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The effects of hybridization on growth allometry and craniofacial form in Sulawesi macaques

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Abstract

The present research investigates the effects of hybridization between *Macaca maurus* and *M. tonkeana* on adult male form and patterns of growth allometry. Comparisons of adult hybrid mean phenotypic values with the adult averages of the parental species indicate a condition of heterosis for cranial vault length and crown–rump length. Negative heterosis is indicated for body mass. Regression parameters describing growth allometry are generated for four craniofacial measurement variables and one body measurement using both least squares and reduced major axis regression. Comparisons of hybrid and parental regression slopes and intercepts using analysis of covariance and *t*-tests suggest that there is a hybrid pattern of growth allometry characterized by an increase in regression slope values coupled with lower intercept values compared to those of the parental species and the parental averages for most regression parameters. Multivariate analyses of the adult and ontogenetic morphometric data indicate significant differences across species taxa in form and shape during development and adulthood. Our finding of significant differences between hybrids and their parental taxa in growth allometry and craniofacial form and shape during development challenges the assumption often made regarding the reproductive and taxonomic significance of observed

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ontogenetic divergence between Neandertals and modern humans. We propose that anthropological primatology, with its goal of developing nonhuman primate models for investigating human evolution, can provide a biologically relevant means by which to empirically estimate the taxonomic significance of morphological and ontogenetic divergence observed in the hominid fossil record.

Keywords: Ontogeny; Heterosis; Hybrids; Growth and development; Neandertals; Human evolution; Anthropological primatology; Species recognition

Introduction

Although macaque hybridization on the Indonesian island of Sulawesi has been the focus of considerable research for over fifteen years, there has not been any research on the effects of this hybridization on growth and development. Moreover, with the exception of human primates, there has been virtually nothing published on hybridization and growth by primatologists or biological anthropologists. Here, we present findings from our study on the effects of hybridization between *Macaca maurus*[1] and *M. tonkeana* on patterns of bivariate growth allometry. The potential consequences of the observed pattern differences in growth allometry on adult form are examined using formal comparisons of adult measurements, as well as multivariate vectors describing overall body size and shape. Specifically, we address the following research questions:

1) Does hybridization between these congeners cause heterosis resulting in increased adult cranial and somatic dimensions?
2) If heterosis in adult hybrid size exists, is it associated with increased regression slopes reflecting a stronger magnitude of allometric growth[2] in our cross-sectional ontogenetic sample?
3) If pattern differences in growth allometry among the taxonomic groupings are observed, are these pattern differences associated with differences in adult form (i.e., size + shape)?

Increasingly, comparative studies of ontogeny are becoming a well-accepted means to investigate taxonomy and reproductive isolation in the hominid fossil record. Given the dearth of literature on growth among hybridizing primate species, our study on macaque hybrid growth has relevance not only to the field of primatology, but also to the study of hominid evolution. In particular, we believe that our findings have implications for interpreting the evolutionary and taxonomic significance of the well-described ontogenetic divergence between Neandertals and modern humans.

Research on Neandertal growth and taxonomy

A number of recent studies have compared Neandertal and modern human craniofacial and postcranial growth (e.g., Minugh-Purvis, 1988; Krovitz, 2000; Williams, 2000; Ponce de León and Zollikofer, 2001; Minugh-Purvis, 2002; Williams et al., 2002a; Coqueugniot and Minugh-Purvis, 2003; Krovitz, 2003; Williams et al., 2003; Ramirez Rozzi and Bermudez de Castro, 2004; Zollikofer and Ponce de León, 2004). Despite differences in analytical techniques, most of these studies have described a significantly divergent pattern of growth and development for the Neandertals when compared to modern humans (but see Minugh-Purvis, 2002; see also Ackermann and Krovitz, 2002). For example, the study by Ponce de León and Zollikofer (2001), which employed computerized fossil reconstruction and

[1] Here, we use the species name *Macaca maurus* in place of *M. maura* (Cuvier: 1823) in accordance with convention allowing the use of separate gender in latin for genus and species names in macaque taxonomic nomenclature, e.g., *Macaca sylvanus* and *M. silenus*.

[2] It is important to note that an increased magnitude of allometric growth does not neccesarily correspond with increased growth rates (see Gould, 2000).