

A geometric morphometric analysis of heterochrony in the cranium of chimpanzees and bonobos

Daniel E. Lieberman^{a,*}, Julian Carlo^b,
Marcia Ponce de León^c, Christoph P.E. Zollikofer^c

^a Peabody Museum, Harvard University, Cambridge MA, 02138, USA

^b Harvard Medical School, 220 Longwood Ave, Boston MA, 02115, USA

^c Anthropologisches Institut, Universität Zürich-Irchel, Winterthurerstrasse 190, CH- 8057 Zürich, Switzerland

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Abstract

Despite several decades of research, there remains a lack of consensus on the extent to which bonobos are paedomorphic (juvenilized) chimpanzees in terms of cranial morphology. This study reexamines the issue by comparing the ontogeny of cranial shape in cross-sectional samples of bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*) using both internal and external 3D landmarks digitized from CT scans. Geometric morphometric methods were used to quantify shape and size; dental-maturation criteria were used to estimate relative dental age. Heterochrony was evaluated using combined size-shape (allometry) and shape-age relationships for the entire cranium, the face, and the braincase. These analyses indicate that the bonobo skull is paedomorphic relative to the chimpanzee for the first principal component of size-related shape variation, most likely via a mechanism of postformation (paedomorphosis due to initial shape underdevelopment). However, the results also indicate that not all aspects of shape differences between the two species, particularly in the face, can be attributed to heterochronic transformation and that additional developmental differences must also have occurred during their evolution.

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Introduction

This study uses geometric morphometric (GM) methods to consider the extent to which the skull of the bonobo (*Pan paniscus*) is paedomorphic (juvenilized) compared to that of the chimpanzee (*Pan troglodytes*). A second, related goal is to test for any dissociation of heterochronies in the skull between facial and neurocranial regions in these two species. Applying heterochrony models to analyze differences between the bonobo and chimpanzee has not only been the subject of much

previous research but also a major test case for theoretical debates concerning heterochrony theory (Shea, 1983a; 1984, 1992; Godfrey and Sutherland, 1996; Alba, 2002; Cobb and O'Higgins, 2004; Mitteroecker et al., 2004, 2005; Ponce de León and Zollikofer, 2006). Yet, despite this attention, bonobo and chimpanzee skulls differ morphologically in ways that have yet to be completely described or understood in terms of their developmental causes and evolutionary implications. While some authors (e.g., Shea, 1992) support the hypothesis that bonobos are paedomorphic relative to chimpanzees, others do not completely support this heterochronic diagnosis for several reasons. Godfrey and Sutherland (1996) used a multivariate allometric model to suggest that the bonobo cranium cannot be described as either paedomorphic or peramorphic relative to chimpanzees because of nonuniform allometries

* Corresponding author.

E-mail addresses: danlieb@fas.harvard.edu (D.E. Lieberman), julian_carlo@hms.harvard.edu (J. Carlo), Marcia@ifi.unizh.ch (M. Ponce de León), zolli@aim.unizh.ch (C.P.E. Zollikofer).

between the two species (see below). Additional studies by Williams et al. (2002), Mitteroecker et al. (2005), and Ponce de León and Zollikofer (2006) found that allometric scaling and multivariate analyses can explain only partially the differences between bonobo and chimpanzee crania. Mitteroecker et al. (2004, 2005), moreover, have raised questions about the utility of multivariate analyses such as GM to infer heterochronic transformations.

Here, we expand in several ways upon these earlier studies by using a landmark-based GM approach to compare ontogenetic changes in cranial shape and size between bonobos and chimpanzees using both external and internal landmarks, many of which represent key sites of craniofacial growth. We also use approximate estimates of age based on dental stages in the two species, and we examine multivariate size-shape and age-shape relationships throughout the cranium as a whole and within various regions. Given the potentially confusing nature of research on heterochrony, particularly in light of different methods and terminologies, we begin with a brief review of the GM heterochronic transformation model used here. We then review previous research on whether the bonobo skull is paedomorphic relative to the chimpanzee skull, and outline the hypotheses to be tested and the methods we employ.

Heterochrony model

Ever since Gould (1977), there has been considerable interest in heterochrony, the analysis of changes in the timing and/or rate of developmental events among ancestor and descendant individuals or taxa. Traditionally, heterochronic processes are quantified with respect to three parameters: *shape*, *size*, and *time*. Size and shape describe the *form* of an organism, with size representing a scalar measure of the magnitude of form, and shape referring to aspects of form independent of scale (O'Higgins, 2000). Time can be quantified in several ways, typically as absolute age (chronological time relative to a homologous event such as birth), or in relative terms using a series of stages or events during ontogeny such as tooth eruptions (de Beer, 1958; Smith, 2001).

Implementation of the basic parameters of heterochronic transformation has varied considerably among studies, sometimes leading to alternative methodologies and terminologies (e.g., Gould, 1977; Alberch et al., 1979; McKinney and McNamara, 1991). A major source of confusion and debate has been the issue of time, for which reliable data are often unavailable in many samples. In the absence of good data on the ages of individuals in a sample, researchers typically use size as a proxy to compare size-shape relationships between ontogenetic samples of two or more taxa, effectively converting the analysis to a comparative ontogenetic allometry (Gould, 1977; Fleagle, 1985; McKinney and McNamara, 1991; Godfrey and Sutherland, 1996). Heterochrony and allometry provide complementary but not necessarily equivalent analytic frameworks for analyzing the evolution of ontogenetic trajectories (Klingenberg, 1998). Allometry tests for size-related shape changes; it cannot test directly for temporal differences in development, such as changes in rate and time of offset.

Although there exists a general covariance between size and ontogenetic time, the correspondence between allometry and heterochrony can be complex, making it difficult to infer heterochronic transformation from allometry. Alternative (and often confusing) terminologies have stemmed from multiple models that apply the same terms to heterochronic and allometric plots, which use different parameters to define the ontogenetic changes they portray. Allometry nonetheless sheds light on heterochronic transformations between two species when there is a strong covariance between size and age because heterochronic processes can create various patterns of scaling (McKinney and McNamara 1991; Godfrey and Sutherland, 1995a, b; Godfrey et al., 1998; Leigh et al., 2003).

Allometry, the relationship between size and shape, is used here explicitly as part of our analysis of heterochronic transformation. Changes in allometric trajectories indicate heterochronic transformation, but reflect only indirectly the effects of ontogenetic time (McKinney and McNamara 1991; Godfrey and Sutherland, 1995a, b; Klingenberg 1998; Smith, 2001; Leigh et al., 2003). The evolution of both allometric growth trajectories and aspects of developmental timing are therefore crucial for the understanding of heterochronic transformations because changes in the relationship between size and shape may be independent of that between shape and ontogenetic development.

Size and shape have also been treated in multiple ways. Until recently, most heterochrony studies assessed size using linear measurements, mass, areas, volumes, or occasionally the first principal component of variation of a set of linear measurements (for review, see Alba, 2002). Shape, a dimensionless parameter, has most often been quantified using ratios of two linear measurements. One problem with these measures of size and shape is the issue of size-shape covariation. Lengths, areas, and volumes are not always independent of shape, and the first principal component of multivariate analyses that are not computed from size-corrected data typically includes some component of size-related shape change (Jungers et al., 1995; Mitteroecker et al., 2004).

Geometric morphometric methods that use landmark data are a useful way to measure shape in heterochrony analyses because they can effectively quantify size and 3D shape independently (Zelditch et al., 1995; Penin et al., 2002, Berge and Penin 2004; Cobb and O'Higgins, 2004; Zollikofer and Ponce de León, 2004; Mitteroecker et al., 2004, 2005). Geometric morphometric methods first quantify the form (size and shape) of each specimen according to the location in space of a set of anatomical landmarks that are homologous among individuals. Shape and size are then separated using a Procrustes superimposition of landmarks, which translates the landmarks to a common origin, scales them to a common size, and rotates them to minimize their summed squared landmark distances (Rohlf and Slice, 1990; Zelditch et al., 2004). Procrustes superimposition thus enables one to quantify shape as the multidimensional deviation of a specimen's landmarks from a reference configuration, typically an average of the entire sample. Shape covariation is then quantified using principal components analysis (PCA), a dimension reduction technique

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