



# Craniomandibular form and body size variation of first generation mouse hybrids: A model for hominin hybridization

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## ABSTRACT

Hybridization occurs in a number of mammalian lineages, including among primate taxa. Analyses of ancient genomes have shown that hybridization between our lineage and other archaic hominins in Eurasia occurred numerous times in the past. However, we still have limited empirical data on what a hybrid skeleton looks like, or how to spot patterns of hybridization among fossils for which there are no genetic data. Here we use experimental mouse models to supplement previous studies of primates. We characterize size and shape variation in the cranium and mandible of three wild-derived inbred mouse strains and their first generation (F<sub>1</sub>) hybrids. The three parent taxa in our analysis represent lineages that diverged over approximately the same period as the human/Neanderthal/Denisovan lineages and their hybrids are variably successful in the wild. Comparisons of body size, as quantified by long bone measurements, are also presented to determine whether the identified phenotypic effects of hybridization are localized to the cranium or represent overall body size changes. The results indicate that hybrid cranial and mandibular sizes, as well as limb length, exceed that of the parent taxa in all cases. All three F<sub>1</sub> hybrid crosses display similar patterns of size and form variation. These results are generally consistent with earlier studies on primates and other mammals, suggesting that the effects of hybridization may be similar across very different scenarios of hybridization, including different levels of hybrid fitness. This paper serves to supplement previous studies aimed at identifying F<sub>1</sub> hybrids in the fossil record and to introduce further research that will explore hybrid morphologies using mice as a proxy for better understanding hybridization in the hominin fossil record.

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## 1. Introduction

### 1.1. Hybridization and its phenotypic consequences in primates

Hybridization, the interbreeding between individuals from genetically differentiated lineages, is an important mechanism facilitating evolution (Stebbins, 1959; Lewontin, 1966; Arnold,

1992; Dowling and DeMarais, 1993; Dowling and Secor, 1997; Barton, 2001; Seehausen, 2004; Schwenk et al., 2008; Arnold and Martin, 2009; Feder et al., 2012; Abbott et al., 2013; Dittrich-Reed and Fitzpatrick, 2013; Kronforst et al., 2013). While botanists have embraced hybridization as normal and abundant among diversifying taxa, it is often overlooked in studies involving animals (Mallet, 2005). Despite this, animal hybrids are quite common, with 10% of animal species producing hybrids and with occasional “phylogenetic hotspots” having greater hybridization rates in animals than in plants (Mallet, 2005; Stelkens and Seehausen, 2009). Hybridization occurs across a wide range of mammalian lineages,

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including (but not limited to) whales (Árnason et al., 1991; Bérubé and Aguilar, 1998), wildebeest (Brink, 2005; Ackermann et al., 2010), bison and domestic cattle (Baranov and Zakharov, 1997), coyotes, wolves, and dogs (Mahan et al., 1978; Vilà et al., 2003; Benson et al., 2012; Khosravi et al., 2013; Monzón et al., 2014), squirrels (Goodwin, 1998; Chaves et al., 2011), and many primate taxa (Jolly, 2001; Detwiler et al., 2005; Arnold and Meyer, 2006; Cortés-Ortiz et al., 2007; Zinner et al., 2011).

In primates, hybridization in the wild occurs within all major lineages. In strepsirrhines, hybridization has been reported among subspecies and species of lemurs, and especially taxa within the genus *Eulemur* (Curtis and Zaramody, 1998; Wyner et al., 2002; Pastorini et al., 2009). In platyrrhines, hybridization has been observed among howler monkeys (genus *Alouatta*; Gregorin, 2006; Aguiar et al., 2007, 2008; Kelaita and Cortes-Ortiz, 2009; Cortés-Ortiz et al., 2015), spider monkeys (genus *Ateles*; Rossan and Baerg, 1977), saddle-back tamarin (*Saguinus fuscicollis*) subspecies (Cheverud et al., 1993; Peres et al., 1996; Kohn et al., 2001), and among different species of marmoset (Coimbra-Filho et al., 1993; Tagliaro et al., 1997; Marroig et al., 2004; Malukiewicz, 2013; Fuzessy et al., 2014; Malukiewicz et al., 2014). Within Old World Monkeys, baboons (genus *Papio*), macaques (genus *Macaca*), and guenon species (genus *Cercopithecus*) exhibit inter- and intra-specific hybridization (Fooden, 1964; Bergman and Beehner, 2004; Wildman et al., 2004; Detwiler et al., 2005; Schillaci et al., 2005; Zinner et al., 2009). Hybridization among ape taxa is less common than in monkeys, no doubt in part because there are simply fewer closely related, sympatric ape taxa. However, hybridization between siamangs and gibbons (genera *Symphalangus* and *Hylobates*, respectively) has occurred in captivity (Myers and Shafer, 1979), and other instances of hybridization have occurred between closely related species both in captivity and in the wild (Montagu, 1950; Brockelman and Srikosamatar, 1984; Marshall and Sugardjito, 1986). Within-genus hybridization among great ape species and subspecies (perhaps even between-genus hybridization) may occur (see discussion in Arnold, 2008), but evidence for it is limited and restricted to the genome (Ackermann, 2010; Prado-Martinez et al., 2013; but see Ackermann and Bishop, 2010). Furthermore, hybridization between distinct hominin lineages (e.g., Neanderthals, Denisovans, ancient Africa-derived people) has occurred multiple times during the Pleistocene, both outside and within Africa (Patterson et al., 2006; Green et al., 2010; Krause et al., 2010; Reich et al., 2010, 2011; Hammer et al., 2011; Abi-Rached et al., 2011; Meyer et al., 2012; Lachance et al., 2012; Sankararaman et al., 2012, 2014; Wall et al., 2013; Fu et al., 2013, 2014, 2015, 2016; Huerta-Sánchez et al., 2014; Kim and Lohmueller, 2015; Kuhlwilm et al., 2016).

The current literature indicates that there can be considerable variation in the morphological expression of hybridization, with hybrids resembling either parent taxon, being intermediate between the parent taxa (additive outcome), or having morphologies that are extreme or novel (Cheverud et al., 1993; Rieseberg et al., 1999; Stelkens and Seehausen, 2009; Ackermann, 2010). Heterosis or dysgenesis, positive or negative deviations from the intermediate outcome, are terms typically used to describe fitness; for morphology, larger or smaller size is a proxy for increased/decreased fitness. Phenotypic changes in plants, resulting from large scale changes in genomic regulation due to the combining of divergent genomes, is referred to as “genomic shock” (Comai et al., 2003). Similar effects (like the unusual expression of growth-related genes) have also been implicated in the unusually large size of *Peromyscus* (field mouse) hybrids (Duselis and Vrana, 2010).

Although the skeletons of most primate taxa have not been examined for evidence of hybridization *per se*, wide ranges of

morphological variation—especially pelage and body size variation—among primate hybrids have been observed and described (Arnold, 2008; Ackermann, 2010). The work that has been done on the skeleton of primate and other mammalian hybrids shows that hybrids are extreme in size (transgressive) and sometimes express high frequencies of novel traits relative to the parents (Ackermann et al., 2006, 2014; Ackermann, 2010). These include a prevalence of atypical traits associated with a breakdown in the coordination of early development, such as supernumerary teeth and sutural anomalies (Goodwin, 1998; Ackermann et al., 2006, 2010, 2014; Ackermann and Bishop, 2010). In terms of craniometric analyses of hybrids, research has focused on understanding heterosis and dysgenesis (i.e., where the hybrids are significantly larger or smaller, respectively, than the additive effect of intermediacy expected based on parental size). Analyses that have examined baboons, gorillas, and tamarins indicate that hybrids (or purported hybrids in the case of the gorillas) are heterotic in the majority of traits tested (Cheverud et al., 1993; Ackermann et al., 2006; Ackermann and Bishop, 2010). The statistical significance of cranial heterosis varies among primate hybrids, with tamarin hybrids exhibiting more significant heterotic cranial traits than baboon hybrids. It is not known how many generations cranial heterosis persists after hybridization has taken place, though there is some suggestion that it might be observable for a considerable amount of time (Ackermann and Bishop, 2010).

The link between unusual hybrid morphology and the phylogenetic distances among parents is difficult to determine. Stelkens and colleagues (2009) noted a tight correlation between genetic distance and transgressive size in cichlid fish, although this link was most correlated in the F2 generation. Similarly, in the literature of both plants and animal hybrids, transgressive behavioral, morphological, and physiological traits showed a tighter correlation with genetic distance than phenotypic distance (Stelkens et al., 2009). This implies that much of the transgression seen in hybrids is the result of complementary gene action or epistasis. However, when studying hybrid skeletal traits, such relationships are less clear. For instance, despite being relatively closely related, the baboon hybrids studied by Ackermann and colleagues (2006, 2014) display high levels of supernumerary dentition and relatively low levels of heterosis.

Primates are excellent models for understanding hominin hybrid morphology, but they have limitations. In particular, slow breeding time, expense, and ethical issues make experimental work with primates unfeasible. Observational data in the wild, or data collected from museum specimens, can be used, but often the degree of introgression is unknown or unknowable. Moreover, collecting skeletal data on wild animals is complicated (and expensive if it involves capture and radiography/scanning). Known genealogies of hybrid primates are rare, with skeletal collections such as the Southwest National Primate Research Center (SNPRC) baboons (Ackermann et al., 2006, 2014) having limited samples beyond the first generation. Additionally, both the SNPRC collection and many museum collections are of crania only; information regarding the postcranial skeleton of hybrids is practically non-existent.

Here we present data obtained from mouse crosses that have been chosen and bred to provide a more comprehensive approach to assessing variation in the hybrid skeletal phenotype. This is the first study from an ongoing project that is examining multi-generation mouse recombinants of several closely related subspecies and two species, designed to generate large samples of mice with various degrees of introgression in the wild. The data generated will ultimately include skeletal cranial and postcranial data, as well as soft-tissue (pelage, muscle) variation, in the context of known genotypes. This paper serves as an introduction to this

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