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Further evidence for phenotypic signatures of hybridization in descendent baboon populations

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Abstract

Hybridization may have played a substantial role in shaping the diversity of our evolving lineage. Although recent genomic evidence has shown that hybridization occurred between anatomically modern humans (AMHS) and Neanderthals, it remains difficult to pin down precisely where and when this gene flow took place. Investigations of the hybrid phenotype in primates and other mammals are providing models for identifying signatures of hybridization in the fossil record. However, our understanding of intra- and inter-taxon variation in hybrids is still limited. Moreover, there is little evidence from these studies that is pertinent to the question of how long hybrid skeletal traits persist in descendants, and therefore it is not clear whether observed hybrid phenotypes are evidence of recent (e.g., F_1) or much earlier hybridization events. Here, we present an analysis updating a previous study of cranial variation in pedigreed olive and yellow baboons and their hybrids. Results suggest that traits previously associated with hybrids in baboons and other mammalian species are also present in this expanded data set; many of these traits are highly heritable, confirming a genetic basis for their variation in this mixed population. While F_1 animals – and especially F_1 males – still have the highest number of dental anomalies, these and other atypical traits persist into later hybrid generations (such as F_2 and B_1). Moreover, non- F_1 recombinants also show extremely rare trait variations, including reduced canines and rotated teeth. However, these results must be considered in light of the possibility that some founding individuals may have themselves been unrecognized hybrids. Despite this, the data are compelling, and indicate once again that further controlled research remains to be done on primates and other mammals in order to better understand variation in the hybrid phenotype.

Keywords

Gene flow; *Papio cynocephalus*; *Papio anubis*; Supernumerary teeth; Cranial variation

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Introduction

Hybridization has played a significant role in shaping primate diversity, causing important and occasionally large-scale evolutionary changes such as the formation of new species (e.g., *Macaca arctoides*; (Tosi et al. 2000)). Similarly, hybridization may have been influential in shaping the diversity of our own evolving lineage (Arnold 2009; Arnold and Meyer 2006), however, the evidence for this is somewhat limited. Although there is evidence that gene flow likely occurred early on at the initial divergence of the hominin and chimpanzee lineages (Mailund et al. 2012), and also later between closely-related sympatric hominin species, currently our best evidence for hybridization in human evolution comes from recent genomic studies that have shown that hybridization occurred between archaic human peoples (e.g., Neanderthals, Africans, Denisovans) (Green et al. 2010; Meyer et al. 2012; Reich et al. 2010; Sánchez-Quinto et al. 2012). Unfortunately, genetic evidence has limited power for pinning down precisely where and when this gene flow took place. Moreover, the vast bulk of hominin species are not candidates for genetic analyses. In such cases, our greatest insights can only come from morphology, and depend on our ability to recognize the signatures of hybridization in the phenotype.

Hybridization can produce some striking phenotypes in mammals, including variation in coat colour, as well as often dramatic changes in body size, tooth number, and chromosome number, among other things. For primates, considerable variation in coat colour and pattern is particularly well-documented in hybrid zones (see review in (Ackermann 2010)). But of course skin and hair do not fossilize, and only studies of bony morphology are useful for interpreting the fossil past. Previous work on hybrid skeletons has shown that dental and sutural anomalies are common in hybrid mammals, including baboons, gorillas, and wildebeest (Ackermann 2007; Ackermann 2010; Ackermann and Bishop 2010; Ackermann et al. 2010; Ackermann et al. 2006). The human fossil record also reveals similar anomalies – and arguably evidence of hybridization – in a handful of fossils, including Neanderthals and anatomically modern humans (AMHS) living in the Middle East and nearby regions circa 100 thousand years ago (Ackermann 2010). However, considerable work remains to be done to understand the expression of hybridization in the primate skeleton. Most pressing, we need a better understanding of variation in living hybrid populations, a more thorough grasp of how long traits associated with hybridization persist in descendants and further investigations into the universality of these traits across taxa with varying degrees of temporal divergence.

Here we contribute to these goals through an analysis of purebred and hybrid pedigreed baboons. This analysis is an update of a previous study (Ackermann et al. 2006) of cranial variation in pedigreed olive and yellow baboons and their hybrids. That research was based on what was then a collection of 252 skulls, with 169 animals with known pedigrees (112 purebreds, 57 hybrids). This collection allowed for the analysis of first generation F_1 hybrids, and a small number of backcrossed B_1 hybrids. Since that time the collection has grown as more material has become available. The collection is now closed and comprises 985 skulls. Although there are a few other primate species (e.g., hamadryas baboons) in the collection, it primarily comprises yellow baboons (*Papio cynocephalus*), olive baboons (*P. anubis*), and their hybrids (including F_1 , B_1 , F_2 , B_2 and other recombinants).

Materials and methods

Our sample derives from the captive population of pedigreed baboons at the Southwest National Primate Research Center (SNPRC) at the Texas Biomedical Research Institute (previously Southwest Foundation for Biomedical Research, or SFBR), San Antonio, Texas. When skeletal material became available following an animal's natural death, skulls were collected at necropsy, then cleaned, and are currently curated in the Department of Biology at Loyola University Chicago. Because the precise genealogical relationships among individuals are known, we are able to distinguish different types of hybrids (e.g., F_1 , B_1). Proportional ancestry for hybrids is determined from the pedigree data. The wild-derived founding colony members were assigned to taxa based on their phenotypes and as a result there is a some possibility of admixture in a few of these founding individuals (as will be addressed further in the discussion); some of the original collection of wild animals occurred in or near an olive-yellow hybrid zone in southern Kenya (Jolly 1967; Maples and McKern 1967). For subsequent generations, proportional ancestry (e.g., 75% olive, 25% yellow), as well as precise hybrid status (e.g., F_1 , B_1) is inferred from the pedigree data. Individuals for whom pedigree information is not known at all, as well as individuals labelled as purebreds but where pedigrees are only partially known (and therefore may not actually be purebreds), are removed for the purposes of this study. The final sample size for analysis is 570 (278 purebreds, 292 hybrids), and includes the 169 animals previously analysed in the 2006 study. The final purebred sample is heavily biased towards olive baboons with only three female (and no male) yellow baboons included in the analysis. Therefore, purebreds of both taxa are pooled for all analyses. Importantly, this does not mean that the hybrids are descended from only three yellow baboon females, simply that their *P. cynocephalus* ancestors are not included in the skeletal collection as most of these baboons died before the collecting began.

We focus here on qualitative trait variation in the sample, given the results of the 2006 study, which showed a preponderance of both supernumerary teeth and additional zygomatic sutures in hybrids relative to purebreds. In the 2006 study, we also evaluated heterosis based on cranial measurements; an extensive quantitative analysis of size and shape variation (including analyses of heterosis, integration, and asymmetry) in these crania is currently underway and will be reported on elsewhere. To analyse qualitative trait variation, individual crania were examined and scored for the presence of a suite of cranial non-metric traits: supernumerary teeth, extra sutures in the zygomaxillary region, dental crowding, remnant metopic sutures, ossicles at lambda and asterion, bregmatic bones, coronal ossicles, epipteric bones, and parietal notch bones. We discarded the trait called 'ruggedness' observed in the 2006 study in order to avoid concerns about inter-observer subjectivity, as data were collected by both RRA and LS. This trait is currently being evaluated in a separate quantitative study of the crania, mentioned above. Samples were divided by sex to determine whether males and females show different hybrid morphologies. A chi-square test (one-way) was used to test the hypothesis that hybrids have a higher frequency of atypical non-metric traits than purebreds. Additionally, we estimated the narrow-sense heritability (h^2) for these traits scored as absent (0) or present (1) using the SOLAR quantitative genetic software package (Almasy and Blangero 1998). This package estimates the heritable variance as a

proportion of the total phenotypic variance after accounting for the effects of covariates using a maximum likelihood model (Almasy and Blangero 1998). We tested for sex differences as a covariate in the model. If the sexes were significantly different at the 10% level, sex was retained in the model when calculating heritability. If sex failed to reach the 10% significance level, it was deleted from the model estimating heritability. Associated probabilities indicate the chance of obtaining the observed heritability, or an even more extreme one, when the true population heritability is 0.0.

Supernumerary teeth in the permanent dentition can be quite variable, ranging from normal morphology to very rudimentary forms (Batra et al. 2005). They are generally classified into four types: conical (peg-shaped, typically maxillary mesiodens), tuberculate (barrel shaped with tubercles, typically found in the palate), supplemental (near normal size/shape found in dentition), and odontomas (disorganised mass of dental tissues) (Garvey et al. 1999). We also record the supernumerary dental type, indicate where supernumerary teeth are completely normal (or near-normal) size/shape versus reduced in size, and indicate whether the latter retain some cusp morphology. The most likely cause of supplemental teeth, including distomolars, is a split in the tooth germ (tooth germ dichotomy theory) or hyperactivity of the dental lamina; heredity is also believed to be an important factor (Wang and Fan 2011). To test whether supplementary teeth result from finer subdivisions of the molar dental field versus a longer molar dental field divided into normal sized segments, we also measured molar lengths for all hybrids with distomolars, and compared the summed lengths of M1–M3 for the left maxillary and mandibular rows between hybrids and a sample of purebreds using a MANOVA.

Results

Qualitative differences exist among the hybrid and purebred samples. Table 1 reports the trait frequencies of those traits that exist at a frequency greater than zero in the sample. Frequencies are given for purebreds and hybrids as well as each hybrid group, broken down by sex. The incidence of supernumerary teeth, atypical sutures, and remnant metopic sutures is significantly higher in the hybrid males, relative to the purebreds. The incidence of tooth crowding, atypical sutures and remnant metopic sutures is also higher than expected in the hybrid females, relative to the purebreds. Atypical sutures as a category includes additional sutures in the zygomatic (as described in (Ackermann et al. 2006), but also sutures that have unusual spicules or ossicles. However, unlike in the 2006 study, we also analysed the presence of additional sutures in the zygomatic separately, and found that hybrids do not have significantly higher frequencies, indicating that frequency differences in atypical sutures seen between the groups are not attributable to this trait. Although trait significance does differ somewhat by sex, the overall pattern is similar, with four of the six values being at or close to (e.g., $p < 0.1$) significance in both sexes. The majority of these traits are also significantly heritable, including supernumerary teeth (as well as distomolars only), tooth crowding, rotated teeth and remnant metopic suture (Table 2). Most of these heritabilities are high. Atypical sutures (inclusive of zygomatic sutures) are significantly heritable at the 10% level while zygomatic suture does not reach significance. Significant heritabilities support the results of the hybrid/purebred comparisons by indicating that differences

between hybrids and purebreds seen in the non-metric traits are segregating as heritable variance in this baboon population.

All of the supernumerary teeth are permanent teeth, with one exception. W957, a female olive baboon, has a small supernumerary tooth buccal to the left upper canine, between the canine and p3; this is clearly an un-erupted deciduous canine. This specimen was eliminated from all statistical analyses. Fifty-eight individuals in the sample have permanent supernumerary teeth (22 (7.9%) purebreds; 36 (12.3%) hybrids; see descriptions in Table 3). All of the supernumerary teeth are distomolars, i.e., additional teeth at the end of the tooth row, with a few exceptions. Three purebred animals have supernumerary premolars (one of these also has a maxillary distomolar), while one hybrid with an incomplete pedigree has a supernumerary premolar. Additionally, one F1 male has bilateral full-sized supernumerary maxillary canines, reported on elsewhere (Ackermann et al. 2006). The bulk of the distomolars are at or near normal shape/size. However, although most of the distomolars can be classified as supplemental, in the sense that they occupy a position in the tooth row and look like molars (as opposed to pegs or disorganised masses), there is considerable variation in distomolar morphology. These fourth molars range from being morphologically indistinguishable from third molars, to looking like molars but with clear size and cusp reduction, to being seriously reduced in size and barrel-shaped with two or three cusps, to a conical form with only a single cusp (see Table 3). These latter two may be classifiable as tuberculate or conical, although they do not appear in the positions typically associated with these types (e.g., incisor region, palate). We are, however, wary of dividing this continuous trait variation into categories (and concerned about the integrity of these categories) given that this range likely results from a common aetiology where fairly small changes in gene regulation ('tinkering') result in small differences in the rate and timing of cusp development but have more visible effects on molar cusp morphology (Jernvall and Thesleff 2012).

The 36 hybrid individuals with supernumerary teeth listed in Table 3 are the descendants of 33 dams and 19 sires, with most individual dams (30/33) and sires (12/19) producing just one hybrid offspring, three dams and two sires producing two offspring, three sires producing three offspring, one sire producing four, and one sire producing seven. For the purebreds, again the offspring with supernumerary teeth are the descendants of a number of individuals (19 dams, 10 sires), with most individual dams (17/19) and sires (6/10) producing only one offspring with supernumerary teeth, one dam and two sires producing two offspring, one dam and one sire producing three, and a single sire producing nine. These pedigree data are available on request.

The majority of the supernumerary teeth seen in hybrids occur in individuals from the F₁ generation ($n = 14$), as seen in the 2006 study, but they also occur in F₂ ($n = 1$), B₁ ($n = 4$), and other recombinant generations (see Tables 1 and 3). Although numbers of individuals are lower in post-F₁ generations, this nonetheless represents a significant advance on the previous study and indicates that these traits can persist into later generations. There are also 14 hybrids with incomplete pedigrees that have supernumerary teeth. From the information we have, most of these incompletely characterized hybrid individuals appear to be backcrosses, rather than F₁ animals. Fifteen of the 36 hybrid individuals with supernumerary

teeth (i.e., 42%) have bilateral mandibular molars, while six hybrid individuals have both maxillary and mandibular full-sized distomolars bilaterally. In contrast, five of the 22 purebred individuals with supernumerary teeth (23%) have bilateral mandibular molars, with only one having both bilateral maxillary and bilateral mandibular molars. Although this frequency in the purebreds is lower than the hybrids, it is still higher than in the 2006 study; possible causes of this will be further explored in the Discussion.

Additional molars in the tooth row beyond the third molar may be caused by either a split in the tooth germ or hyperactivity of the dental lamina (Wang and Fan 2011). Quantitative differences among male hybrids with supernumerary distomolars ($n = 19$), purebreds without supernumerary distomolars ($n = 12$), and purebreds with supernumerary distomolars ($n = 10$) suggest that the alveoli (measured as the total length of M1–M3) are comparably sized (MANOVA; $P = 0.759$), regardless of whether or not the specimens have distomolars. Separate tests for the mandible (ANOVA; $p = 0.649$) and the maxilla (ANOVA; $p = 0.746$) support this conclusion. Quantitative differences among female hybrids with supernumerary distomolars ($n = 17$), purebreds without supernumerary distomolars ($n = 13$), and purebreds with supernumerary distomolars ($n = 14$) indicate size differences in the alveoli among the groups (MANOVA; $p = 0.002$), however separate tests for the mandible (ANOVA; $p = 0.065$) and the maxilla (ANOVA; $p = 0.562$) suggest that these differences are not substantial. These results suggest that distomolar formation is due to hyperactivity of the dental lamina, a form of heterosis.

The trait frequencies of supernumerary teeth for each hybrid group differ considerably (Table 1). The frequency of supernumerary teeth in hybrids is greatest in the F_1 males (31%). The males also continue to have a fairly high frequency of supernumerary teeth in the B_1 and B_3 crosses (12% and 10%, respectively). Other recombinants of known pedigree have no individuals with supernumerary teeth, but it is important to remember that the sample sizes become extremely small ($n < 4$). For females, the frequency in the F_1 generation is 8%, while the B_1 ($F_1 \times$ yellow) hybrids have a very low frequency of just over 2%. Although supernumerary teeth do exist in other female recombinants, sample sizes are too small to have any confidence in the frequency values.

In the 2006 study we also found extremely unusual traits in F_1 animals. Here, for the first time, we have such traits in non- F_1 individuals. One backcrossed specimen (SNPRC ID# 1X4161, B_1 female) has a very small conical tooth where the maxillary right canine belongs, and what looks like a very tiny tooth broken off at the root (and therefore of unknown morphology) on the left. This appears to be the perfect counterpart for the F_1 male with double canines from the 2006 study (Figure 1). Two specimens (SNPRC ID# 14263, F_1 male; SNPRC ID# 9774, unknown pedigree hybrid female) have rotated teeth (Figure 2), one of which is a rotated distomolar. For the first time there is an individual with ossicles at asterion (SNPRC ID# 14270), and one with a wormian bone (SNPRC ID# 8291), both unknown pedigree hybrids (Figure 3).

Discussion

Previous work on the known hybrid baboons from the SNPRC colony has shown that these animals exhibit a suite of non-metric traits that indicate the breakdown in the coordination of early development (Ackermann 2007; Ackermann et al. 2006). F₁ animals in particular were shown to have a higher frequency of supernumerary teeth and unusual zygomatic sutures relative to purebreds; later generations of recombinants were not well-represented in the sample. Additionally, F₁ hybrids tended to show a pattern of expression for supernumerary teeth that differed from 'normal' trait variation (Ackermann et al. 2006). In humans, supernumerary teeth, like other rare non-metric traits, are usually single and unilateral (Hallgrímsson et al. 2005; Wang and Fan 2011), and are most often incisors (Ferres-Padro et al. 2009; Garvey et al. 1999). What was observed among the baboons, however, was distomolars that were often bilateral and typically mandibular. One baboon individual also had bilateral double canines, a trait that has also been observed in a baboon drawn from a wild hybrid zone (Ackermann et al. 2006; Freedman 1963).

The results presented here generally support the results of the 2006 study. Once again, we see an increased prevalence of supernumerary teeth in hybrids, including mandibular distomolars that are often bilateral. The frequency of atypical zygomatic sutures and residual metopic sutures is also high in hybrids. Although the frequency of supernumerary teeth in F₁ animals is lower than seen in the smaller 2006 sample (31% versus 50%), it nonetheless remains the highest frequency of all the compared groups. There are also a number of individuals with very unusual traits, including a B₁ female with bilateral reduced canines, two specimens with rotated teeth, and first occurrences (for this SNPRC sample) of individuals with ossicles at asterion and lambda. This is the first time we have found such traits in baboon hybrids, although rotated teeth are present in wildebeest hybrids (Ackermann et al. 2010) and in hominins (Ackermann 2010). Importantly, the observed dental and sutural non-metric traits persist into further generations, including F₂, B₁, and other recombinant generations.

Our understanding of how long hybrid skeletal traits persist in descendants, as we start to look at multigenerational recombinants, is poor, and the present study provides the first solid evidence that they persist beyond the F₁ generation. This has important implications for considering the fossil record. Traditional thinking was that the phenotypic effects of gene flow would disappear quite rapidly in populations that hybridized either in a once off event or for a limited time, due to backcrossing into the parental animals. However, we have very little quantitative evidence to speak to this issue. In fact, research on plants (Buerckle and Rieseberg 2008) has shown that 'new' variation that enters a system through gene flow can persist for a considerable amount of time in the population, even hundreds of generations, before the hybrid genome becomes stabilized; this persistence is especially marked if the traits are not directly linked to fitness. Presumably the phenotype would respond similarly, retaining signatures of hybridization long after the event, though perhaps in a manner more subtle than has been appreciated. Although it is difficult to assess the longevity of hybrid phenotypic traits in primates because of their long generation times, it is possible to gain some insight into this issue in multi-generational studies, especially if signatures of hybridization are indeed short-lived. The results presented here suggest that hybrid traits

persist for at least a few generations, and suggest that the presence of such traits in the human fossil record, rather than indicating F₁ animals, could provide evidence of earlier initial hybridization events.

Moreover, the observation of heterosis in the F₁ population for dental lamina activity, combined with the high levels of heritability for these hybrid traits in later generations, indicate that the initial heterosis was most likely due to epistatic interactions between loci rather than directional dominance at individual loci. Heritability (h^2) is a measure of the proportion of total variance that is due to additive genetic variance, not dominance genetic variance, so the segregation of additive gene effects in the population after hybridization show the ‘conversion’ of epistatic effects into heritable variation. This heritable variation can contribute to an evolutionary response to selection.

Although this study generally supports previous work, the fact that the frequency of supernumerary teeth in the purebreds is greater than that seen in the 2006 study (8% versus 3%) is unexpected. Permanent, full sized supernumerary teeth are uncommon in modern humans and other primates (Lavelle and Moore 1973; Rajab and Hamdan 2002), with multiple supernumerary teeth extremely rare in individuals with no other associated diseases or syndromes (e.g., cleft lip/palate, cleidocranial dysostosis, Gardner syndrome). Our best data come from studies of modern humans, which report the prevalence of supernumerary teeth at 0.5% to 5.3% in adults, with geographic variation in frequency ((Wang and Fan 2011) and references therein), making a frequency of 8% somewhat high for a ‘normal’ primate population, though certainly not of the magnitude seen in the hybrid sample. Why the purebreds would show a value above ~5% is unclear. One possible explanation is that increased frequencies of these traits result from inbreeding, which may be especially acute in a contained, captive colony. A few studies of captive-bred primates have attributed skeletal malformations to inbreeding, including anencephaly (Rawlins and Kessler 1983), polydactyly and syndactyly (Chalifoux and Elliot 1986), and limb malformations (Nakamichi et al. 1997). However, there is no direct evidence from wild or captive primates that inbred matings result in additional teeth (or other anomalies discussed herein) (see (Charpentier et al. 2007) and references therein). Eastern lowland gorillas, which do show these traits (Ackermann and Bishop 2010), may indeed be inbred (Prado-Martinez et al. 2013); however, the historical museum ($n = 78$) and extant genomic ($n = 3$) samples used in these studies are not directly comparable and sample different regions and time periods. We do know that for the mountain gorilla, in which the morphological evidence for inbreeding (i.e., strabismus and syndactyly) is well-known (Fossey 1983), there are no dental or sutural anomalies (Ackermann and Bishop 2010). But while the absence of good evidence for such traits in documented inbred primate populations suggests that this is not the cause of the increased frequency seen here, most compellingly, all but three of the purebred baboons with supernumerary teeth (and many of the hybrids as well) are the direct descendants of founding individuals. It is therefore unlikely that these animals are inbred. Finally, although we have focussed this discussion of inbreeding on the increased frequency of supernumerary teeth in the purebreds, it is important to remember that the hybrids have, in previous studies, shown evidence for increased size and variation (Ackermann 2007; Ackermann et al. 2006),

phenomena that are well-known to result from hybridization, not inbreeding (see discussion in (Ackermann 2010)).

A second possibility is that the relatively high proportion of supernumerary teeth is a founding effect, whereby colony founders with supernumerary teeth were sampled at a high frequency from the wild. In this case the trait would exist at a higher frequency than expected in their offspring, given the high heritability of this trait demonstrated here. This is difficult to test, as we do not have the skulls of the founding individuals, only those of descendants. However, this explanation would predict that supernumerary teeth would be present equally across the pedigree, rather than in higher frequency in hybrids versus purebreds as is seen here. Interestingly, closer examination of the pedigree information shows that 50% of the purebred individuals with supernumerary teeth are the direct descendants (either a child ($n = 9$) or grandchild ($n = 2$)) of a single male individual (SNPRC ID# 1X3162; marked with a * in Table 3) who was a founding male. Indeed, he sired more individuals with supernumerary teeth than seen for any other male or female in the sample (mean number of offspring with supernumerary teeth = 1.6; mode = 1). He did not father any of the hybrid offspring with supernumerary teeth. Importantly, while this chance event might offer some explanation for the higher frequency seen in the purebreds, again it would not explain the high frequency seen in the hybrids, who are not largely descended from one (or a few) individuals.

However, we believe that a more probable explanation for the high frequency of supernumerary teeth in purebreds is that this male individual (SNPRC ID# 1X3162), his descendants, and perhaps others in the ‘purebred’ group, are themselves actually unrecognized hybrids. Founding individuals for this colony were assigned to their respective taxa by researchers at the SNPRC based on external morphology. Many of the founder baboons were trapped in the Darajani region of southern Kenya (Maples and McKern 1967) and this region does contain some olive-yellow hybrid baboons (Jolly 1967). While it is not possible to demonstrate unambiguously, it is quite possible that some of the founding baboons were indeed hybrids of one degree or another. Certainly field studies at other sites have shown us that hybridization in the wild between olive and yellow baboons has a long history (Charpentier et al. 2012; Tung et al. 2008), and that hybrid individuals are both viable and reproductively active in the wild. For the founding male discussed above we have no pedigree information, nor skull. Although we do not know what he looked like, the skulls of many of his descendants look like ‘classic’ known hybrids, with bilateral mandibular distomolars, and even combinations of atypical traits (extra teeth, sutures) and size/robusticity (RRA, Personal observation). The only purebred individual with bilateral mandibular and maxillary distomolars is also his descendant. When you eliminate the descendants of this one male, only 4% of purebreds have supernumerary teeth, much more in line with expected frequencies of non-metric trait variation in ‘normal’ human populations and in line with the previous 2006 study. Importantly, as this individual case demonstrates, if some of the founding animals presumed to be purebred are in fact cryptic hybrids, it is reasonable to presume that the differences in frequencies of observed traits between actual ‘true’ purebreds and the SNPRC known hybrids would be even greater than the differences reported here. So while the ambiguous status of the presumed purebreds

from SNPRC is frustrating, it does not weaken the overall results but only suggests that the effect we observed may be an underestimate of the real effect on phenotype.

Finally, Ackermann (2010) provided some discussion of the potential genetic determinants of dental and sutural anomalies in hybrids, suggesting that they are likely to result from divergence in regions of the genome that code for regulatory genes, with the merger of these divergent genomes during hybridization resulting in perturbed morphology. The relatively high heritability of these traits in this mixed population raises the possibility of quantitative trait locus mapping for distomolar formation and the other nonmetric traits investigated here. This study also provides further insight into the developmental underpinnings of distomolars. Relatively little is known about the developmental/genetic mechanisms underlying supernumerary tooth formation (Wang and Fan 2011). Histological studies of tooth replacement in a series of animal models (see (Wang and Fan 2011) and references therein) indicate that successional teeth are initiated from the dental lamina, and therefore maintenance or reactivation of the dental lamina is essential for supernumerary tooth formation (Jarvinen et al. 2009; Tummers and Thesleff 2009). In developmental studies, it has been shown that increased canonical Wnt signalling induces supernumerary tooth formation (Wang and Fan 2011), while Sox2 may function to inhibit the formation of supernumerary teeth by inhibiting epithelial growth (Juuri et al. 2013). Visual examination of the supernumerary teeth here shows that the morphology of the first three molars in individuals with distomolars is normal, while the morphology of full-sized distomolars most often resembles the third molar (though this is variable). This pattern, as well as the statistical tests performed here, suggests that the supernumerary teeth result from a longer molar dental field (i.e., hyperactivity of the dental lamina), as opposed to finer subdivision of a normal sized dental field. This may be the result of an extension of tooth morphogenesis in these hybrids, possibly due to overall extension of growth, especially in males.

Conclusion

Our understanding of the persistence of phenotypic signatures of hybridization in populations that have undergone fairly short-term hybridization events is poor. We know that hybridization in plants results in signatures in the genome even after hundreds of generations, though how this translates to the mammalian or primate phenome is not known. The data presented here, though limited, suggest that non-metric traits that have previously been shown only in F_1 hybrids are expressed beyond the F_1 generation in baboons, as hybrids backcross into the parental species, and that this produces additive genetic variation in the mixed population that persists over generations. There are also previously unobserved, atypical and even novel dental and sutural trait variants in some backcrossed individuals. However, we still have little evidence to support the presence of a hybrid phenotype 200+ generations after a hybridization event (e.g., the Lagar Velho child; (Duarte et al. 1999)). Unfortunately, such deep multi-generational data simply do not exist. With this in mind, it is clear that continued multi-generational studies of primates, but also other mammals with shorter generation times, will further add to our understanding of the longevity of hybrid traits. We also need studies that focus on the effects that other processes (e.g., founding effects, inbreeding) might have on the skeleton, in order to better differentiate among causal

agents of atypical trait variation. Such studies will be essential in interpreting the fossil record of primate and human evolution.

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References

- Ackermann, RR. 284 NFS. Tinkering: the micro-evolution of development. Chichester: Wiley; 2007. Craniofacial variation and developmental divergence in primate and human evolution; p. 262–279.
- Ackermann RR. Phenotypic traits of primate hybrids: recognizing admixture in the fossil record. *Evolutionary Anthropology*. 2010; 19:258–270.
- Ackermann RR, Bishop JM. Morphological and molecular evidence reveals recent hybridization between gorilla taxa. *Evolution*. 2010; 64:271–290. [PubMed: 19804402]
- Ackermann RR, Brink JS, Vrahimis S, de Klerk B. Hybrid wildebeest (*Artiodactyla: Bovidae*) provide further evidence for shared signatures of admixture in mammalian crania. *S Afr J Sci*. 2010; 106(11/12):Art # 423.
- Ackermann RR, Rogers J, Cheverud J. Identifying the morphological signatures of hybridization in primate and human evolution. *J Hum Evol*. 2006; 51:632–645. [PubMed: 16962160]
- Almasy L, Blangero J. Multipoint quantitative trait linkage analysis in general pedigrees. *Am J Hum Genet*. 1998; 62:1198–1211. [PubMed: 9545414]
- Arnold, M. Reticulate Evolution and Humans: Origins and Ecology. Oxford University Press; 2009.
- Arnold M, Meyer A. Natural hybridization in primates: One evolutionary mechanism. *Zoology*. 2006; 109:261–276. [PubMed: 16945512]
- Batra P, Duggal R, Parkash H. Non-syndromic multiple supernumerary teeth transmitted as an autosomal dominant trait. *J Oral Pathol Med*. 2005; 34:621–625. [PubMed: 16202084]
- Buerckle CA, Rieseberg LH. The rate of genome stabilization in homoploid hybrid species. *Evolution*. 2008; 62:266–275. [PubMed: 18039323]
- Chalifoux LV, Elliot MW. Congenital anomalies in two neonatal tamarins (*Saguinus oedipus* and *Saguinus fuscicollis*). *J Med Primatol*. 1986; 15:329–340. [PubMed: 3027346]
- Charpentier M, Fontaine M, Cherel E, Renoult J, Jenkins T, Benoit L, Barthes N, Alberts S, Tung J. Genetic structure in a dynamic baboon hybrid zone corroborates behavioural observations in a hybrid population. *Molecular ecology*. 2012; 21(3):715–731. [PubMed: 21988698]
- Charpentier MJE, Widdig A, Alberts SC. Inbreeding depression in non-human primates: a historical review of methods used and empirical data. *Am J Primatol*. 2007; 69:1370–1386. [PubMed: 17486606]
- Duarte C, Maurício J, Pettitt PB, Souto P, Trinkaus E, Plicht Hvd, Zilhão J. The early Upper Paleolithic human skeleton from the Abrigo do Lagar Velho (Portugal) and modern human emergence in Iberia. *Proc Nat Acad Sci USA*. 1999; 96:7604–7609. [PubMed: 10377462]
- Ferres-Padro E, Prats-Armengol J, Ferres-Amat E. A descriptive study of 113 unerupted supernumerary teeth in 79 pediatric patients in Brcelona. *Med Oral Patol Oral Cir Bucal*. 2009; 14:E146–E162. [PubMed: 19242396]
- Fossey, D. Gorillas in the mist. Boston: Houghton Mifflin; 1983.
- Freedman L. A biometric study of *Papio cynocephalus* skulls from Northern Rhodesia and Nyasaland. *J of Mammalogy*. 1963; 44:24–43.

- Garvey M, Barry H, MB. Supernumerary teeth - An overview of classification, diagnosis and management. *J Can Dent Assoc.* 1999; 65:612–616. [PubMed: 10658390]
- Green RE, Krause J, Briggs AW, Maricic T, Stenzel U, Kircher M, Patterson N, Li H, Zhai W, Fritz MH-Y, et al. A Draft Sequence of the Neandertal Genome. *Science.* 2010; 328(5879):710–722. [PubMed: 20448178]
- Hallgrímsson B, Donnabháin BÓ, Blom DE, Lozada MC, Willmore KT. Why are rare traits unilaterally expressed?: trait frequency and unilateral expression for cranial nonmetric traits in humans. *Am J Phys Anthropol.* 2005; 127 In press.
- Jarvinen E, Tummers M, Thesleff I. The role of the dental lamina in mammalian tooth replacement. *J Exp Zool B Mol Dev Evol.* 2009; 312B:281–291. [PubMed: 19137538]
- Jernvall J, Thesleff I. Tooth shape formation and tooth renewal: evolving with the same signals. *Development.* 2012; 139:3487–3497. [PubMed: 22949612]
- Jolly, CJ. The evolution of the baboons. In: Vagtborg, H., editor. *The Baboon in Medical Research.* Vol. II. Austin, Texas: University of Texas Press; 1967. p. 23-50.
- Juuri E, Jussila M, Seidel K, Holmes S, Wu P, Richman J, Heikinheimo K, Chuong C-M, Arnold K, Hochedlinger K. Sox2 marks epithelial competence to generate teeth in mammals and reptiles. *Development.* 2013; 140(7):1424–1432. [PubMed: 23462476]
- Lavelle CL, Moore WJ. The incidence of agenesis and polygenesis in the primate dentition. *Am J Phys Anthropol.* 1973; 38:671–679. [PubMed: 4633574]
- Mailund T, Halager AE, Scally A. A new isolation with migration model along complete genomes infers very different divergence processes among closely related great ape species. *PLOS Genetics.* 2012; 8:e1003125. [PubMed: 23284294]
- Maples, W.; McKern, T. A preliminary report on classification of the Kenya baboon. In: Vagtborg, H., editor. *The Baboon in Medical Research.* Vol. II. Austin, Texas: University of Texas Press; 1967. p. 13-22.
- Meyer M, Kircher M, Gansauge M, Li H, Racimo F, Mallick S, Schraiber J, Jay F, Prüfer K, de Filippo C, et al. A high-coverage genome sequence from an archaic Denisovan individual. *Science.* 2012; 338:222–226. [PubMed: 22936568]
- Nakamichi M, Nobuhara H, Nobuhara T, Nakahashi M, Nigi H. Birth rate and mortality rate of infants with congenital malformations of the limbs in the Awajishima free-ranging group of Japanese monkeys (*Macaca fuscata*). *Am J of Primatol.* 1997; 42:225–234. [PubMed: 9209587]
- Prado-Martinez J, Sudmant PH, Kidd JM, Li H, Kelley JL, Lorente-Galdos B, Veeramah KR, Woerner AE, O'Connor TD, Santpere G. Great ape genetic diversity and population history. *Nature.* 2013
- Rajab LD, Hamdan MAM. Supernumerary teeth: review of the literature and a survey of 152 cases. *Int J Paediatric Dentistry.* 2002; 12:244–254.
- Rawlins RG, Kessler MJ. Congenital and hereditary anomalies in the rhesus monkeys (*Macaca mulatta*) of Cayo Santiago. *Teratology.* 1983; 28:169–174. [PubMed: 6648821]
- Reich D, Green R, Kircher M, Krause J, Patterson N, Durand E, Viola B, Briggs A, Stenzel U, Johnson P, et al. Genetic history of an archaic hominin group from Denisova Cave in Siberia. *Nature.* 2010; 468:1053–1060. [PubMed: 21179161]
- Sánchez-Quinto F, Botigué L, Civit S, Arenas C, Ávila-Arcos M, Bustamante C, Comas D, Lalueza-Fox C. North African Populations Carry the Signature of Admixture with Neandertals. *PLoS One.* 2012; 7(10):e47765. [PubMed: 23082212]
- Tosi A, Morales J, Melnick D. Comparison of Y chromosome and mtDNA phylogenies leads to unique inferences of macaque evolutionary history. *Mol Phy Evol.* 2000; 17:133–144.
- Tummers M, Thesleff I. The importance of signal pathway modulation in all aspects of tooth development. *J Exp Zool B Mol Dev Evol.* 2009; 312B:309–319. [PubMed: 19156667]
- Tung J, Charpentier M, Garfield D, Altmann J, Alberts S. Genetic evidence reveals temporal change in hybridization patterns in a wild baboon population. *Molecular Ecology.* 2008; 17(8):1998–2011. [PubMed: 18363664]
- Wang X-P, Fan J. Molecular genetics of supernumerary tooth formation. *Genesis.* 2011; 49:261–277. [PubMed: 21309064]

Figure 1. Supernumerary (SNPRC ID# 1X3997, F₁ male, left) and severely reduced (SNPRC ID# 1X4161, B₁ female, right) canines in hybrid baboons.

Figure 2. Rotated teeth in hybrid baboons. SNPRC ID# 14263 F₁ male, left; SNPRC ID# 9774, unknown pedigree hybrid female, right.

Figure 3. Cranial ossicle at asterion (SNPRC ID# 14270, unknown pedigree hybrid, left), and wormian bone at lambda (SNPRD ID# 8291, unknown pedigree hybrid, right)

Table 1

Examined samples, percentage ancestry (*anubis/cynocephalus*), sample sizes (*n*), and frequency of nonmetric traits for males and females.

Sample	Percentage ancestry (A/C)	Sex	n	Supernumerary permanent teeth	Tooth crowding	Atypical sutures	Zygomatic sutures	Rotated Teeth	Remnant Metopic suture
Purebreds	100	F	204	0.064	0.029	0.039	0.010	0.000	0.074
All Hybrids	Variable	F	187	0.091	0.053	0.075	0.016	0.005	0.112
F1 Hybrids (olive × yellow)	50/50	F	62	0.081	0.065	0.048	0.016	0.000	0.065
F2 Hybrids (F1 × F1)	50/50	F	4	0.000	0.250	0.250	0.250	0.000	0.000
F1F2 Hybrid (F1 × F2)	50/50	F	0	0.000	0.000	0.000	0.000	0.000	0.000
B1 Hybrids (F1 × olive)	75/25	F	43	0.023	0.070	0.047	0.000	0.000	0.116
B2 Hybrids (F1 × yellow)	25/75	F	3	0.333	0.000	0.000	0.000	0.000	0.333
B3 Hybrids (B1 × B1)	75/25	F	2	0.000	0.000	0.000	0.000	0.000	0.000
B4 Hybrids (B1 × olive)	87.5/12.5	F	5	0.200	0.200	0.000	0.000	0.000	0.000
B5 Hybrids (B1 × yellow)	12.5/87.5	F	1	0.000	0.000	0.000	0.000	0.000	0.000
B6 Hybrids (variable)	63/37	F	7	0.000	0.143	0.143	0.143	0.000	0.000
B7 Hybrids (F1B1×F2)	56/44	F	1	0.000	0.000	0.000	0.000	0.000	0.000
B8 Hybrids (B2×B1)	81/19	F	0	0.000	0.000	0.000	0.000	0.000	0.000
Unknown Hybrids	Incomplete	F	59	0.153	0.000	0.136	0.017	0.017	0.169
Chi-squared (Hybrids versus Purebreds)					3.386	5.685	0.646	-	3.323
p value					0.033	0.009	0.211	-	0.034
Purebreds	100	M	74	0.122	0.054	0.041	0.027	0.000	0.014
All Hybrids	Variable	M	111	0.171	0.063	0.117	0.018	0.009	0.045
F1 Hybrids (olive × yellow)	50/50	M	29	0.310	0.069	0.207	0.000	0.034	0.000
F2 Hybrids (F1 × F1)	50/50	M	4	0.000	0.250	0.000	0.000	0.000	0.250
F1F2 Hybrid (F1 × F2)	50/50	M	1	0.000	1.000	0.000	0.000	0.000	0.000
B1 Hybrids (F1 × olive)	75/25	M	17	0.118	0.000	0.000	0.000	0.000	0.000
B1 Hybrids (F1 × yellow)	25/75	M	0	0.000	0.000	0.000	0.000	0.000	0.000
B2 Hybrids (B1 × B1)	75/25	M	1	0.000	0.000	0.000	0.000	0.000	1.000

Sample	Percentage ancestry (A/C)	Sex	<i>n</i>	Supernumerary permanent teeth	Tooth crowding	Atypical sutures	Zygomatic sutures	Rotated Teeth	Remnant Metopic suture
B2 Hybrids (B1 × olive)	87.5/12.5	M	2	0.000	0.000	0.000	0.000	0.000	0.000
B2 Hybrids (B1 × yellow)	12.5/87.5	M	0	0.000	0.000	0.000	0.000	0.000	0.000
B3 Hybrids (variable)	63/37	M	10	0.100	0.200	0.000	0.000	0.000	0.000
B4 Hybrids (F1B1×F2)	56/44	M	2	0.000	0.000	0.000	0.000	0.000	0.000
B5 Hybrids (B2×B1)	81/19	M	1	0.000	0.000	0.000	0.000	0.000	0.000
Unknown Hybrids	Incomplete	M	46	0.109	0.043	0.130	0.043	0.000	0.087
Chi-squared (Hybrids versus Purebreds)				11.672	2.290	35.425	0.104	-	16.862
<i>p</i> -value				0.000	0.065	0.000	0.374	-	0.000

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Chi-square and *p*-values* given for tests of hybrids versus purebreds.

* Values shown in bold are significant at *p* < 0.05

Table 2

A table showing heritability estimates (h^2), probability values for the test of sex as a covariate ($p(\text{sex})$), and standard error ($\text{SE}(h^2)$) and probability values ($p(h^2)$) of the heritability estimate.

Trait	All supernumerary permanent teeth	Distomolars only	Tooth crowding	Atypical sutures	Zygomatic sutures	Rotated Teeth	Remnant Metopic suture
h^2	0.671	0.801	0.277	0.178	0.254	0.774	0.619
$p(\text{sex})$	0.014	0.019	0.025	0.178	0.069	0.666	0.000
$\text{SE}(h^2)$	0.229	0.254	0.106	0.122	0.237	0.274	0.282
$p(h^2)$	0.002	0.001	0.004	0.072	0.143	0.002	0.014

Table 3

Individuals with supernumerary teeth, sorted by status (A=*anubis*; other crosses as indicated in Table 1). The skull collection ID, original colony ID (SNPRC ID), sex, and percent ancestry information are provided. Teeth are marked as full sized (normal or near-normal size/shape) or reduced (typically less than 50% size); further detailed information on morphological variation is provided in notes. Groups of animals of the same status are shaded similarly to aid visualization. Descendants of male individual SNPRC ID# 1X3162 marked with an asterisk.

Collection ID	SNPRC ID	Sex	Status	% Known Ancestry	% <i>anubis</i>	% <i>cynocephalus</i>	Max L	Max R	Mand L	Mand R	Other	Notes
W255	1X3928	F	A	1	1	0	Full-sized	Reduced				Supplemental distomolars. Right distomolar less than half normal size (tuberculate?) but retains some occlusal morphology.
W300	1X3952	F	A	1	1	0	Full-sized	Full-sized				Supplemental distomolars. Normal morphology similar to M3s.
W386	1X4241	F	A	1	1	0	Reduced	Full-sized				Supplemental distomolars. Left distomolar less than half normal size (tuberculate?) but retains some occlusal morphology.
W609	9515	F	A	1	1	0					Premolar	Supplemental premolar. Supernumerary left maxillary p3, lingual and slightly between p3 and p4. Normal morphology, but rotated.
W658	10509	F	A	1	1	0			Full-sized			Supplemental distomolar. Left distomolar near normal size, slightly out of tooth row due to crowding from ascending ramus.
W795	9963	F	A	1	1	0	Full-sized	Full-sized				Supplemental distomolars. Near normal size/shape similar to M3s.
W916	10393	F	A	1	1	0			Full-sized	Full-sized		Supplemental distomolars. Normal morphology identical to M3s.
W964	8116	F	A	1	1	0			Full-sized	Full-sized		Supplemental distomolars. Normal morphology identical to

Collection ID	SNPRC ID	Sex	Status	% Known Ancestry	% <i>anubis</i>	% <i>cynocephalus</i>	Max L	Max R	Mand L	Mand R	Other	Notes
												- missing all teeth o - missing all teeth o - missing all teeth o - missing all teeth o Mann et al.
W436	6725	M	A	1	1	0				Reduced		M3s. Mandible pathological M3s. Mandible pathological M3s. Mandible pathological M3s. Mandible pathological Tuberculate distomolar. Barrel-shaped, approximately half the size of M3. Some occlusal morphology.
W586	6609	M	A	1	1	0	Full-sized					Supplemental distomolar. Near normal size/shape similar to M3.
W616	9326	M	A	1	1	0			Reduced	Full-sized		Supplemental distomolars. Left distomolar very small (approximately 1/3 size of typical m3) and tuberculate(?), but retaining some occlusal morphology.
W206*	1X4108	F	A	1	1	0	Full-sized					Supplemental distomolar. Distomolar slightly reduced but near size/ shape of M1.
W289*	1X4236	F	A	1	1	0	Full-sized	Reduced	Full-sized			Supplemental distomolars. Right maxillary barrel shaped and reduced to approximately half size; retains some occlusal morphology. Mandibular still in crypt - appears near normal.
W291*	1X2594	F	A	1	1	0	Full-sized		Full-sized			Supplemental distomolars. Normal shape size identical to M3s.
W568*	10099	F	A	1	1	0	Reduced				Premolar	Supplemental distomolar and premolar. Left maxillary distomolar reduced to approximately half size, but with cusp morphology resembling a premolar. Supernumerary premolar in tooth row between P3 and P4 (missing postmortem).

Collection ID	SNPRC ID	Sex	Status	% Known Ancestry	% <i>anubis</i>	% <i>cynocephalus</i>	Max L	Max R	Mand L	Mand R	Other	Notes
W579*	1X4866	F	A	1	1	0			Full-sized	Reduced		Supplemental distomolar/ Conical distomolar. Left distomolar slightly reduced (about the size of M1) but with near normal morphology; slightly out of alignment with tooth row (crowding). Right distomolar in line with tooth row and conical in shape.
W235*	6977	M	A	1	1	0	Reduced					Supplemental distomolar. Still in crypt; appears reduced in size.
W469*	8292	M	A	1	1	0	Full-sized	Full-sized				Supplemental distomolars. Identical to M3 in size/shape.
W490*	9976	M	A	1	1	0	Full-sized	Full-sized				Supplemental distomolars. Near normal size/shape.
W705*	14796	M	A	1	1	0					Premolar	Tuberculate premolars. Bilateral, tuberculate supernumerary maxillary premolars, located on lingual side of tooth row between p3 and p4. Left missing postmortem.
W872*	8601	M	A	1	1	0	Full-sized					Supplemental distomolar. Near normal size/shape.
W951*	14039	M	A	1	1	0	Reduced	Full-sized	Full-sized	Full-sized		Supplemental distomolars. Left maxillary one is in crypt, but looks small.
W890	9040	F	B1(AC)	1	0.75	0.25			Full-sized	Full-sized		Supplemental distomolars. Slightly reduced in size and barrel-shaped, but near normal with good multi-cusp occlusal morphology.
W356	10875	M	B1(AC)	1	0.75	0.25	Full-sized	Full-sized	Full-sized	Full-sized		Supplemental distomolars. Normal morphology similar to M3s.
W622	8615	M	B1(AC)	1	0.75	0.25				Reduced		Tuberculate distomolar. Barrel-shaped,

Collection ID	SNPRC ID	Sex	Status	% Known Ancestry	% <i>anubis</i>	% <i>cynocephalus</i>	Max L	Max R	Mand L	Mand R	Other	Notes
												approximately half-size with two simple cusps.
												approximately half-size with two simple cusps.
W267	1X2000	F	B1(CA)	1	0.25	0.75				Reduced		Tuberculate distomolar. Barrel-shaped, approximately half-size with simple cusps. Out of alignment with tooth row buccal to posterior portion of M3.
W853	12720	F	B2A	1	0.875	0.125				Full-sized		Supplemental distomolar. Still partially unerupted; appears near normal size/shape.
W666	15283	M	B3A	1	0.625	0.375			Full-sized			Supplemental distomolar. In crypt, but appears normal size/shape.
W124	1X1374	F	F1(AC)	1	0.5	0.5			Full-sized	Full-sized		Supplemental distomolars. Slightly atypical morphology but similar to M3s.
W343	1X4265	F	F1(AC)	1	0.5	0.5			Full-sized	Full-sized		Supplemental distomolars. Identical to M3s.
W419	1X4276	F	F1(AC)	1	0.5	0.5				Full-sized		Supplemental distomolar. Still in crypt, impacted. Appears to be somewhat reduced in size, but still with good multi-cusp occlusal morphology.
W781	12460	F	F1(AC)	1	0.5	0.5			Full-sized	Full-sized		Supplemental distomolars. Still in crypt but appear near normal size/shape.
W971	1X4243	F	F1(AC)	1	0.5	0.5			Full-sized	Full-sized		Supplemental distomolars. All at or near-normal size/shape.
W18	1X3475	M	F1(AC)	1	0.5	0.5			Full-sized	Full-sized		Supplemental distomolars. Like M3 in size/shape. Right M4 still partially erupting.
W68	1X3758	M	F1(AC)	1	0.5	0.5			Reduced	Reduced		Tuberculate distomolars. Single large cusp with small accessory cusp.
W97	1X3705	M	F1(AC)	1	0.5	0.5			Full-sized	Full-sized		Supplemental distomolars. Impacted right mandibular molar

two simple cusps.
two simple cusps.
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Collection ID	SNPRC ID	Sex	Status	% Known Ancestry	% <i>anubis</i>	% <i>cynocephalus</i>	Max L	Max R	Mand L	Mand R	Other	Notes
W107	1X3997	M	F1(AC)	1	0.5	0.5					Canine	might be slightly reduced in size (hard to see), b might be slightly reduced in size (hard to see), b might be slightly reduced in size (hard to see), b might be slightly reduced in size (hard to see), b
W135	1X3809	M	F1(AC)	1	0.5	0.5			Full-sized	Reduced		Supplemental distomolars. Left slightly reduced in size but with multiple cusps. Right tuberculate. Peglike lateral incisors.
W155	1X3837	M	F1(AC)	1	0.5	0.5			Full-sized	Full-sized		Supplemental distomolars. Look full size, but are in ascending ramus and hard to see.
W159	1X4331	M	F1(AC)	1	0.5	0.5	Full-sized	Full-sized	Full-sized	Full-sized		Supplemental distomolars. All at or near full size/shape.
W199	1X3144	M	F1(AC)	1	0.5	0.5			Reduced			Tuberculate distomolar. Oddly shaped - looks almost like one third of a tooth in terms of morphology.
W376	1X3796	M	F1(AC)	1	0.5	0.5	Full-sized	Full-sized	Full-sized	Full-sized		Supplemental distomolars. Identical in size/shape to M3s.
W683	17214	M	F2	1	0.5	0.50	Full-sized	Full-sized	Full-sized	Full-sized		Supplemental distomolars. Size/shape of typical M3s.
W685	14508	M	F2	1	0.5	0.50	Full-sized					Supplemental distomolar. Typical M3-like size/shape.
W313	14322	F	UX(AC)	0,375	0.25	0.125					Premolar	Supernumerary lower left P4 - conical with no cusp morphology, lingual to adult tooth.
W364	13715	F	UX(AC)	0,625	0.5	0.125	Full-sized	Full-sized				Supplemental distomolars. Still in crypt but look near normal size/shape.
W394	8919	F	UX(AC)	0,5	0.375	0.125	Full-sized	Full-sized	Full-sized	Full-sized		Supplemental distomolars. Slightly small but with multiple cusps.

Collection ID	SNPRC ID	Sex	Status	% Known Ancestry	% <i>anubis</i>	% <i>cynocephalus</i>	Max L	Max R	Mand L	Mand R	Other	Notes
W409	9774	F	UX(AC)	0,5	0,375	0,125		Full-sized				Supplemental distomolar. Near normal size/shape. Rotated and slightly out of alignment with tooth row.
W462	9791	F	UX(AC)	0,5	0,25	0,25			Full-sized	Full-sized		Supplemental distomolars. Still in crypt but appear normal.
W651	1X4593	F	UX(AC)	0,5	0,25	0,25	Reduced	Reduced				Supplemental distomolars. Left is reduced to about half-size, with multiple cusps but atypical looking morphology (especially occlusal outline). Right is tuberculate.
W707	12513	F	UX(AC)	0,625	0,375		0,25		Reduced			Conical distomolar - single cusp.
W930	10492	F	UX(AC)	0,75	0,5	0,25			Reduced			Conical distomolar - single cusp.
W983	10052	F	UX(AC)	0,5	0	0,5			Reduced			Distomolar. Reduced (possibly tuberculate?) in crypt (impacting).
W315	14081	M	UX(AC)	0,75	0,625	0,125	Reduced	Reduced				Distomolars. Extremely reduced (conical?) and fell out postmortem.
W327	7842	M	UX(AC)	0,5	0,25	0,25			Full-sized	Full-sized		Supplemental distomolars. Right slightly reduced in size but with multiple cusps; impacted.
W601	16330	M	UX(AC)	0,375	0,1562	0,2188				Full-sized		Supplemental distomolar. In crypt; normal size/shape.
W613	14758	M	UX(AC)	0,5	0,375	0,125		Full-sized				Supplemental distomolar. In crypt; normal size/shape.
W625	14275	M	UX(AC)	0,5	0,3125	0,1875	Full-sized					Supplemental distomolar. In crypt; normal size/shape.