

17. Speciation by distance and temporal overlap: a new approach to understanding Neanderthal evolution

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Abstract

Neanderthals are the best-known fossil hominid group, but at the same time many aspects of their evolution are still poorly understood. The variation of numerous characters in Neanderthal populations shows a geographical gradient. From west to east, characters become less and less Neanderthal-like and more and more modern human-like. Moreover, in Central Europe and the Near East, post-Neanderthal populations still exhibit some Neanderthal features, which is not the case in Western Europe. The spread of the first humans into Europe involved differentiation of this species by distance, whereas consecutive populations were linked by gene flow. Hence, from Western Europe to the Near East, there was a succession of human populations that developed, over time, Neanderthal characters that were more and more marked from east to west. Then, modern humans spread rapidly into Europe at about 40,000 years ago, but at least in the western part of the continent, no convincing evidence of hybridization with Neanderthals has been found. By contrast, interbreeding was still possible in the eastern part of Europe and in the Near East, but became less and less so towards the west. This hypothesis implies that the ancestors of Neanderthals arrived and evolved in Europe at a time when gene flow between Western Europe and Near Eastern populations was very limited. Hence, Near East Neanderthals cannot be interpreted as the result of a migration of a European population toward the east, but as a continuum in space and time of European inhabitants. Thus, as they moved westwards, modern humans integrated local populations in the Near East and Central Europe and replaced populations in Western Europe.

Introduction

Although Neanderthals are among the best-known fossil hominids, many aspects of their

evolutionary history, especially their extinction and taxonomic position relative to modern humans, are still poorly understood. There are two main schools of thought on this last

topic: (1) Neanderthals and modern humans are two distinct species (e.g., Rak, 1993; Hublin et al., 1996; Stringer and McKie, 1996; Bermúdez de Castro et al., 1997; Krings et al., 1997; Stringer, 1998, 2002; Bocquet-Appel and Demars, 2000; Hublin, 2000; Arsuaga et al., 2001; Bräuer, 2001; Schillaci and Froehlich, 2001; Rak et al., 2002; Harvati, 2003; Harvati et al., 2004); and (2) Neanderthals and modern humans are a single species, with or without two subspecies (Thoma, 1965; Trinkaus, 1983, 1991; Smith et al., 1989a, 2005; Smith, 1991; Smith and Trinkaus, 1991; Frayer, 1992; Wolpoff and Caspari, 1996; Duarte et al., 1999; Wolpoff et al., 2000; Relethford, 2001, 2003; Ahern et al., 2002, 2004; Curnoe and Thorne, 2003). Explanations of Neanderthal extinction depend in great part on how scholars consider their taxonomic status. If Neanderthals and modern humans belong to the same species, then Neanderthal morphology disappeared because Neanderthals were genetically absorbed into modern human populations. On the other hand, if Neanderthals and modern humans were two distinct species, the disappearance of the former is likely the result of competition with modern humans when they arrived in Europe. However, some scholars consider that Neanderthals and modern humans may never have met (d'Errico et al., 1998; Zilhão and d'Errico, 2000; d'Errico and Sánchez Goni, 2003), and that Neanderthal extinction was not related to their taxonomic status. Whatever the case, in the following analysis and discussion I will simply treat these two human groups as distinct populations without taking a position on their taxonomy.

In this study, I propose a new interpretation of the relationships between these two human groups. First, I briefly present an overview of Neanderthal characters and their variation in western and eastern populations. Then, I explain this variation in the context of "speciation by distance" and the migration of modern humans into Europe.

A West to East Morphological Cline

At the transition between the Middle and Upper Paleolithic in Western Europe, all fossil humans clearly belong to one of two groups: Neanderthals or modern humans. Everyone agrees that there were two distinct populations in this region of the world (whether they belong to two different species or not). Since 1999, the Lagar Velho child (Duarte et al., 1999) has been at the center of discussion, being the earliest human fossil in Western Europe about which no consensus exists. As we will see below, the Lagar Velho fossil fits well with my hypothesis. However, in Eastern Europe, and more evidently in the Near East, the two populations are less clear-cut. As noted by Smith et al. (1989a: 50) "there is little evidence of evolutionary trends in the modern human direction among the west European Neanderthals. ... However, in central Europe, there are possible indications of diachronic trends within the Neanderthals, in the direction of the modern European condition." The debate begins with early remains, such as the Zuttiyeh fossil, which are alternatively considered pre-*sapiens* (Vandermeersch, 1989a), related to Asian Paleolithic populations (Sohn and Wolpoff, 1993), or pre-Neanderthal (Smith et al., 1989a; Simmons et al., 1991). In the same way, more recent remains are considered to belong only to archaic *Homo sapiens* (Arensburg, 1989; Smith, 1991; Wolpoff, 1999; Arensburg and Belfer-Cohen, 1998; Kramer et al., 2001), with no Neanderthals existing in the Near East. Alternatively, others consider that Neanderthals do exist in the Near East (e.g., Condemi, 1991; Rak, 1998; Stringer, 1998; 2002; Trinkaus, 1983, 1991). This disagreement is primarily due to the variation of Neanderthal morphology from east to west. In Western Europe, Neanderthal morphology is well marked and easily distinguishable from that of modern humans, while differences are less pronounced in the Near East. In other