

4. Inquiries into Neanderthal craniofacial development and evolution: “accretion” versus “organismic” models

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Abstract

The origin and evolutionary significance of the Neanderthals is still unresolved. Several basic questions about the biological processes determining the apomorphic morphology of this human group are still pending resolution. In this paper we present a general outline of the lines of research we are currently following in the exploration of Neanderthal anatomy. We focus our approach on three different aspects: (1) a methodological and theoretical component based on system theory; (2) specific morphological problems, such as the effects of body size and brain development on craniofacial shape in Neanderthals; and (3) the analysis of these aspects by geometric morphometric and paleohistological methods.

Presently, Neanderthals are considered the end point of an evolutionary lineage rooted in the European Middle Pleistocene fossil record. The “tempo and mode” in the evolution of the Neanderthal lineage are here evaluated by comparison of two different perspectives: the “accretion model” (Hublin, 1998a) and the “organismic model”. In the former, stochastic processes are invoked to account for the “gradual tempo and a mosaic mode” for the emergence of the Neanderthal anatomy. By contrast, the “organismic model” presented here, sets out the hypothesis that the Neanderthal skull form may result from two interconnected effects at different levels of organization: (1) body-face interactions via organismic-level effects (e.g., allometry, physiological demands), and (2) brain-face interactions via integration principles.

We propose a conceptual framework in which the evolutionary process experienced by the Neanderthal lineage was primarily dominated by two distinct and successive phases. The first to appear in time was that producing midfacial prognathism, which may be related to mid-sagittal growth dynamics, in which body size and cranial base orientation are primarily involved. This evolutionary phase is accompanied by significant variation, which is still poorly understood. Here it is associated with increased body size and sexual dimorphism variation, and its concomitant craniofacial compensatory mechanisms. A second evo-devo process, largely related to the relative size increase of the occipital and temporal neural areas, affects the organization of the skull, via cascading effects resulting from integration mechanisms (at times assimilated to pleiotropic effects). In this two-phase evolutionary process, facial changes may be connected with processes affecting the variation of the sagittal cranial base, whereas temporal bone modification may be related to processes affecting bilateral, middle cranial fossa variation. Occipital modifications remain open to interpretation, although a complex interplay between increased encephalization and head position (perhaps as an indirect result of body shape) might be considered.

Taxonomically, the “accretion model” considers the Neanderthal lineage as a continuum of evolving populations, which are temporally associated with two different *nomina*: *H. heidelbergensis* and *H. neanderthalensis*, on the basis of a single chronospecies concept. In an alternative view, we favor the hypothesis that the species *H. neanderthalensis* emerges as a distinct biological entity (morph) after a speciation event (or change in morphological quality). The main point of this paper is to evaluate the “accretion model” versus a two-phase hypothesis of Neanderthal speciation in the Middle Paleolithic.

Introduction

The natural history of Neanderthals is among the oldest and most exciting topics in human evolution. Understanding the role of Neanderthals in our own ancestry has aroused many conceivable ways of approaching its study, and it has strongly challenged the intellectual capacity of scientists. Beyond attempts to clarify the genealogical position of Neanderthals in our own ancestry, from the viewpoint of morphology as a science, we face one of the most elusive and challenging case studies in human evolution.

While, for most of their scientific existence, the Neanderthals were those enigmatic people living in Europe during the Würm glaciation (Late Pleistocene, OIS 4–3), today the term Neanderthal is used in a twofold sense. On the one hand, we refer to Neanderthals as the human populations inhabiting the western end of the Eurasian continent, from approximately 80,000–30,000 years ago, also called Würm Neanderthals or “Classic” Neanderthals (further geographic subdivision may consider the Levant Neanderthals). Nowadays, a majority of scholars consider classic Neanderthals as a distinct species, *Homo neanderthalensis* (e.g.,