genetic differences among subspecies of the saddle-back tamarin (*Saguinus fuscicollis*): evidence from hybrids. *Am. J. Primatol.* 31, 23–39.
- Condemi, S., Mounier, A., Giunti, P., Lari, M., Caramelli, D., Longo, L., 2013. Possible interbreeding in late Italian Neanderthals? New data from the Mezzena Jaw (Monti Lessini, Verona, Italy). *PloS ONE* 8, 1–9.
- Dean, D., Hublin, J.J., Holloway, R., Ziegler, R., 1998. On the phylogenetic position of the pre-Neandertal specimen from Reilingen, Germany. *J. Hum. Evol.* 34, 485–508.
- Duarte, C., Muarico, J., Pettitt, P.B., Souto, P., Trinkaus, E., van der Plicht, H., Zilhão, J., 1999. The Early Upper Paleolithic Human Skeleton from the Abrigo Do Lagar Velho (Portugal) and Modern Human Emergence in Iberia. *Proc. Natl. Acad. Sci. USA* 96, 7604–7609.
- Endicott, P., Ho, S.Y., Stringer, C., 2010. Using genetic evidence to evaluate four palaeoanthropological hypotheses for the timing of Neanderthal and modern human origins. *J. Hum. Evol.* 59, 87–95.
- Falconer, D.S., Mackay, T.F.C., 1996. Introduction to quantitative genetics. Longman, Harlow.
- Franciscus, R.G., 1999. Neandertal nasal structures and upper respiratory tract “specialization.” *Proc. Natl. Acad. Sci.* 96, 1805–1809.
- Franciscus, R.G., 2003. Internal nasal floor configuration in *Homo* with special reference to the evolution of neandertal facial form. *J. Hum. Evol.* 44, 701–729.
- Franciscus, R.G., Holliday, T.W., 2013. Crossroads of the Old World: Late hominin evolution in Western Asia. In: Smith, F.H., Ahern, J.C.M. (Eds.), *The Origins of Modern Humans: Biology Reconsidered*. John Wiley and Sons, New York, pp. 45–88.
- Friess, M., Marcus, L.F., Reddy, D.P., Delson, E., 2002. The use of 3D laser scanning techniques for the morphometric analysis of human facial shape variation. *BAR IS.* 1049, 31–35.
- Fu, Q., Li, H., Moorjani, P., Jay, F., Slepchenko, S.M., Bondarev, A.A., Johnson, P.L.F., Aximu-Petri, A., Prüfer, K., de Filippo, C., Meyer, M., Zwyns, N., Salazar-García, D.C., Kuzmin, Y.V., Keates, S.G., Kosintsev, P.A., Razhev, D.I., Richards, M.P., Peristov N.V., Lachmann, M., Douka, K., Higham, T.F.G., Slatkin, M., Hublin, J.-J., Reich, D., Kelso, J., Viola, T.B., Pääbo, S., 2014. Genome sequence of a 45,000-year-old modern human from western Siberia. *Nature* 514, 445–449.
- Fu, Q., Hajdinjak, M., Moldovan, O.T., Constantin, S., Mallick, S., Skoglund, P., Patterson, N., Rohland, N., Lazardis, I., Nickel, B., Viola, B., Prüfer, K., Meyer, M., Kelso, J., Reich, D., Pääbo, S., 2015. An early modern human from Romania with a recent Neanderthal ancestor. *Nature* 524, 216–219.

- Fuzessy, L.F., Silva, I.O., Malukiewicz, J., Silva, F.F.R., Pônzio, M.C., Boere, V., Ackermann, R.R., 2014. Morphological variation in wild marmosets (*Callithrix penicillata* and *C. geoffroyi*) and their hybrids. *Evol. Biol.* 41, 480–493.
- Green, R.E., Malaspina, A.S., Krause, J., Briggs, A.W., Johnson, P.L., Uhler, C., Meyer, M., Good, J.M., Marcic, T., Stenzel, U., Prüfer, K., Siebauer, M., Burbano, H.A., Ronan, M., Rothberg, J.M., Egholm, M., Rudan, P., Brajković, D., Kuan, Ž., Gušić, I., Wirkstöm, M., Laakkonen, L., Kelso, J., Slatkin, M., Pääbo, S., 2008. A complete Neandertal mitochondrial genome sequence determined by high-throughput sequencing. *Cell* 134, 416–426.
- Green, R.E., Krause, J., Briggs, A.W., Maricic, T., Stenzel, U., Kircher, M., Patterson, N., Li, H., Zhai, W., Fritz, M.H.-Y., Hansen, N.F., Durand, E.Y., Malaspina, A.-S., Jensen, J.D., Marques-Bonet, T., Alkan, C., Prüfer, K., Meyer, M., Burbano, H.A., Good, J.M., Schultz, R., Aximu-Petri, A., Butthof, A., Höber, B., Höffner, B., Siegemund, M., Weihmann, A., Nusbaum, C., Lander, E.S., Russ, C., Novod, N., Affourtit, J., Egholm, M., Verna, C., Rudan, P., Brajković, D., Kucan, Ž., Gušić, I., Doronichev, V.B., Golovanova, L.V., Lalueza-Fox, C., de la Rasilla, M., Jorde, J., Rosas, A., Schmitz, R.W., Johnson, P.L.F., Eichler, E.E., Falush, D., Birney, E., Mullikin, J.C., Slatkin, M., Nielsen, R., Kelso, J., Lachmann, M., Reich, D., Pääbo, S., 2010. A draft sequence of the neandertal genome. *Science* 328, 710–722.
- Harrison, R., 1986. Pattern and process in a narrow hybrid zone. *Heredity* 55, 337–349.
- Harvati, K., Gunz, P., Grigorescu, D., 2007. Cioclovina (Romania): affinities of an early modern European. *J. Hum. Evol.* 53, 732–746.
- Harvati, K., Hublin, J.J., Gunz, P., 2010. Evolution of middle-late Pleistocene human cranio-facial form: A 3-D approach. *J. Hum. Evol.* 59, 445–464.
- Ito, T., Kawamoto, Y., Hamada, Y., Nishimura, T.D., 2015. Maxillary sinus variation in hybrid macaques: implications for the genetic basis of craniofacial pneumatization. *Biol. J. Linnean Soc.* 115, 333–347.
- Hu, Y., Wang, Y., Ding, Q., He, Y., Wang, M., Wang, J., Xu, S., Jin, L., 2014. Genome-wide scan of archaic hominin introgressions in eurasians reveals complex admixture history. *arXiv: 1404.7766*.
- Jiggins, C.D., Mallet, J., 2000. Bimodal hybrid zones and speciation. *Trends Ecol. Evol.* 15, 250–255.
- Jones, N., 2001. The nose and paranasal sinuses physiology and anatomy. *Adv. Drug Deliv. Rev.* 51, 5–19.
- Key, K., 1968. The concept of stasipatric speciation. *Syst. Zool.* 17, 14–22.
- Klein, R.G., 2003. Whither the Neanderthals? *Science* 299, 1525–1527.
- Kohn, L.A.P., Langton, L.B., Cheverud, J.M., 2001. Subspecific genetic differences in the saddle-back tamarin (*Saguinus fuscicollis*) postcranial skeleton. *Am. J. Primatol.* 54, 41–56.

- Krings, M., Stone, A., Schmitz, R.W., Krainitzki, H., Stoneking, M., Pääbo, S., 1997. Neandertal DNA sequences and the origin of modern humans. *Cell* 90, 19–30.
- Lynch, M., Walsh, B., 1998. Genetics and analysis of quantitative traits. Sinauer Associates Inc., Sunderland.
- Márquez, S., Pagano, A.S., Delson, E., Lawson, W., Laitman, J.T., 2014. The nasal complex of neanderthals: An entry portal to their place in human ancestry. *Anat. Rec.* 297, 2121–2137.
- Mlynski, G., Grutzenmacher, S., Plontke, S., Mlynski, B., Lang, C., 2001. Correlation of nasal morphology and respiratory function. *Rhinology* 39, 197–201.
- Newman, T.K., Jolly, C.J., Rogers, J., 2004 Mitochondrial phylogeny and systematics of baboons (*Papio*). *Am. J. Phys. Anthropol.* 124, 17–27.
- Noback, M.L., Harvati, K., Spoor, F., 2011. Climate-related variation of the human nasal cavity. *Am. J. Phys. Anthropol.* 145, 599–614.
- Nolte, A.W., Tautz, D., 2010. Understanding the onset of hybrid speciation. *Trends Genet.* 26, 54–58.
- Prüfer, K., Racimo, F., Patterson, N., Jay, F., Sankararaman, S., Sawyer, S., Heinze, A., Renaud, G., Sudmant, P.H., de Filippo, C., Li, H., Mallick, S., Dannemann, M., Fu, Q., Kircher, M., Kuhlwilm, M., Lachmann, M., Meyer, M., Ongyerth, M., Siebauer, M., Theunert, C., Tandon, A., Moorjani, P., Pickrell, J., Mullikin, J.C., Vohr, S.H., Green, R.E., Hellmann, I., Johnson, P.L.F., Blanche, H., Cann, H., Kitzman, J.O., Shendure, J., Eichler, E.E., Lein, E.S., Bakken, T.E., Golovanova, L.V., Doronichev, V.B., Shunkov, M.V., Derevianko, A.P., Viola, B., Slatkin, M., Reich, D., Kelso, J., Pääbo, S., 2014. The complete genome sequence of a neanderthal from the Altai Mountains. *Nature* 505, 43–49.
- Rieseberg, L.H., Archer, M.A., Wayne, R.K., 1999. Transgressive segregation, adaptation and speciation. *Heredity* 83, 363–372.
- Rougier, H., Milota, S., Rodrigo, R., Gherase, M., Sarcin, L., Moldovan, O., Zilhão, J., Constantin, S., Franciscus, R.G., Zollikofer, C.P.E., de León, M.P., Trinkaus, E., 2007. Peștera cu Oase 2 and the cranial morphology of early modern Europeans. *Proc. Natl. Acad. Sci. USA* 104, 1165–1170.
- Sankararaman, S., Patterson, N., Li, H., Pääbo, S., Reich, D., 2012. The date of interbreeding between Neandertals and modern humans. *PLoS Genet.* 8, e1002947.
- Schwartz, J.H., Tattersall, I., 1996. Significance of some previously unrecognized apomorphies in the nasal region of *Homo neanderthalensis*. *Proc. Natl. Acad. Sci. USA* 93, 10852–10854.
- Schwartz, J.H., Tattersall, I., Teschler-Nicola, M., 2008. Architecture of the nasal complex in neanderthals: Comparison with other hominids and phylogenetic significance. *Anat. Rec.* 291, 1517–1534.
- Seehausen, O., 2004. Hybridization and adaptive radiation. *Trends Ecol. Evol.* 19, 198–207.

- Smith, F.H., Jankovic, I., Karavanic, I., 2005. The Assimilation Model, Modern Human Origins in Europe, and the Extinction of Neandertals. *Quatern. Int.* 137, 7–19.
- Soficaru, A., Petrea, C., Dobosi, A., Trinkaus, E., 2006. Early modern humans from the Peștera Muierii, Baia de Fier, Romania. *Proc. Natl. Acad. Sci. USA* 103, 17196–17201.
- Sollas, W.J., 1908. On the cranial and facial characters of the Neandertal race. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 199, 281–339.
- Stringer, C.B., 2008. Modern Human Origins: Progress and Prospects. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 357, 563–579.
- Stringer, C.B., Andrews, P., 1988. Genetic and fossil evidence for the origin of modern humans. *Science* 239, 1263–1268.
- Tattersall, I., Schwartz, J., 1999. Hominids and Hybrids: The Place of Neanderthals in Human Evolution. *Proc. Natl. Acad. Sci. USA* 96, 7117–7119.
- Tattersall, I., Schwartz, J., 2008. The Distinctiveness and Systematic Context of *Homo neanderthalensis*. In: Harvati, K., Harrison, T. (eds.), *Neanderthals Revisited: New Approaches and Perspectives*. Springer, New York, pp. 9–22.
- Trinkaus, E., Constantin, S., Silhco, J., 2013. *Life and Death at the Peștera cu Oase. A Setting for Modern Human Emergence in Europe*. Oxford University Press, New York.
- Tung, J., Charpentier, M.J.E., Mukherjee, S., Altmann, J., Alberts, S.C., 2012. Genetic effects on mating success and partner choice in a social mammal. *Am. Nat.* 180, 113–129.
- Wolpoff, M.H., Hawks, J., Frayer, D.W., Hunley, K., 2001. Modern human ancestry at the peripheries: a test of the replacement theory. *Science* 291, 293–297.
- Wolpoff, M.H., Mannheim, B., Mann, A., Hawks, J., Caspari, R., Rosenberg, K.R., Frayer, D.W., Gil, G.W., Clark, G., 2004. Why Not the Neandertals? *World Archaeol.* 36, 527–546.
- Wu, C.I., 2001. The genic view of the process of speciation. *J. Evol. Biol.* 14, 851–865.
- Zilhão, J., Trinkaus, E. (Eds.), 2002. Portrait of the Artist as a Child. The Gravettian Human Skeleton from the Abrigo do Lagar Velho and its Archeological Context. *Trabalhos de Arqueologia* 22.
- Zinner, D., Groeneveld, L.F., Keller, C., Roos, C., 2009. Mitochondrial phylogeography of baboons (*Papio spp.*)—Indication for introgressive hybridization? *BMC Evol. Biol.* 9, 83.

Figure legends

Figure 1. a) Coronal section of the anterior bony cavity, b) coronal section of the nasopharynx, c) sagittal section of the nasal cavity, and d) location of five CT images further analyzed for each specimen.

Figure 2. Representation of nasal cavity features that were found to be statistically significant between a) parental taxa and hybrids with pooled sexes, after correction for sexual dimorphism; b) female parental taxa and female hybrids; and c) male olives and male hybrids.

Figure 3. Principal Component Analysis (PCA) of a-b) parental taxa and F₁ hybrids prior to correction for sexual dimorphism: a) PC1 against PC2, b) PC2 against PC3; PCA of c-d) parental taxa and F₁ hybrids after correction: c) PC1 against PC2, d) PC2 against PC3.

Figure 4. Canonical Discriminant Analysis (CDA) of a) parental taxa and F₁ hybrids separated by sex, b) parental taxa and F₁ hybrids with pooled sexes and after correction for sexual dimorphism, c) male parental taxa and male F₁ hybrids, and d) female parental taxa and female F₁ hybrids.

Figure 1

Figure 2

Figure 3

Figure 4