

5. Neanderthals and modern humans – chimps and bonobos: similarities and differences in development and evolution

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Abstract

Being our closest living relatives, chimps and bonobos provide the best available comparative evidence to study the evolutionary split between our sister taxon – the Neanderthals – and ourselves. Here, we analyze craniofacial development in these taxa from birth to adulthood using geometric morphometric methods. In both *Homo* and *Pan*, ontogenetic trajectories of sister taxa differ by their length, position and/or direction in shape space, as well as in the relationship between cranial size and shape. Modern human and bonobo ontogenies represent “abridged” versions of Neanderthal and chimp spatiotemporal developmental patterns, respectively, where “shortening” of trajectories is likely to represent evolutionary novelty. When examined in detail, however, the Neanderthal-human and chimp-bonobo splits do not represent equivalent forms of evolutionary developmental diversification. Rather, it appears that each bifurcation is the result of a different unique evolutionary event, during which the ancestral mode of growth and development was modified in a taxon-specific manner.

Introduction

For almost 150 years Neanderthals have been recognized as a fossil human taxon exhibiting a suite of morphological features that differentiate them both from earlier *Homo* and from contemporaneous anatomically modern

humans (AMH) (Stringer and Gamble, 1993). With the advent of new analytical methods, the classical morphology-based view of Neanderthals has been modified and complemented. Among these new developments, two directions of research have proven especially promising: analysis of fossil mitochondrial

DNA (mtDNA) and quantitative analysis of three-dimensional morphology.

Successful extraction and sequencing of ancient DNA from several Neanderthal individuals has provided evidence of an early evolutionary split between Neanderthals and anatomically modern humans (Krings et al., 1997, 1999; Ovchinnikov et al., 2000), essentially supporting the view that no significant interbreeding between these taxa occurred (Krings et al., 2000; Serre et al., 2004). New morphometric methods have been implemented concurrently. Most notably, the methodological framework of Geometric Morphometrics (GM) permits quantitative analysis of shape variability in complex three-dimensional forms (Dryden and Mardia, 1998). The growing popularity of GM methods has provided new insights into the distinction between Neanderthal and AMH cranial architecture and development (Ponce de León et al., 2001; Harvati et al., 2004). Studies at a smaller morphological scale have revealed previously unrecognized Neanderthal features, such as distinct tooth cusp patterns (Bailey, 2002, 2004), and a more rapid pace of tooth development that indicates divergent Neanderthal and modern human life histories (Guatelli-Steinberg et al., 2005; Ramirez Rozzi and Bermúdez de Castro, 2004). These studies consolidate the notion of two contemporaneous but independently evolving *Homo* lineages during the Middle to Late Pleistocene.

In this study we focus on the evolutionary bifurcation of a hypothetical common ancestor into Neanderthal and anatomically modern human populations. Evolutionary lineage splits are attributed traditionally to divergent adaptation often arising from habitat shifts. In the case of Neanderthals, the functionally adaptive value of several distinguishing features such as the size and shape of paranasal sinuses, limb proportions, and pelvic form remains highly controversial (Rak, 1986; Trinkaus, 1987, 2003; Churchill, 1998;

Franciscus, 1999, 2003; Franciscus and Churchill, 2002; O'Connor et al., 2005). An evolutionary developmental perspective offers an alternative approach to investigating Neanderthal morphology. Rather than studying the potential adaptive significance of a novel trait, attention is directed toward how processes of growth and development are modified to bring about evolutionary novelty. From this perspective, Neanderthal morphology is considered as an integrated whole rather than an array of more or less independent features. This approach frees us from the shackles of adaptationist reasoning (Gould and Lewontin, 1979) since it puts more weight on the role of developmental constraints during the evolution of new morphologies. As we demonstrated in an earlier study (Ponce de León et al., 2001), Neanderthals and AMH exhibit clear morphological differences at an early stage of ontogeny, but follow a shared ancestral pattern of postnatal development. Henceforth, contrary to the widespread notion that only adult specimens exhibit the requisite autapomorphic features required to define a species, juvenile specimens are equally relevant in performing this task.

Studying development in an evolutionary context by comparing fossils encounters substantially more limitations compared to developmental studies that use extant taxa. Most notably, developmental processes and their modifications cannot be followed *in vivo* using the fossil record but must be inferred from patterns of morphological change between fossil specimens. It is essential, therefore, to carry out comparative studies addressing similar questions in living species from which more complete data can be derived. Fortunately, hominoid evolution has provided an ideal test case. Our closest relatives, the chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*), represent sister species with distinct morphologies and life histories (Barriel, 1997; D'Aout et al., 2004; Doran, 1993; Gagneux et al., 1999; Parish and