

6. Cranial growth models: heterochrony, heterotopy, and the kinematics of ontogeny

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Abstract

In fossil hominins, phyletic diversification – the process by which ancestral species give rise to descendant ones – can only be inferred through analysis of patterns of morphological diversity displayed in the fossil record. These patterns are interpreted typically in terms of selection/adaptation and related to environmental change. From an organism-centered perspective, evolutionary modification of developmental processes is an equally important source of phyletic diversity. Here, we use model systems to simulate cranial growth and to explore how mutations in the “genes” of an “ancestral” morphogenetic system may affect “descendant” ontogenies and “adult” morphologies. Intriguingly, a model that assumes basic epigenetic interactions between developmental processes is capable of producing a wide variety of patterns of developmental modification, many of which are not foreseen in classic heterochronic theory. Also, small changes in developmental “genes” often have complex effects on patterns of ontogeny. With regard to the evolutionary split between Neanderthals and modern humans, these model considerations shall be an incentive to look at taxon-specific character complexes from the perspective of developmental as opposed to functional constraints.

Introduction

Morphological change in the cranium during human evolution is typically seen as a suite of functional adaptations to changing environmental conditions and/or specialization to an

ecological niche. A paramount example can be seen in the Neanderthals, who are often thought to represent a human species adapted to the harsh climatic conditions of mid-Pleistocene Europe (Churchill, 1998; Lahr and Foley, 1998). However, establishing

correlations and causal links between varying environmental factors and variation in character states faces both practical and theoretical obstacles. First, due to the incompleteness of paleoenvironmental and fossil records, reconstruction of past key events and inferences regarding their impact on the course of human evolution should remain tentative. Second, it is typically impossible to interpret changes in a particular body structure in terms of specific functional changes, i.e., adaptations to a specific task or a specific environmental condition. Rather, it appears that morphological alterations involve correlated sets of characters and reflect a network of changing functional requirements. Disentangling these networks is a challenging task because it is often difficult to discriminate between cause and effect. Third, evolutionary modification of morphology is typically channeled by developmental constraints. As a consequence, in highly integrated systems such as the hominin skull, every conceivable morphology cannot be realized, thus morphology becomes a compromise between external (environmental) constraints and requirements, and internal (developmental) constraints and requirements.

These arguments merit further attention. Using the metaphor of supply and demand, it is developmental variation that supplies evolutionary novelty and diversity, while selection reduces diversity by restricting demands to a small fraction of the supply. Accordingly, how and why the form of the hominin cranium changes over evolutionary time spans can be tackled in two complementary ways. On the one hand, we may investigate the adaptive and functional context of change, while on the other hand, we may study how change is brought about through modification of developmental programs.

The latter approach is adopted here. First, we devise a general model of cranial growth and use computer simulations to explore how changes in model parameters – which stand for “developmental genes” and epigenetic

interactions – affect developmental paths and result in cranial morphological diversity. Second, we ask how our results comply with existing theoretical frameworks of evolutionary developmental modification, notably with current concepts of heterochrony, heterotopy, and ontogenetic allometry. These concepts are central to evolutionary developmental reasoning, but there is no consensus on how to define them theoretically and apply them during empirical data analysis. In the study presented here, we refrain from adopting one or the other existing theoretical framework. Rather, we use insights from simulations to reveal limitations of current concepts of heterochrony and heterotopy, and we propose a combination of geometric-morphometric analysis and kinematic analysis to quantify the widest possible diversity of patterns of evolutionary modification of developmental pathways.

Measuring and Interpreting Ontogenetic Modifications

The central role of ontogenetic modification as a promoter of phylogenetic ramification was recognized by Haeckel (1866), who coined the terms *heterochrony* and *heterotopy* to denote evolutionary modification of temporal and spatial properties of developmental programs, respectively. Analyzing ancestor-descendant relationships in terms of heterochronic and heterotopic modification of ontogeny has proven extremely fruitful in generating insights into developmental paths of phyletic diversification: Since the conceptual foundations were provided in Stephen Jay Gould's *Ontogeny and Phylogeny* (Gould, 1977), heterochronic theory has diversified into two principal schools of thought. The first, which may be named “pan-heterochrony” (McKinney and McNamara, 1991; McKinney, 1999; McNamara, 2002) proposes that most observed instances of developmental