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Identifying the morphological signatures of hybridization in primate and human evolution

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Abstract

Recent studies point to contact and possible admixture among contemporaneous hominin species during the Plio-Pleistocene. However, detection of hybridization in fossils—and especially fossil hominins—is contentious, and it is hindered in large part by our lack of understanding about how morphological hybridity is manifested in the primate skeleton. Here, we report on a study of known-pedigree, purebred yellow and olive baboons ($n = 112$) and their hybrids ($n = 57$), derived from the baboon colony of the Southwest Foundation for Biomedical Research. The hybrids were analyzed in two different groups: (1) $F_1 = olive \times yellow$ first-generation hybrids; (2) $B_1 = olive \times F_1$ backcross hybrids. Thirty-nine metric variables were tested for heterosis and dysgenesis. Nonmetric data were also collected from the crania. Results show that these primate hybrids are somewhat heterotic relative to their parental populations, are highly variable, and display novel phenotypes. These effects are most evident in the dentition and probably indicate the mixing of two separately coadapted genomes and the breakdown in the coordination of early development, despite the fact that these populations diverged fairly recently. Similar variation is also observed in museum samples drawn from natural hybrid zones. The results offer a strategy for detecting hybrid zones in the fossil record; implications for interpreting the hominin fossil record are discussed.
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Keywords: Hybrid phenotype; *Papio*; Yellow and olive baboons; Supernumerary teeth; Epigenesis; Heterosis; Pleistocene hominins

Introduction

The role played by natural hybridization in evolution is generally underappreciated. Strikingly, hybridization can facilitate evolutionary diversification in both plants and animals, including the evolution of ecological diversity, as well as the origin of new species (Arnold, 1997; Rieseberg, 1997; Arnold, 2004; Grant et al., 2005; Schwarz et al., 2005). Hybridization can allow populations to move into new ecological niches. This is especially true when a hybrid zone occurs in a region that is ecologically marginal for both parent populations, where the hybrids might find underutilized niches in which they are better ecologically adapted, enjoying equal or higher fitness than their parents (Seehausen, 2004). For example, Lewontin and Birch (1966) showed that hybridization can produce the increase in genetic variation that is necessary for range expansion and rapid evolution, resulting in physiological adaptation to extreme temperatures in flies; this new phenotype evolved even though the initial hybridization was disadvantageous (Lewontin and Birch, 1966). Hybridization can also lead to evolutionary innovation, especially via the production of novel genotypes/phenotypes (Anderson and Stebbins, 1954; Svärdson, 1970; Rieseberg et al., 2003). Introgressive hybridization occurs frequently among extant sympatric ancestral and descendent populations [such as wild taxa and their

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domesticates (Arnold, 2004)] and can result in the genetic enrichment of descendent populations, particularly when they have passed through a population bottleneck. Such hybridization also leads to a higher degree of genetic similarity (and by extension morphological similarity) among these populations than expected in a branching evolutionary model; this is important for thinking about the past, as in such situations an evolutionary web (rather than a diverging tree) might better represent phylogenetic relationships (Arnold, 1992).

Hybridization occurs frequently in nonhuman primates. For example, hybridization among primates in the wild has been reported for gibbons (Brockelman and Srikosamatara, 1984; Marshall and Sugardjito, 1986), tamarins (Peres et al., 1996), baboons (Phillips-Conroy and Jolly, 1986; Phillips-Conroy et al., 1991; Jolly et al., 1997; Alberts and Altmann, 2001), and macaques (Fooden, 1964; Bernstein, 1966; Supriatna, 1991; Froehlich and Supriatna, 1996; Bynum et al., 1997; Evans et al., 2001), among others. For some primates, hybridization at species contact zones is nearly ubiquitous (i.e., baboons and Sulawesi macaques). Hybridization occurs across a variety of taxonomic levels, and even primate genera with old evolutionary divergence times exchange migrants (Jolly et al., 1997; Jolly, 2001). Yet, despite such abundant evidence for hybridization in extant primates, the possibility and implications of frequent hybridization rarely enter the discourse on human evolution or shape hominin phylogenetic interpretations (see discussions in Jolly, 2001; Schillaci and Froehlich, 2001; Holliday, 2003; Schillaci et al., 2005). Although molecular and fossil evidence indicate that our evolutionary lineage is shallow by paleontological standards (Ruvolo, 1997; Haile-Selassie, 2001; Senut et al., 2001; Brunet et al., 2002), it is populated by a wide array of species, with most researchers currently accepting between ten and twenty distinct taxa. As pointed out by Jolly (2001), one nearly universal characteristic of this bushy hominin tree is its depiction of a pattern including branching and extinction but no reticulation.

Yet, a number of recent studies suggest that admixture between contemporaneous hominin species may have been more widespread than previously appreciated. Direct genetic evidence may indicate gene introgression among late Pliocene *Homo* in Africa (Stefansson et al., 2005), while indirect genetic evidence supports physical contact among Pleistocene *Homo* in Asia (Reed et al., 2004). Additionally, fossil evidence may indicate contact, and in some instances admixture, between early modern humans and their contemporaries in Asia (Swisher et al., 1996; Brown et al., 2004) and Europe (Zilhao and Trinkaus, 2002; Trinkaus, 2005). Most recently, hybridization between the earliest hominins and chimpanzee ancestors following their initial divergence has been proposed as an explanation for a wide range of locus-specific divergence times (Patterson et al., 2006). In the most prominent debate over hybridization in human evolution—that between Neandertals and modern humans—there has been movement in recent years towards interpretations that invoke a small amount of gene flow, which may have contributed only a little, if at all, to the modern gene pool (see discussions in Smith et al., 1989; Stringer, 2002; Holliday, 2003; Smith et al., 2005; Trinkaus, 2005). This movement of the discussion of the ''Neandertal problem'' into one that focuses on the relative degree of gene flow and the influence of population expansion places it firmly into the realm of ''general hybrid-zone theory'' (Jolly, 2001). Yet, the criteria for testing for hybridization based on skeletal data remain poorly delineated (Lieberman, 2003); it is largely unknown what hominin hybrids should look like (Tattersall and Schwartz, 1999). Clearly, there is a need to develop strategies for detecting morphological hybrids and hybrid zones in the fossil record.

Baboons, in particular, have recently been proposed as valuable analogues for considering issues of hybridization in human evolution (Jolly, 2001). One of the main reasons for this is that they probably resemble hominins—more than extant humans or apes do—in terms of their population structure and diversity (Jolly, 2001). Baboon morphs are genetically distinct and have a complex history of diversification and subsequent genetic exchange. This complexity includes the formation of hybrid zones wherever baboon allotaxa come into contact. Another point of analogy relates to evolutionary time depth, as the divergence of all extant baboons from their most recent common ancestor began circa 1.8 Ma, around the time of the emergence of the genus *Homo* [excluding *H. habilis* and *H. rudolfensis* (sensu Wood and Collard, 1999)]. In this light, the phylogenetic positioning of baboons as allotaxa that represent both biological subspecies and phylogenetic species may be analogous to Pleistocene hominin relationships, such as that between Neandertals and their contemporaries (Jolly, 2001).

Although extant primates make important analogues for considering these issues, relatively few studies have concentrated on the hybrid-primate phenotype, and even fewer on the hybrid-primate skeleton. Those that have focused on the skeleton have largely been concerned with the detection of body-size and size-related-shape differences among parental taxa and their hybrids, and they have shown that hybrid skeletons are often morphologically distinct from those of their parent species, being larger (heterosis) or smaller (dysgenesis) than expected. Heterosis, also known as ''hybrid vigor,'' reflects the degree of genetic differentiation among hybridizing populations and will not exist if these populations do not differ in gene frequencies or in dominance deviations. Negative heterosis, or dysgenesis, can occur when hybrids form between parental populations with separately coadapted gene complexes (Falconer and Mackay, 1996; Kohn et al., 2001), resulting in the breakdown of these complexes (Templeton, 1987), and is not generally expected when parental taxa share similar environments. Studies of heterosis and dysgenesis in nonhuman primates have focused on callitrichids (Cheverud et al., 1993; Kohn et al., 2001) and cercopithecoids (Smith and Scott, 1989; Schillaci et al., 2005). Cheverud et al. (1993) found heterosis in most dimensions of the skull of hybrids between saddle-back tamarin subspecies, though the amount and significance of heterosis varied depending on which pairs of subspecies were hybridizing. Similarly, Kohn et al. (2001) found heterosis in dimensions of the hybrid-tamarin postcranium. Smith and Scott (1989) described large body lengths and weights in crosses of rhesus macaques. Most recently, in their

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study of Sulawesi macaques, Schillaci et al. (2005) detected heterosis in hybrids for cranial-vault length and crown-rump length, but dysgenesis in body mass. To date, no study has focused on both quantitative and qualitative skeletal-trait variation in hybrid primates.

Here, we test whether primate hybrids differ morphologically from their parental populations by examining quantitative and qualitative trait variation in the crania of a known-pedigree sample of yellow and olive baboons drawn from a captive population. In particular, we test: (1) whether there are significant quantitative differences among purebred populations and their hybrids; (2) if so, whether hybrids show heterosis or dysgenesis (i.e., sizes larger or smaller than expectations); and (3) whether there are any nonmetric differences among these populations, especially increased qualitative morphological variation relative to purebreds, or novel morphologies. We also discuss parallel evidence for similar trait variation in natural baboon hybrids drawn from museum collections.

Materials and methods

Baboon phylogeny

Baboon diversity is represented by at least five major phena: chacma, Guinea, olive (anubis), yellow, and hamadryas baboons (Jolly, 1993, 2001; Newman et al., 2004). Whether these forms are distinctive at the specific (*Papio ursinus*, *P. papio*, *P. anubis*, *P. cynocephalus*, and *P. hamadryas*, respectively) or subspecific (within *P. hamadryas*) level is a matter of debate, as they freely form hybrid zones wherever the populations come into contact but are also readily diagnosable as distinct morphs (Jolly, 1993). The phylogenetic relationships among these five forms are not entirely clear. One study of mitochondrial DNA sequences drawn from individuals representing all five baboon morphs provides the following relationships: (chacma(Guinea(hamadryas(yellow + olive)))), along with estimates of divergence times, including the divergence of yellow and olive baboons at 160 ka and separation of the chacma baboon lineage from the rest of the baboons at approximately 1.8 Ma (Newman et al., 2004). Morphological evidence, including aspects of cranial morphology (Frost et al., 2003), as well as detailed features of hair structure and overall pelage (Jolly, 1993), suggests that yellow baboons may cluster more closely with southern chacma baboons, as opposed to the more northern olive baboons.

Data collection and analysis

Our sample derives from a captive population of known-pedigree baboons at the Southwest Foundation for Biomedical Research (SFBR), San Antonio, Texas. As these animals die of natural causes, their skulls are cleaned and curated in the Department of Anatomy and Neurobiology at Washington University. This sample is unique because the precise genealogical relationships among individuals are known; among other things, this allows us to distinguish between different kinds of hybrids. In this study, we examined the crania of 169 yellow baboons, olive baboons, their first-generation hybrids ($F_1 = olive \times yellow$), and backcrosses formed from the mating of first-generation hybrids with olive baboons ($B_1 = olive \times F_1$). These hybrids represent either crosses between recently diverged subspecies (i.e., 160,000 years) or possibly crosses between older lineages (i.e., divergence time of 500,000–1,000,000 years; see above).

Metric data are represented by 39 Euclidean distances, derived from three-dimensional coordinates of 36 unilateral and midline neurocranial and facial landmarks, which were chosen to represent the overall morphology of the cranium without redundancy (Table 1). These variables closely mirror those presented in an earlier study of tamarin hybrids (Cheverud et al., 1993). The trait mean values, standard deviations, and sample sizes for the olive baboons, yellow baboons, and F_1 and B_1 hybrids are given in Table 2.

Table 1
Landmarks recorded from baboon crania using the three-dimensional digitizer and the linear measurements derived from these landmarks*

Landmarks
1. Nasion (NA)
2. Nasale (NSL)
3. Anterior nasal spine (ANS)
4. Intradentale superior (IS)
5. Premaxillary-maxillary suture at the alveolus (PM)
6. Frontal-maxillary-nasal junction (FMN)
7. Zygomaxillare superior (ZS)
8. Zygomaxillare inferior (ZI)
9. Fronto-malare (FM)
10. Zygotemporal superior (ZTS)
11. Zygotemporal inferior (ZTI)
12. Maxillary tuberosity (MT)
13. Pterion (PT)
14. Asterion (AS)
15. Superior pterygo-palatine fossa (PPF)
16. Anterior petrous temporal (APET)
17. Jugular process (JP)
18. External auditory meatus (EAM)
19. Posterior nasal spine (PNS)
20. Inferior vomer-sphenoid junction (VS)
21. Basion (BA)
21. Opisthion (OPI)
23. Bregma (BR)
24. Lambda (LD)

Measurements		
1. IS-PM	14. BR-APET	27. MT-PNS
2. IS-NA	15. PT-FM	28. PNS-APET
3. IS-PNS	16. PT-APET	29. APET-BA
4. PM-ZS	17. PT-BA	30. APET-VS
5. PM-ZI	18. PT-EAM	31. BA-EAM
6. PM-MT	19. PT-ZTI	32. EAM-ZTI
7. NSL-NA	20. PT-PPF	33. ZTI-PPF
8. NSL-ZS	21. FM-ZS	34. LD-AS
9. NSL-ZI	22. FM-MT	35. BR-LD
10. NA-BR	23. ZS-ZI	36. OPI-LD
11. NA-FM	24. ZI-MT	37. PT-AS
12. NA-PNS	25. ZI-ZTI	38. JP-AS
13. BR-PT	26. ZI-PPF	39. BA-OPI

* Landmarks adapted from Cheverud et al. (1993). All unilateral measurements were taken on the left side of the cranium.

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Table 2
Sample sizes (n), means*, standard deviations (SD), and univariate probabilities (p) of intergroup differences in cranial measurements among all four groups and among pairs of taxa

Variable	Olive baboons			Yellow baboons			F_1 hybrids			B_1 hybrids			p	Pairwise comparison probabilities				
	n	Mean	SD	n	Mean	SD	n	Mean	SD	n	Mean	SD		OY	OF1	YF1	OB1	YB1
IS-PM	88	2.211	0.251	7	2.210	0.262	33	2.246	0.248	15	2.138	0.238	0.73	0.99	0.50	0.73	0.30	0.53
IS-NA	89	9.673	0.793	7	9.872	0.785	33	10.044	0.677	15	9.641	0.691	0.46	0.52	0.02	0.56	0.88	0.49
IS-PNS	89	8.086	0.582	7	8.452	0.549	33	8.269	0.583	15	8.025	0.483	0.80	0.11	0.13	0.45	0.70	0.08
PM-ZS	90	7.107	0.629	7	7.412	0.720	34	7.486	0.622	16	7.026	0.519	0.46	0.22	0.00	0.78	0.63	0.16
PM-ZI	90	6.089	0.523	7	6.275	0.509	34	6.261	0.495	16	5.952	0.403	0.95	0.36	0.10	0.94	0.32	0.12
PM-MT	80	6.537	0.418	7	6.690	0.371	28	6.657	0.489	15	6.381	0.444	0.84	0.35	0.21	0.87	0.19	0.13
NSL-NA	102	5.442	0.479	9	5.058	0.606	40	5.407	0.406	17	5.326	0.456	0.17	0.03	0.68	0.04	0.36	0.22
NSL-ZS	102	4.676	0.379	9	4.373	0.536	40	4.628	0.352	17	4.468	0.368	0.15	0.03	0.49	0.08	0.04	0.60
NSL-ZI	101	5.425	0.345	9	5.146	0.340	39	5.247	0.300	17	5.221	0.281	0.01	0.02	0.01	0.38	0.02	0.55
NA-BR	103	6.127	0.369	9	6.093	0.331	40	6.223	0.317	17	6.278	0.296	0.65	0.79	0.15	0.28	0.11	0.16
NA-FM	103	3.588	0.139	9	3.632	0.209	40	3.595	0.177	17	3.647	0.155	0.22	0.38	0.79	0.58	0.11	0.84
NA-PNS	99	5.333	0.327	8	5.584	0.348	38	5.522	0.315	17	5.582	0.264	0.03	0.04	0.00	0.62	0.00	0.99
BR-PT	103	4.541	0.296	9	4.650	0.366	40	4.677	0.374	17	4.752	0.300	0.24	0.30	0.02	0.85	0.01	0.45
BR-APET	102	6.106	0.237	9	6.007	0.256	40	6.231	0.319	17	6.236	0.202	0.08	0.24	0.01	0.06	0.04	0.02
PT-FM	103	2.524	0.277	9	2.284	0.294	40	2.446	0.241	17	2.413	0.172	0.07	0.02	0.12	0.09	0.11	0.17
PT-APET	102	4.180	0.215	9	4.030	0.162	40	4.149	0.284	17	4.181	0.177	0.20	0.04	0.49	0.23	0.98	0.04
PT-BA	86	5.651	0.209	9	5.519	0.214	32	5.606	0.282	17	5.733	0.248	0.04	0.08	0.36	0.40	0.15	0.04
PT-EAM	103	3.818	0.253	9	3.908	0.206	40	3.818	0.279	17	3.763	0.246	0.53	0.30	1.00	0.37	0.40	0.14
PT-ZTI	99	3.997	0.298	9	3.778	0.299	39	3.914	0.286	17	3.789	0.277	0.09	0.04	0.14	0.21	0.01	0.93
PT-PPF	103	3.395	0.293	9	3.300	0.355	40	3.415	0.311	17	3.359	0.216	0.60	0.36	0.71	0.33	0.63	0.60
FM-ZS	103	2.103	0.170	9	2.129	0.189	40	2.096	0.136	17	2.215	0.208	0.26	0.67	0.80	0.54	0.02	0.31
FM-MT	80	5.677	0.384	8	5.962	0.361	29	5.975	0.364	16	5.924	0.311	0.06	0.05	0.00	0.93	0.02	0.79
ZS-ZI	102	3.084	0.264	9	3.099	0.326	39	3.088	0.202	17	3.118	0.235	1.00	0.87	0.94	0.90	0.62	0.87
ZI-MT	80	2.866	0.288	8	2.857	0.236	29	2.955	0.286	16	2.865	0.161	0.68	0.94	0.15	0.38	0.99	0.92
ZI-ZTI	99	3.300	0.258	9	3.383	0.209	39	3.360	0.260	17	3.232	0.220	0.43	0.35	0.22	0.81	0.31	0.10
ZI-PPF	102	2.744	0.161	9	2.581	0.182	39	2.608	0.156	17	2.648	0.214	0.01	0.01	0.00	0.66	0.03	0.43
MT-PNS	80	1.913	0.200	8	1.852	0.178	29	1.889	0.211	16	1.863	0.202	0.52	0.40	0.57	0.65	0.36	0.90
PNS-APET	99	2.517	0.176	8	2.389	0.248	38	2.434	0.243	17	2.398	0.167	0.07	0.06	0.03	0.64	0.01	0.92
APET-BA	86	2.179	0.146	9	2.044	0.140	32	2.103	0.175	17	2.222	0.141	0.07	0.01	0.02	0.36	0.27	0.01
APET-VS	102	0.923	0.126	9	0.828	0.148	40	0.932	0.119	17	0.915	0.130	0.37	0.03	0.71	0.03	0.79	0.14
BA-EAM	86	4.395	0.187	9	4.164	0.198	32	4.388	0.226	17	4.353	0.116	0.26	0.00	0.86	0.01	0.37	0.01
EAM-ZTI	99	3.341	0.229	9	3.217	0.279	39	3.318	0.220	17	3.343	0.228	0.74	0.13	0.59	0.24	0.98	0.23
ZTI-PPF	99	3.786	0.203	9	3.705	0.195	39	3.792	0.193	17	3.649	0.179	0.21	0.25	0.87	0.23	0.01	0.47
LD-AS	103	3.902	0.285	9	3.581	0.348	40	3.804	0.375	17	3.841	0.395	0.10	0.00	0.09	0.11	0.44	0.11
BR-LD	103	4.641	0.487	9	4.831	0.511	40	4.716	0.415	17	4.794	0.449	0.53	0.27	0.39	0.48	0.23	0.85
OPI-LD	103	4.311	0.296	9	4.150	0.238	40	4.474	0.367	17	4.363	0.305	0.15	0.12	0.01	0.02	0.50	0.08
PT-AS	103	5.425	0.342	9	5.446	0.337	40	5.383	0.314	17	5.350	0.331	0.74	0.86	0.50	0.59	0.40	0.49
JP-AS	95	3.462	0.245	9	3.426	0.282	36	3.522	0.331	17	3.467	0.265	0.93	0.68	0.26	0.43	0.93	0.72
BA-OPI	71	2.015	0.187	7	1.901	0.198	24	2.002	0.171	12	1.938	0.172	0.73	0.13	0.76	0.19	0.19	0.67

* Measurements are in centimeters.

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A multivariate analysis of variance (MANOVA) including all traits indicates statistically significant morphological differences between the sexes ($p < 0.0001$). Males are larger than females for all 39 traits. Univariate analysis of variance (ANOVA) indicates that 38 of the 39 traits (excepting BR-LD) are significantly different between males and females at the $p = 0.01$ level of significance. Because of these differences, all traits were corrected to the female mean prior to the analysis [adjusted male value = original male value + (female mean − male mean)] in order to eliminate the potentially confounding effect of sexual dimorphism.

To test for significant quantitative differences among the four samples (yellow baboons, olive baboons, F_1 hybrids, B_1 hybrids), a MANOVA was performed on these sex-adjusted variables. Following this procedure, each of the 39 measurements was analyzed individually using ANOVA to test for differences between the four groups. For each of the 39 variables, the means of the purebred groups were then compared to one another and to the means of each hybrid sample using *t*-tests to assess the significance of observed differences. Following these multivariate and univariate comparisons, each hybrid sample was then tested for heterosis by judging it relative to an expected value; heterosis was then measured as the difference between the hybrid and expected values (Turner and Young, 1969). The expected value for the F_1 hybrids is the midparental value (PO) of the means of the pooled-sex olive and yellow purebreds. Assuming no dominance, the expected value for the backcross with the olive baboons (B_1) is half the distance between PO and the olive baboon value (Falconer, 1981; Lynch and Walsh, 1998). If the hybrids are significantly larger than their expected value, the cross exhibits heterosis, while significantly smaller values indicate negative heterosis (dysgenesis). The statistical significance of heterosis was evaluated using a *t*-test, where the standard error of the expected value is half the square root of the sum of the sampling variances obtained from the parental samples. Because of small sample sizes, our males and females were pooled in these analyses of heterosis. In order to test whether this pooling affected our results—as heterosis is not always expressed to the same magnitude in males and females—we also tested for a sex-by-taxon interaction. Further details on these methods can be found in Cheverud et al. (1993) and Kohn et al. (2001).

To analyze qualitative trait variation, individual crania were examined and scored for the presence of a suite of cranial nonmetric traits. Of these, only supernumerary teeth, extra sutures or ossicles in the zygomaxillary region, dental crowding, residual metopic sutures, and large overall size and associated "ruggedness" were present in the sample (variables described further in Table 3; other traits examined but not present include: ossicles at lambda and asterion, bregmatic bones, coronal ossicles, epipteric bones, and parietal-notch bones). "Ruggedness," while subjective, is included in the study both because we would expect a more "robust" morphology in hybrids (especially males) due to heterosis and because a similar morphology was observed in museum specimens; examples of different expressions of this trait can be seen in Figures 2 and 6. Samples were divided by sex, in order to test whether males and females show different hybrid morphologies. Differences between the purebred and hybrid baboons were tested for statistical significance with a chi-square test. We also performed MANOVAs to test for a relationship between the presence of heterosis and nonmetric traits.

Table 3
Descriptions of cranial nonmetric traits identified in the sample

Trait	Description
Supernumerary teeth	Teeth additional to the normal complement, either full-sized or reduced in size; here, with one exception, all extra teeth are molars within the tooth row
Tooth crowding	A misalignment of the tooth row, especially in the region of the premolars
Zygomaxillary suture abnormalities	Extra suture or ossicle in the malar; this suture generally runs perpendicular to the zygomaxillary suture
Extreme facial size/robustness	Extreme size and ruggedness, especially in the snout, causing a "boxy" appearance
Residual metopic suture	Tiny remnant of the suture on the frontal, superior to nasion

Results

Quantitative differences among purebred populations and their hybrids are significant (MANOVA; $n = 95$; 74 cases deleted due to missing data; $p = 0.001$). Additionally, univariate tests indicate significant differences among the four groups for 10% of the traits, whereas only 5% are expected to be significant by chance (Table 2). The purebred olive and yellow baboons are significantly different from each other for 33% of the traits. The F_1 hybrid values are significantly larger than both purebred populations for one trait (OPI-LD), while they are significantly larger than olive baboons for six traits (ISNA, PM-ZS, NA-PNS, BR-PT, BR-APET, FM-MT) and larger than yellow baboons for three traits (NSL-NA, APET-VS, BAEAM). The F_1 hybrids are also significantly smaller than olive baboons for four traits (NSL-ZI, ZI-PPF, PNS-APET, APET-BA). The B_1 hybrids are significantly larger than both purebred populations for one trait (BR-APET), while they are significantly larger than olive baboons for four traits (NA-PNS, BR-PT, FM-ZS, FM-MT) and larger than yellow baboons for four traits (PT-APET, PT-BA, APET-BA, BAEAM). The B_1 hybrids are also significantly smaller than olive baboons for six traits (NSL-ZS, NSL-ZI, PT-ZTI, ZI-PPF, PNS-APET, ZTI-PPF).

Both hybrid samples exhibit heterosis. Heterosis in F_1 hybrids is displayed in 28 traits (72%) and is significant in three traits (8%) at the $p = 0.05$ level (BA-EAM, BR-APET, OPI-LD; Fig. 1; Table 4); there is no significant dysgenesis. In the B_1 generation, heterosis is displayed in 19 traits (49%) and is significant in seven traits (18%) at the $p = 0.05$ level (NA-BR, NA-PNS, BR-PT, BR-APET, FM-ZS, FM-MT, APET-BA; Fig. 1; Table 4). There is no substantial dysgenesis in the B_1 generation. Although two traits are significantly

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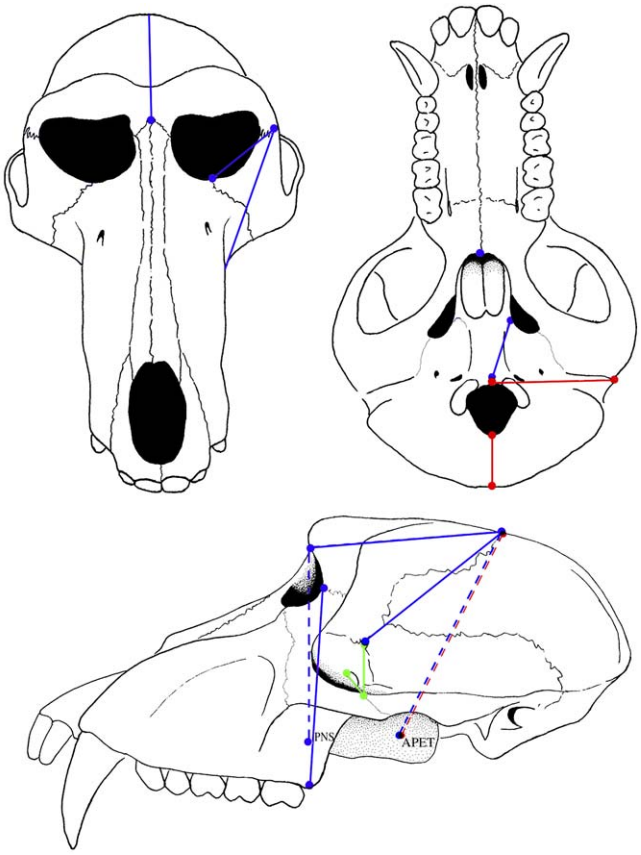

Fig. 1. Variables that show significant heterosis or dysgenesis in hybrids: red, F_1 heterosis; blue, B_1 heterosis; green, B_1 dysgenesis.

Table 4
Heterosis values for F_1 (*olive* × *yellow*) and B_1 (F_1 × *olive*) hybrids*

Trait	F_1		B_1	
	Heterosis	*t*-value	Heterosis	*t*-value
IS-PM	0.035	0.52	−0.073	−1.07
IS-NA	0.272	1.40	−0.082	−0.41
IS-PNS	−0.001	0.00	−0.153	−1.10
PM-ZS	0.226	1.29	−0.157	−1.04
PM-ZI	0.079	0.60	−0.183	−1.58
PM-MT	0.044	0.37	−0.194	−1.58
NSL-NA	0.157	1.29	−0.020	−0.16
NSL-ZS	0.103	0.97	−0.132	−1.30
NSL-ZI	−0.039	−0.51	−0.134	−1.75
NA-BR	0.112	1.46	**0.159**	**2.00**
NA-FM	−0.015	−0.33	0.048	1.13
NA-PNS	0.064	0.78	**0.187**	**2.55**
BR-PT	0.081	0.95	**0.183**	**2.27**
BR-APET	**0.174**	**2.60**	**0.155**	**2.81**
PT-FM	0.043	0.67	−0.051	−1.00
PT-APET	0.045	0.84	0.039	0.84
PT-BA	0.022	0.35	0.115	1.80
PT-EAM	−0.045	−0.78	−0.078	−1.23
PT-ZTI	0.026	0.38	**−0.154**	**−2.10**
PT-PPF	0.068	0.87	−0.012	−0.19
FM-ZS	−0.020	−0.52	**0.105**	**1.96**
FM-MT	0.155	1.63	**0.176**	**2.01**
ZS-ZI	−0.004	−0.06	0.030	0.47
ZI-MT	0.094	1.35	0.002	0.04
ZI-ZTI	0.019	0.34	−0.089	−1.53
ZI-PPF	−0.055	−1.37	−0.055	−1.01
MT-PNS	0.006	0.12	−0.035	−0.65
PNS-APET	−0.019	−0.32	−0.087	−1.85
APET-BA	−0.009	−0.23	**0.077**	**2.06**
APET-VS	0.056	1.78	0.015	0.44
BA-EAM	**0.108**	**2.05**	0.015	0.44
EAM-ZTI	0.039	0.66	0.033	0.53
ZTI-PPF	0.047	1.02	**−0.117**	**−2.45**
LD-AS	0.062	0.74	0.019	0.19
BR-LD	−0.020	−0.18	0.105	0.88
OPI-LD	**0.244**	**3.40**	0.092	1.18
PT-AS	−0.053	−0.69	−0.081	−0.93
JP-AS	0.078	1.06	0.014	0.20
BA-OPI	0.044	0.84	−0.048	−0.88

* F_1 heterosis is the difference between the mean of the hybrids and the value halfway between the means of the olive and yellow baboons. B_1 heterosis is the difference between the hybrid mean and the value halfway between the midparental value and the olive baboon value. Significant heterosis (or dysgenesis) values at $p = 0.05$ are shown in bold.

smaller than expected at $p = 0.05$ (PT-ZTI, ZTI-PPF), and two more at $0.05 < p < 0.10$, this frequency is what we would expect by chance. A MANOVA including the heterotic variables indicates no statistically significant sex-by-taxon interaction ($p = 0.393$). Post-hoc power analyses indicate that the samples are of reasonable size for detecting differences, with 80% power to detect a difference of 0.4 standard deviations. Note that the variables that are heterotic in the two hybrid groups differ, with heterosis in the B_1 hybrids concentrated in measurements in the middle portion of the cranium, including the anterior neurocranium and upper face, while F_1 hybrids display heterosis primarily in inferior regions, especially the basicranium.

Qualitative differences also exist among the hybrid and purebred populations (Figs. 2–4). The incidence of both supernumerary teeth and large, rugged facial morphology is higher than expected in the hybrid males, while the incidence of unusual zygomaxillary sutures (Fig. 4) is higher in the hybrid females (Table 5). All of the supernumerary teeth are permanent teeth. With one exception, all of the supernumerary teeth are additional molars in the tooth row beyond the third molar (Table 6). Such distomolars result from either a long alveolus during dental lamina formation or missegmentation of the lamina in the molar region. The majority of the supernumerary teeth are in hybrids, all from the F_1 generation. Nine of the ten F_1 hybrids with supernumerary teeth are male. Eight of the ten hybrid individuals with extra teeth have bilateral mandibular molars, 71% of which are full-sized molars. Two individuals with full-sized bilateral mandibular molars also have full-sized bilateral maxillary molars. Supernumerary teeth exist in three of the purebreds, but their overall incidence is low (<5%), and they differ in expression from the hybrid teeth, being maxillary fourth molars only, with two reduced in size and unilaterally expressed. One of the F_1 hybrid male baboons displays bilateral, supernumerary, full-sized permanent canines (Fig. 5), a novel morphological trait not seen in any of the other SFBR specimens. There is no significant relationship between the magnitude of heterosis displayed in those variables identified as heterotic and the presence of extra teeth (MANOVA; $n = 45$; 12 cases deleted due to missing data;

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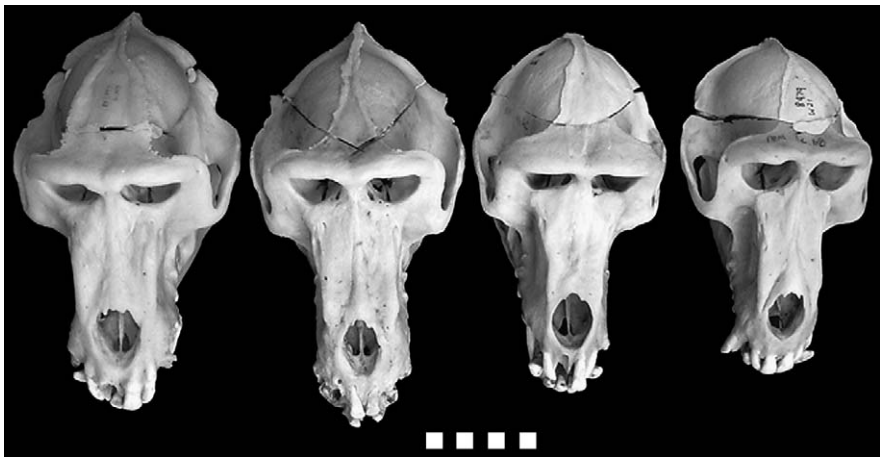

Fig. 2. Male SFBR purebreds and hybrids, from left to right: F_1 hybrid W107, F_1 hybrid W135, yellow purebred W6, olive purebred W21. The F_1 hybrid males shown here exhibit the ruggedness and boxy facial morphology seen in many hybrids, possibly associated with their overall large size.

$p = 0.290$) or unusual sutures ($p = 0.784$) in the hybrids. However, univariate tests do indicate a significant relationship between two variables (OPI-BA and FM-MT) and the presence of extra teeth; the latter variable likely reflects an elongation of the tooth row.

Discussion

Yellow and olive baboons diverged more than 160,000 years ago (Newman et al., 2004), and the first goal of this study was to test for heterosis in their hybrids. In populations that are

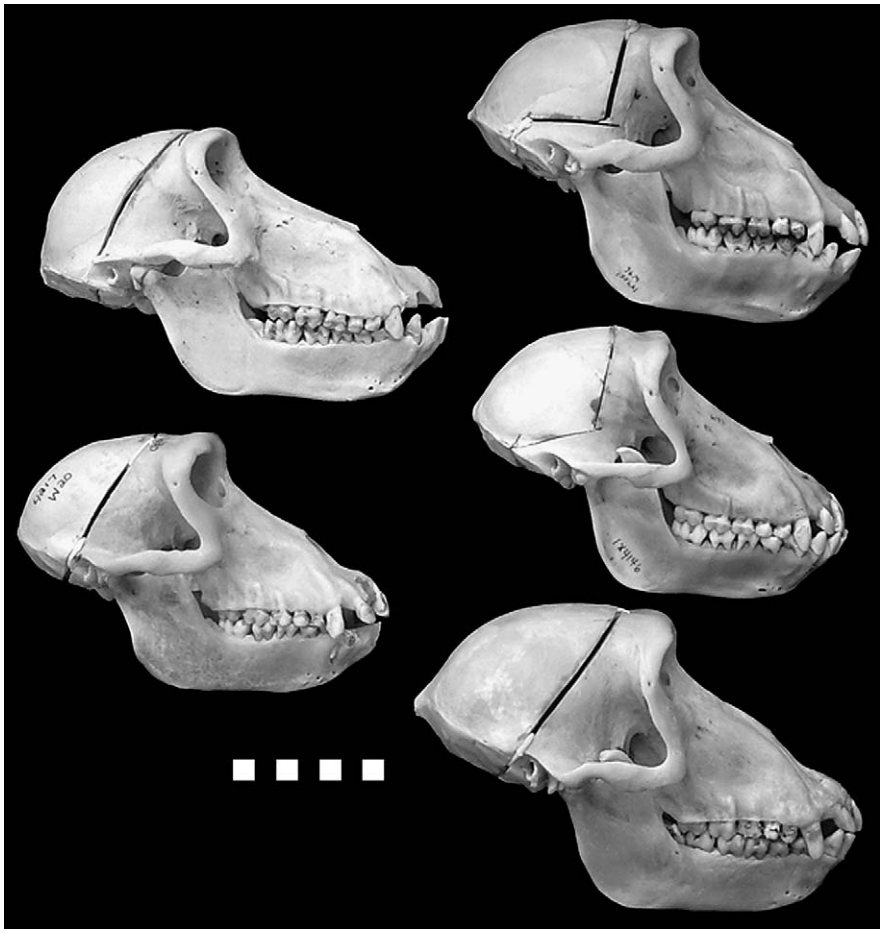

Fig. 3. Female SFBR purebreds and hybrids, clockwise from top left: olive purebred W88, F_1 hybrid W96, F_1 hybrid W93, F_1 hybrid W124, yellow purebred W20. Hybrid specimens were chosen to illustrate extreme variation in size and morphology; the largest hybrid (W124) is the only female hybrid in this sample with supernumerary teeth (fourth mandibular molars).

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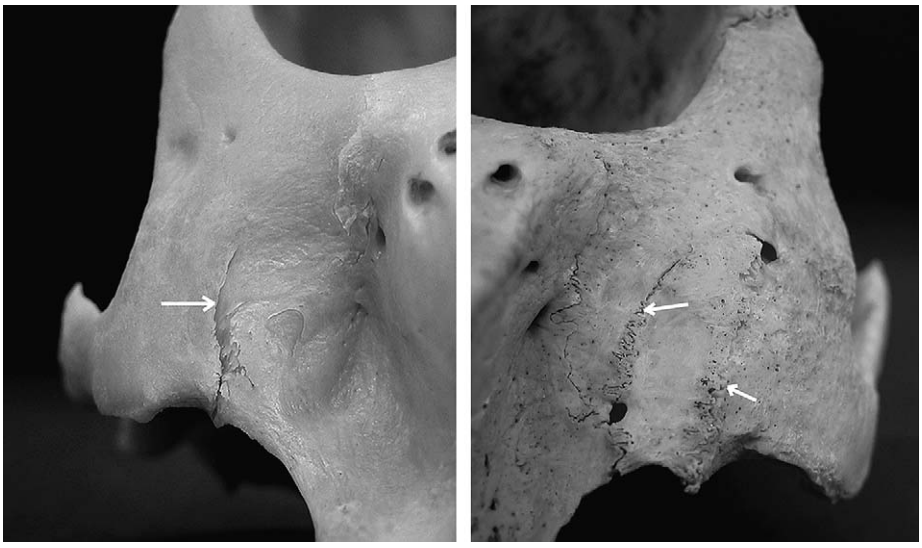

Fig. 4. Unusual zygomaxillary sutures, indicated by arrows, in captive hybrid specimens W127 (left) and W15 (right).

regularly exchanging migrants, where differences among them are due to simple additive effects and small differences in gene frequencies, hybrid morphology will not differ from the midpoint of the parent populations. In those that rarely exchange migrants, hybrids will deviate significantly from this midparental value (Cheverud et al., 1993), as the crossing of isolated strains restores the heterozygosity lost due to genetic drift or selective replacement in the separated gene pools; this results in heterosis (Falconer, 1981; Falconer and Mackay, 1996). Our continuous-trait data show that the hybrid and parental baboon samples are significantly different from each other, and that significant heterosis is present and clearly detectable in the skulls of the hybrids. However, this heterosis was not expressed broadly; it does not affect the majority of traits, nor does it result in hybrids that are significantly larger than both parental means. These levels of heterosis are much lower than those seen in a comparable study of tamarin craniofacial morphology, where, for example, crosses of *Saguinus fuscicollis illigeri* and *S. f. lagonotus* resulted in heterosis across all traits (significant in 56%) and hybrid values were sometimes significantly larger than both parental means (Cheverud et al., 1993). This suggests that, while there are real differences between the parental baboon populations for traits affecting craniofacial morphology, these lineages have not undergone substantial differentiation in the genetic basis of craniofacial development. Yet, the presence of relatively minor heterosis also indicates that the parental taxa remain genetically distinct, although they have not diverged sufficiently to cause recognizable dysgenesis in the skull. The rate of gene flow between these populations (Alberts and Altmann, 2001) may be sufficient to produce this pattern (i.e., they may be exchanging migrants at an evolutionarily significant rate), or dysgenesis in primates may require greater differentiation than that which has accumulated over this period of time.

Yet, these same hybrids show very high levels of nonmetric dental anomalies; it is striking that 50% of F_1 hybrid males have at least one supernumerary tooth, the bulk of which are mandibular, and 90% of these are bilaterally expressed. Permanent, full-sized supernumerary teeth are uncommon in modern humans and other primates, generally with an incidence below 5% (Lavelle and Moore, 1973; Rajab and Hamdan, 2002). Bilateral expression of rare nonmetric traits

Table 5
Frequency of nonmetric traits, with chi-square values* for purebred versus hybrid comparisons

Sample	Sex	*n*	Supernumerary teeth	Tooth crowding	Zygomaxillary suture abnormalities	Facial robustness	Residual metopic suture
Olive purebreds	F	73	0.027	0.233	0.068	0.014	0.219
Yellow purebreds	F	8	0.000	0.125	0.000	0.000	0.000
F_1 hybrids (olive × yellow)	F	22	0.045	0.182	0.273	0.091	0.318
B_1 hybrids (F_1 × olive)	F	10	0.000	0.200	0.200	0.000	0.300
Chi-square (purebreds vs. hybrids)			0.038	0.165	**7.986**	2.233	1.712
Olive purebreds	M	30	0.033	0.267	0.167	0.067	0.000
Yellow purebreds	M	1	0.000	1.000	0.000	0.000	0.000
F_1 hybrids (olive × yellow)	M	18	0.500	0.389	0.222	0.389	0.056
B_1 hybrids (F_1 × olive)	M	7	0.000	0.143	0.143	0.000	0.000
Chi-square (purebreds vs. hybrids)			**10.134**	0.058	0.141	**4.764**	1.263

* Significant chi-square values ($p < 0.05$) are shown in bold.

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Table 6
Supernumerary fourth molars

ID	Taxon	Sex	Left maxillary	Right maxillary	Left mandibular	Right mandibular	Comments
W136	Olive	F	Full-sized	Full-sized	—	—	
W206	Olive	F	Reduced*	—	—	—	
W235	Olive	M	Reduced?	—	—	—	Unerupted and difficult to evaluate
W124	F1 hybrid	F	—	—	Full-sized	Full-sized	
W114	F1 hybrid	M	—	—	Reduced	Full-sized	
W135	F1 hybrid	M	—	—	Reduced	Reduced	
W155	F1 hybrid	M	—	—	Full-sized	Full-sized	Both unerupted
W159	F1 hybrid	M	Full-sized	Full-sized	Full-sized	Full-sized	Right mandibular molar has reduced hypoconulid
W18	F1 hybrid	M	—	—	Full-sized	Full-sized	
W199	F1 hybrid	M	—	—	Reduced	—	
W68	F1 hybrid	M	—	—	Reduced	Reduced	
W97	F1 hybrid	M	Full-sized	Full-sized	Full-sized	Reduced	Occlusal surface of right mandibular molar is turned anteriorly

* "Reduced" refers to supernumerary teeth that are abnormally shaped and smaller in size than usual; these teeth all retain some cusp morphology.

is even less common (Hallgrímsson et al., 2005). Additionally, while supernumerary teeth do occur in the purebreds, it is important to note that the frequency is low and the pattern is consistent with "normal" nonmetric variation in primates, where most supernumerary teeth are anterior (incisors) and maxillary (Lavelle and Moore, 1973; Rajab and Hamdan, 2002).

Canine duplication is highly unusual; the kind seen here is usually ascribed to a split in the original germinal disc for the tooth. To our knowledge, such an anomaly has only been reported once in the primate literature, in a baboon specimen collected from southern Malawi, in a region of known sympatry between chacma and yellow baboons (Freedman, 1963; Fig. 5). This individual has previously been described as a natural hybrid (Freedman, 1963; Hayes et al., 1990). Other specimens from this geographic region display dental anomalies, including bilateral full-sized fourth molars, as well as dental and bone pathologies (Table 7; Fig. 6). Three of these individuals have cranial dimensions much larger than midpoint values of yellow and chacma baboons drawn from nearby regions (Freedman, 1955, 1957, 1963), suggesting heterosis, or at least a wide range of size variation in the region (see Fig. 6). Specimen TM 4078 also has the extreme size and "rugged" morphology seen in a number of the captive male F_1 hybrid baboons. It has been argued that the unusual morphology of TM 4078 resulted in part from spending much of its adult life in a zoo (Freedman, 1955). But the other museum animals were wild-shot, suggesting that the same suite of unusual morphologies observed in the captive hybrids also occurs in natural baboon hybrid zones. This represents corroborating evidence for such traits in a wild population, and shows that the nonmetric anomalies observed in our captive population are not likely to be the result of a founder effect or other special circumstances.

Taken together, the nonmetric data from the captive and wild baboon hybrids demonstrate a high frequency of unusual dental and sutural anomalies, including the presence of a novel

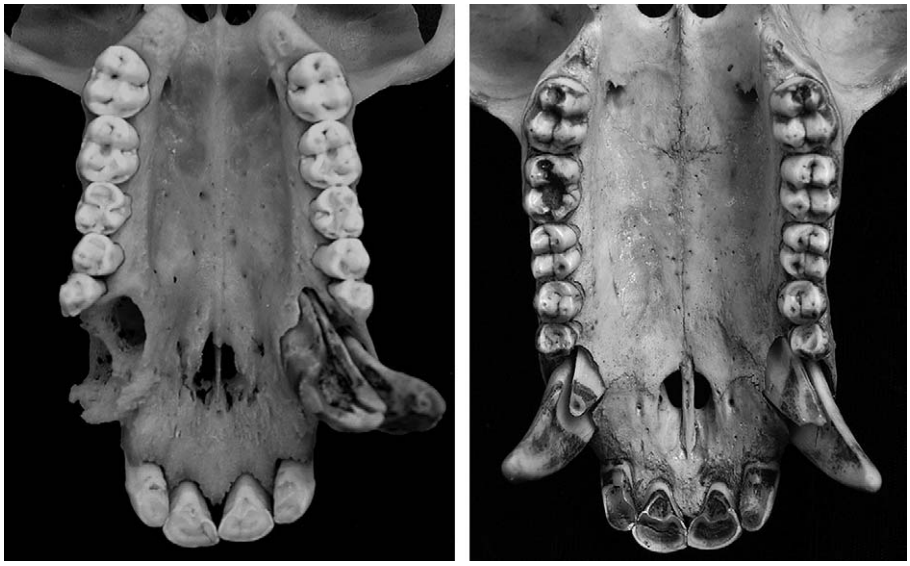

Fig. 5. Bilateral maxillary canines in (left) W107, a captive male F_1 hybrid, and (right) KM 11541, a wild-caught male baboon hybrid.

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Table 7
Museum natural hybrid specimens

Accession number	Date of collection	Place of curation	Locality	Description of anomaly
KM 11541	1946	Amathole Museum, King William's Town	Likabula, Mulanje (=Mlange) Mountains, southern Nyasaland (now Malawi)	Bilateral, full-sized permanent maxillary canines; overall large size
KM 11542	1946	Amathole Museum, King William's Town	Nchisi (=Ntchisi) Mountain, southern (or Central-West in catalogue) Nyasaland (now Malawi)	Crowded lower incisors and abnormally placed left P3 and canine teeth; overall large size
TM 757 (CR 757)	1914 (catalogue), or 1924 (index card)	Transvaal Museum (NFI), Pretoria	Marandellas, South Rhodesia*	Bilateral, full-sized fourth maxillary and mandibular molars
TM 4078	1924	Transvaal Museum (NFI), Pretoria	Marandellas, "Central Rhodesia"*	Dental pathologies, malocclusion, and unusual pitting of the skull/face; overall large size

* The different country designations for Marendellas are as recorded in the museum catalogue; assumedly, this locality is situated in the northern part of South Rhodesia (now Zimbabwe), which is in reasonably close proximity to southwestern Malawi.

morphology—canine duplication—that is undocumented in purebred primates. Traits that appear in hybrid offspring but not in parental animals usually indicate the aberrant effects of mixing two separately coadapted genomes (Falconer and Mackay, 1996; Vrana et al., 2000). The zygomatic and maxillary bones derive from the first pharyngeal arch, and, therefore, the high incidence of unusual zygomaxillary sutures in hybrids may signify a breakdown in the coordination of early development. Similarly, the high frequency of supernumerary teeth in the hybrids may indicate a breakdown of the canalization of dental arch segmentation present in each parental group. Interestingly, although the effects of hybridization on dental morphology in mammals are not well-studied, other documented cases of supernumerary teeth and dental abnormalities in hybrids do exist. In addition to the supernumerary baboon canines reported above (Freedman, 1963; Hayes et al., 1990), supernumerary teeth are also prevalent in both recent (*Spermophilus richardsonii* × *S. elegans*) and late Pleistocene (>120,000 years; *S. richardsonii* complex) ground-squirrel hybrids (Goodwin, 1998). In his study, Goodwin (1998) noted that supernumerary teeth always occur bilaterally in the maxilla, a pattern of expression that is rare in purebred ground squirrels. Dental abnormalities in a monodontid skull have also been attributed to beluga/narwhal hybridization (Heide-Jørgensen and Reeves, 1993). These studies suggest that such dental variation characterizes not just primates, but interspecific mammalian hybridization more broadly.

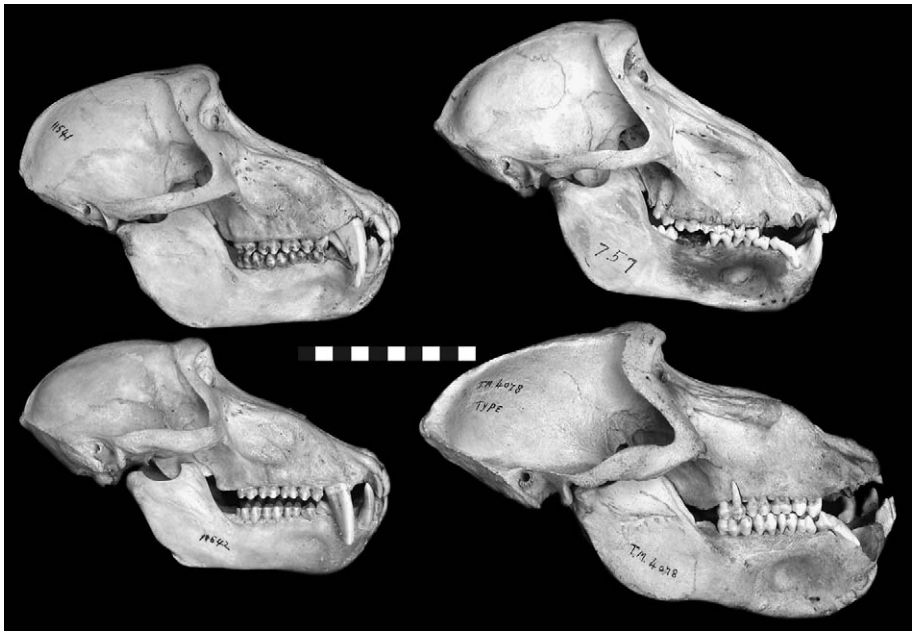

Fig. 6. Museum hybrids, clockwise from top left: KM 11541, TM 757, TM 4078, KM 11542. Note the extreme variation in size among these animals. TM 4078 also exhibits the "robust" phenotype frequently associated with hybrids.

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Heterosis has been used not only to quantify hybrid morphology, but also as an indicator of the presence of hybridization in primates. For example, Natori (1990) used the absence of heterosis in the postcanine dentition of a callitrichid sample relative to putative parental species as a criterion for rejecting the possibility that this was a hybrid population (Natori, 1990). Yet, one of the surprising results of this study is that the morphological variation represented by the suite of hybrid nonmetric anomalies discussed above appears to be a more sensitive indicator of hybridization than heterosis. In other words, even in primate populations that are genetically very similar, and that may express little heterosis, we expect their hybrids to display other qualitative morphological signatures of evolutionary distinctiveness, caused by small differences in the rate or timing of development in the parental populations, the subsequent failure of specific developmental interactions in their hybrids and resultant developmental instability, or other epigenetic phenomena. This cautions against rejection of hybrid status based solely on a lack of detectable heterosis.

So what exactly should a hybrid Pleistocene hominin look like? Detection of hybridization in the fossil record is difficult (Holliday, 2003), but this study contributes by identifying the morphological effects of hybridization in both captive and wild primate populations that have diverged in the Pleistocene. Most importantly, this study emphasizes the fact that primate hybrids are not necessarily a balanced mixture of parental traits, intermediate between parental populations. Rather, hybrids can show a range of morphologies, resembling one parent or the other, or displaying intermediate morphology, depending on dominance and epistatic interactions between alleles fixed or predominant in either parental group. This is shown most clearly in the quantitative analyses, where hybrids exceed expected intermediate values for many traits, but for others may be more like one or the other parental population, depending on which trait is observed. It is also well-illustrated by the range of variation in even the small samples shown in Figures 2 and 3. Hybrids can also fall outside the parental range, as is clearly demonstrated by the nonmetric analyses. What does characterize hybrids, then, is increased *variation*. This is a well-known phenomenon for hybrid populations, which often exhibit a high degree of individual variability and in many cases display levels of phenotypic variation that exceed the combined variation in both parental populations (Arnold, 2004; Seehausen, 2004). A good example of this in primates was reported for wild tamarin hybrids (between *Saguinus fuscicollis fuscicollis* and *S. melanoleucas melanoleucas*), where hybrid coat colors were highly variable and display color combinations not seen in either of the parental groups (Peres et al., 1996). Other studies of primate hybrid zones have also described high degrees of phenotypic variation, often distributed clinally between the morphologies of parental taxa (Phillips-Conroy and Jolly, 1986; Froehlich and Supriatna, 1996; Bynum et al., 1997; Bynum, 2002).

A major impediment to answering the question of whether a comparable range or patterning of skeletal variation exists in the hominin fossil record is that the fossil record samples single individuals and not cross sections of biological populations. Because of this, our ability to test for a population-level phenomenon, such as heterosis or increased trait variation, is virtually nil. In principle, the presence of extreme morphological variation, such as that seen across the earliest modern humans and their contemporaries (see discussion in Trinkaus, 2005), might indicate that hybrid zones are being sampled. However, in practice it would be extremely difficult to distinguish such variation from increased variation resulting from higher levels of sexual dimorphism, the effects of sampling through time or across wide geographic regions, or other such phenomena.

Of more value for considering the fossil record are those signatures of hybridization that highlight distinctly different patterning, especially when they mark individuals. In this light, the results of the nonmetric analysis are most promising. These results reveal a strategy for recognizing hybrid zones in the hominin fossil record (as well as in extant skeletal collections) via skeletal evidence for the breakdown of development, in the form of a prevalence of dental and osteological anomalies such as supernumerary teeth and extra sutures or ossicles. Although hybridization is not necessary for the expression of the bulk of these anomalies, many of which occur at a low frequency in purebred populations, it does significantly increase their expression. As such, even the presence of such anomalies in individuals should be considered a potential indicator of hybridization, particularly when the traits are rare (such as bilateral anomalies), or novel. In this light, it is interesting to consider the possibility that the type skull of *Homo floresiensis* might demonstrate comparable evidence, as it exhibits an unusual bilateral dental anomaly that has not been recorded in any other hominin—rotated maxillary premolars (Brown et al., 2004). Of course, our ability to extrapolate the results of this study to the hominin fossil record depends on the adequacy of our primate analogue, the baboon. However, given documented evidence of heterosis across other primate hybrids (Smith and Scott, 1989; Cheverud et al., 1993; Kohn et al., 2001; Schillaci et al., 2005) and the presence of similar nonmetric anomalies in other Pleistocene and recent mammalian hybrids (Goodwin, 1998), this seems reasonable.

Yet, other evidence for developmental breakdown of the sort seen in the baboon hybrids is limited. Dental crowding and possible molar impactions exist in Neandertals, as well as in eastern African robust and southern African gracile australopiths, while dental crowding alone is more common across hominins (Oppenheimer, 1967; Wolpoff, 1979; Gibson and Calcagno, 1993). Supernumerary teeth have been reported for only two individual hominins. A single robust australopith cranium (SK 83) from Swartkrans, South Africa, has a supernumerary lateral incisor in the right maxilla (Ripamonti et al., 1999); maxillary incisors are the most common type of supernumerary tooth (Lavelle and Moore, 1973; Rajab and Hamdan, 2002). The other hominin with a supernumerary tooth is A.L. 198-1, a left mandibular corpus from Hadar, Ethiopia, which preserves the broken roots of a fourth molar (White and Johanson, 1982). It is impossible to know the crown morphology of this specimen, and it is therefore unclear whether the molar is full-sized, but the root does not suggest anything unusual (W. Kimbel, pers.

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comm.); we cannot know if it was expressed bilaterally. So, while A.L. 198-1 may be evidence for a full-sized supernumerary molar, neither bilateral molars nor supernumerary canines have ever been reported in hominins.

How do we account for the relative scarcity of such traits in the fossil record of human evolution? One obvious explanation is that hybridization was uncommon. But it is unwise to draw definitive conclusions from an absence of evidence, and there remain other plausible explanations. Most importantly, as discussed above, many hybrids are not expected to show any anomalies at all, making them impossible to detect. The paucity of evidence may also result from the sparse fossil record; it is possible that because hybrid zones are narrow (Jolly, 1993, 2001) they simply have not yet been well sampled. It is also possible that individual hybrids within such zones have not yet been sampled, as hybrid zones can comprise a complex mixture of first-generation hybrids, backcrossed hybrids, and parental populations (Jolly, 1993; Barton, 2001). Finally, even in situations where hybrid zones (and the hybrids within them) are adequately sampled, there remains the possibility that those hybridizing hominin populations that were exchanging migrants were doing so at such a high frequency, or were separated for such a short time, that they should not be considered evolutionarily distinct. This is particularly important to keep in mind when considering interpretations of Pleistocene hominin relationships, where other lines of evidence might point towards hybridization (Zilhao and Trinkaus, 2002; Reed et al., 2004; Stefansson et al., 2005; Trinkaus, 2005), as the results presented here indicate that it is unlikely that genetic populations that are very different from each other will hybridize without detectable developmental consequences.

Conclusion

What does a hybrid look like? Although this question is central to our understanding of human evolution, and especially our ability to dissect the fossil record into meaningful taxonomic units, very little is actually known about the hybrid primate skeletal phenotype. The results of this study show that this phenotype can be quite variable, and they caution against simple assumptions that hybrids will display the average of the parental phenotypes. They also indicate that even a small amount of evolutionary divergence among populations, over relatively short time periods, can result in the breakdown in the coordination of development in their hybrids. Because this breakdown was most apparent in the F_1 generation, further studies are necessary to determine whether these traits are transitory, or instead persist into later generations. Teasing this out will be important for understanding the longevity of hybrid zones, and it may give us a better sense of whether we should expect to be able to detect them in the hominin fossil record.

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