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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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