Neanderthals Revisited: New Approaches and Perspectives

Edited by

Katerina Harvati
Max-Planck-Institute for Evolutionary Anthropology
Leipzig, Germany

Terry Harrison
Department of Anthropology, New York University
New York, USA

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This volume is dedicated to the memory of W.W. Howells (1908–2005) for his remarkable and pioneering contributions to the study of human evolution, especially his role in the greater understanding and appreciation of the Neanderthals. He was mentor and source of inspiration to generations of anthropologists, and his work continues to be a tremendous resource for research in human variation and evolution.

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

J.-L. VOISIN
Institut de Paléontologie Humaine
1 rue René Panhard
75013 Paris, France
jeanlucv@mnhn.fr

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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

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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 words, “Neanderthal features are not uniformly spread across the Neanderthal range, with sharp boundaries with other contemporary populations. Instead, they vary clinally, diminishing in frequency to the south east and east. In the Levant, it has been seriously questioned whether the specimens should be called ‘Neanderthal’ at all because they share few diagnostic features with the Europeans [Neanderthal]” (Wolpoff et al., 2004: 529). Other authors have also noted this west to east morphological cline (Vandermeersch, 1989b; Smith, 1991; Rak, 1993; Nara, 1994; Arensburg and Belfer-Cohen, 1998; Moncel and Voisin, 2006).

Osteological Evidence

Table 1 lists characters of the cranium and mandible, postcranial skeleton, and overall stature that show a clinal variation from Western Europe to the Near East. For this study, I used characteristics and data taken from the literature. This is not an exhaustive list, but it does offer examples to illustrate that a morphological cline exists. A more extensive study is currently in progress.

CRANIUM AND MANDIBLE

In their overall proportions, skulls of Near Eastern Neanderthals look more “modern” than those of their Western European counterparts (Table 1). The sharply pointed mastoid process is a Neanderthal autapomorphy that is found in all western individuals. On the contrary, in the Near East this morphology is found only in Shanidar 1 and Tabun 1, but is absent in Shanidar 2 and 5 and in Amud 1 (Vandermeersch, 1981; Trinkaus, 1988; Condemi, 2005). Moreover, in Amud 1 and Shanidar the mastoid process looks more modern than in any other Neanderthal population (Suzuki, 1970). In the same way, Western European Neanderthals have a less rounded occipital region, with a pronounced bun, compared with Central European and Near Eastern Neanderthals (Vandermeersch, 1981; Piveteau, 1983; Trinkaus, 1983; Smith, 1991; Habgood, 2003). The frontal region is larger in Near Eastern than in Western Neanderthals. The difference is not great, but there is no overlap between the two populations (Vandermeersch, 1989b). The cranial vault is higher in Near Eastern Neanderthals than in the Western group (Vandermeersch, 1981; Condemi, 1992), and Amud 1 falls well within the Upper Paleolithic range of variation for this feature (Suzuki, 1970). All hominids, except *Homo sapiens sapiens*, lack a chin on the mandible, but, according to Suzuki (1970) and Bar-Yosef and Vandermeersch (1991), some Near Eastern Neanderthals, like Amud 1, display an incipient development of it. Mid-facial prognathism is less pronounced in Near Eastern than in western Neanderthals (Piveteau, 1983; Habgood, 2003). Habgood (2003) shows that it is possible to separate classic Neanderthals from those from Central Europe on the basis of the overall morphology of the skull and the mandible by multivariate analysis. However, most characters, such as mid-facial prognathism, or sharp mastoid processes, are similar in Central and Western European Neanderthals (Habgood, 2003).

POSTCRANIAL SKELETON

Near Eastern Neanderthals more closely resemble modern humans postcranially than do Western Neanderthals (Table 1). Clavicular morphology is quite different in modern humans and Neanderthals in posterior view (Voisin 2000, 2001, 2004), although the Kebara and Krapina 143 clavicles display a modern morphology (Voisin, 2004). The scapula, which is considered the best postcranial bone for characterizing Neanderthals (Vandermeersch, 1981; Heim, 1982b), displays a morphological cline from west to east, especially in the configuration of its axillary

Table 1. Skull, postcranial, and body proportion differences between western and eastern Neanderthals

	West Europe	*Near East*	*Modern human*	*Authors*
Mastoid process	Sharp pointed	Sharp pointed morphology is not present on all fossils	Never sharp pointed	Vandermeersch, 1981; Trinkaus, 1988
Frontal width	Average = 107.4 mm Min = 106 mm Max = 109 mm	Average = 112.5 mm Min = 110 mm Max = 115 mm	Average = 109 mm Min = 98 mm Max = 113 mm	Vandermeersch, 1981, 1989b
Occipital region	Less rounded with a pronounced torus (i.e., less modern)	More rounded with a torus less pronounced or absent (i.e., more modern)	Rounded without any torus	Trinkaus, 1983; Vandermeersch, 1981, 1989b
Height of the cranial vault (porion-bregma)	Average = 112.5 mm Min = 111 mm Max = 114 mm	Average = 118.5 mm Min = 116 mm Max = 121 mm	Average = 117.4 mm Min = 98 mm Max = 122.5 mm	Vandermeersch, 1981; Condemi, 1992
Position of the auditory meatus	Far from the modern position in regard to the zygomatic arch	Near the modern position in regard to the zygomatic arch	Low in regard to the zygomatic arch	Suzuki, 1970; Vandermeersch, 1989b
Chin	Absent	Incipient	Present	Suzuki, 1970; Bar-Yosef and Vandermeersch, 1991
Clavicle morphology	Two curvatures in dorsal view	Some clavicle show only one curvature in dorsal view, like Modern humans	One curvature in dorsal view (the inferior one)	Voisin, 2000, 2001, 2004
Axillary sulcus of scapula	Dorsal	Bisulcate or ventral	Ventral, sometimes bisulcate	Frayer, 1992; Nara, 1994; Voisin 2000 Hambücken, 1997;
Radius shaft	High curvature	Slight curvature	Slight curvature	Arensburg and Belfer-Cohen, 1998
Pubic length relative to body size	Very long (outside modern range of variation)	Short (within modern range of variation)	Short	Rosenberg (1998)
Stature (of male)	Average = 165.4 cm Min = 162 cm Max = 172	Average = 171.2 cm Min = 163.9 cm Max = 176.5 cm	(Qafzeh and Skhul) Average = 185.2 cm Min = 183.5 cm Average = 187 cm	Vandermeersch, 1981, 1989b
Thorax width	Very large	Smaller (but slightly larger than modern human)	Little bit smaller than the Near East Neanderthal	Endo and Kimura, 1970; Trinkaus, 1983
Limbs	Shorter	Longer	Longer	Trinkaus, 1981
Cold adapted body proportion	More Specialized	Less specialized	Less specialized	Churchill, 1998

border. In Western Europe, all scapulae share a dorsal *axillary sulcus*, but in Central Europe and in the Near East this *sulcus* can be dorsal or bisulcate (Frayer, 1992; Nara, 1994). This feature is important because it relates to arm movements (Boule, 1912; Fraipont, 1927; Stewart, 1962; Trinkaus, 1977; Voisin, 2000) and post-natal growth (Heim, 1982a; Madre-Dupouy, 1991).

Other parts of the postcranial skeleton show differences between western and eastern Neanderthals that make the latter appear closer to *Homo sapiens* than classical Neanderthals. For example, the radius and ulna shafts are straighter in Near Eastern Neanderthals and close to those of Skhul IV and VII or Předmostí males (Endo and Kimura, 1970; Arensburg and Belfer-Cohen, 1998). Also, the Neanderthal upper limb in the Near East is gracile rather than robust (Hambücken, 1995). On the basis of the morphology of the distal extremity of the humerus, Hambücken (1997) separates Neanderthal humeri into two groups: a "classic" group (including La Chapelle-aux-Saints, Combe-Grenal, La Ferrassie, Régourdou, Saint-Césaire, Neanderthal and Spy) and a Mediterranean one (including Hortus, Krapina and Lezetxiki). Both of these groups are more robust in their overall morphology than the humeri of Near Eastern Neanderthals. The length of the pubis, relative to body size, is greatest in Western Europe (with La Ferrassie 1 being outside the range of modern human) and the shortest in the Near East (with Tabun C1 falling within the variation of modern humans). Neanderthals from Central Europe are between these two extremes (with Krapina 208 falling in the upper part of modern human range of variation) (Rosenberg, 1998).

STATURE

Eastern Neanderthals are taller than Western Neanderthals, and the former are closer in estimated stature to individuals from Skhul and Qafzeh (Vandermeersch, 1981, 1989b) (Table 1). This is correlated with body proportions that are adapted to warmer climates, with the Near Eastern Neanderthal populations having longer limbs and a smaller thorax (Endo and Kimura, 1970; Trinkaus, 1981, 1983; Churchill, 1998).

The morphology of the Krapina fossils is typically Neanderthal, but most of the metric values are at the lower extreme of the range of variation in western Neanderthals (Smith and Trinkaus, 1991). Hence, they may not look identical to classic Neanderthals. Although the Vindija remains are fragmentary, and the stature of the individuals cannot be precisely estimated, their overall morphology is less robust than that of classic Neanderthals (Smith and Trinkaus, 1991; Trinkaus and Smith, 1995).

Stature and postcranial morphology show the same west to east cline as skull characters. In other words, the further west that Neanderthals originate, the more they display classical Neanderthal traits. As Smith and Trinkaus (1991: 255) wrote "En Europe centrale, il existe des données importantes qui font penser que la reconnaissance d'une différence morphologique qualitative est moins évidente qu'en Europe occidentale" (In central Europe, there are important data leading to the conclusion that morphological qualitative differentiation is less marked than in Western Europe [my translation]).

Most skull differences are found between European (including Western and Central Europe) and Near East Neanderthal populations, while postcranial characters display a more gradual clinal change from west to east.

NEANDERTHAL CHARACTERS IN POST-NEANDERTHAL POPULATIONS

According to a number of authors, such as Smith et al. (1989b, 2005), Frayer (1992, 1997), Wolpoff et al. (2001, 2004), Trinkaus et al. (2003b), Janković et al. (2006), Ahern (this volume) and Hawks (this volume), some morphological characters in early modern Europeans reflect a Neanderthal influence (Tables 2 and 3). These traits exhibit a higher frequency in early modern Europeans than in later Europeans and non-European Pleistocene samples. This pattern, used to infer a Neanderthal contribution to early modern Europeans, is found only in post-Neanderthal populations of Eastern Europe (Smith, 1991; Smith and Trinkaus, 1991; Frayer, 1992; Smith et al., 2005), and no worker has demonstrated such a contribution to Western European populations (Gambier, 1989; Smith et al., 1989b; Smith, 1991; Smith and Trinkaus, 1991; Frayer, 1992; Hublin et al., 1996; Trinkaus, 2001; Trinkaus et al., 2003). The most striking

Table 2. Frequency of features present in different human populations (from Frayer, 1992; Smith et al., 2005)

	Suprainiac fossa	*Occipital bun*	*H-O*
European Neanderthals	100 (24/24)	80 (8/10)	52.6 (10/19)
Skhul / Qafzeh	14.3 (1/7)	0 (0/5)	/
Early Upper Palaeolithic	38.5 (10/26)	68.4 (13/19)	44.4 (4/9)
Late Upper Palaeolithic	23.7 (9/38)	/	5.3 (2/38)
Mesolithic	19.3 (31/161)	/	1.9 (3/161)
Medieval Hungarians	5.9 (14/237)	/	1.4 (3/208)

Values represent the % of specimens in which the features is present. Number in ( ) indicates the number of individuals exhibiting the feature followed by the sample size. H-O is the occurrence of the horizontal-oval mandibular foramen.

Table 3. Frequencies (%) of axillary scapular border types in Neanderthal, Early Upper Palaeolithic, Late Upper Palaeolithic, Mesolithic and Modern European samples (from Frayer, 1992)

	Dorsal	*Bisulcate*	*Ventral*
Neanderthal	64.1	23.9	12
Early Upper Palaeolithic	12.3	62.4	25.3
Late Upper Palaeolithic	16.8	27.7	55.5
Mesolithic	7.4	18.2	74.4
Modern European	1.2	14.4	84.4

According to Frayer, the high frequency of bisulcate axillary border demonstrates the Neanderthal contribution to the gene pool, because this feature is intermediate between the two other morphologies.

example is the supraorbital torus, which shows a continuous reduction through time in Central Europe without any clear difference between the latest Neanderthals and the first modern human populations. On the contrary, there are sharp boundaries between the last Neanderthals and the first modern humans in Western Europe (Smith et al., 1989b). Although the Lagar Velho child has been interpreted as a hybrid between Neanderthals and modern humans (Duarte et al., 1999), it does not provide convincing evidence for this because: (1) all Neanderthal characters may not be present or may not reach their classical morphology in a four-year-old child, so it becomes difficult to determine if some features are the result of hybridization (Tattersall and Schwartz, 1999); and (2) we do not know whether we are dealing with an F1 generation or not (Tattersall and Schwartz, 1999). Moreover, a hybrid that died before reaching reproductive age could also be interpreted as having a low fitness (see below).

What about DNA?

Since the work of Krings et al. (1997) on Neanderthal mtDNA, other studies of ancient mtDNA have followed (Krings et al., 1999; Ovchinnikov et al., 2000; Scholz et al., 2000; Caramelli et al., 2003; Serre et al., 2004; Serre and Pääbo, this volume). According to these authors, the differences observed between Neanderthal and modern human mtDNA support the interpretation that these two human groups are distinct species, although they do not entirely rule out the possibility of gene flow between them. However, the differences may be due to numerous factors and may not only reflect the replacement of one population by another (Hawks and Wolpoff, 2001). They could show the replacement of an original mtDNA by a new one within the same population through introgression (Mounolou, 1989; Hawks and Wolpoff, 2001). Moreover, mtDNA differences between Neanderthals and modern humans are less profound than the ones observed between two of the three subspecies of *Pan troglodytes* (Relethford, 2001; Barriel and Tillier, 2002).

Phylogenetic trees generated from mtDNA data may be incongruent with those using nuclear DNA (Sota and Vogler, 2001), most notably because selection pressures on these two genomes are not identical. At least in humans, mtDNA is under a high selective pressure, and this invalidates the hypothesis of neutral selection with a constant rate of substitution (Curnoe and Thorne, 2003; Hawks, this volume). In other words, phylogenetic trees obtained from mtDNA may not correctly reflect the evolutionary relationships of Neanderthals and modern humans. In addition, there are numerous difficulties in extracting ancient DNA, especially due to its incompleteness and short length (Cooper and Wayne, 1998), but also because it is fragile. Ancient DNA amplification creates damage that produces mutation artefacts that may artificially enhance differences between Neanderthal and modern human mtDNA (Hansen et al., 2001; Hofreiter et al., 2001; Gutiérrez et al., 2002). Therefore, ancient DNA does not settle the debate about the systematic status of Neanderthals, and more work is needed, especially on the post-mortem diagenesis of DNA (Hofreiter et al., 2001; Geilg, 2002; Smith et al., 2003; Mitchell et al., 2005; Salamon et al., 2005).

An Extreme Example of Speciation by Distance: The Ring Species

In order to explain the east-west morphological cline in Neanderthal populations, as well as their relationships to modern humans, it is useful to look at a peculiar type of speciation: speciation by circular overlap or "ring species". "Ring species provide dramatic evidence that normal genetic divergence within one species can build up to a sufficient level to generate two species" (Ridley, 2004: 388). What is a ring species? Among vertebrates, good examples of ring species are few. These include the Californian salamander *Ensatina eschscholtzii* (Ridley, 2004), the herring gull *Larus argentatus* and lesser black-backed gull *Larus fuscus* (Mayr, 1974). Perhaps the best example is the greenish warbler *Phylloscopus trochiloides* (Wake, 2001) that lives in forests across much of northern and central Asia (Figure 1). In central Siberia, two distinct forms, *P. trochiloides viridanus* and *P. trochiloides plumbeitarsus* are sympatric without interbreeding, and therefore may be considered two species. These two forms are nevertheless connected by a chain of interbreeding populations encircling the Tibetan plateau to the south (*P. trochiloides ludlowi, P.t. trochiloides, P.t. obscuratus*), and traits change gradually in consecutive populations (Irwin et al., 2001a). There is no obvious species boundary along this chain, and the two terminal "species" *viridanus* and *plumbeitarsus* are connected by gene flow (Irwin et al., 2001b). The "species" *trochiloides* has expanded northward following two pathways, one on the east, the second on the west of the Tibetan plateau (Figure 1), evolving several differences as they moved north (Irwin et al., 2001a, b). These include: (1) morphological differences (most notably in their wing bars); (2) song differences (males sing both for attracting females and defending their territories; females of *viridanus* and *plumbeitarsis* do not recognize the song of males of the other form); and (3) genetic differences.

This example shows how differences between two extreme populations (here *P. trochiloides viridanus* and *P. trochiloides plumbeitarsus*) can be important and affect the phenotype as well as the genotype. Between the two forms living in central Siberia morphological traits change gradually in consecutive populations encircling the Tibetan plateau, in the same manner as those of western to eastern Neanderthals. Thus, just before the spread of modern humans into Europe about 40,000 years ago, there was a chain of

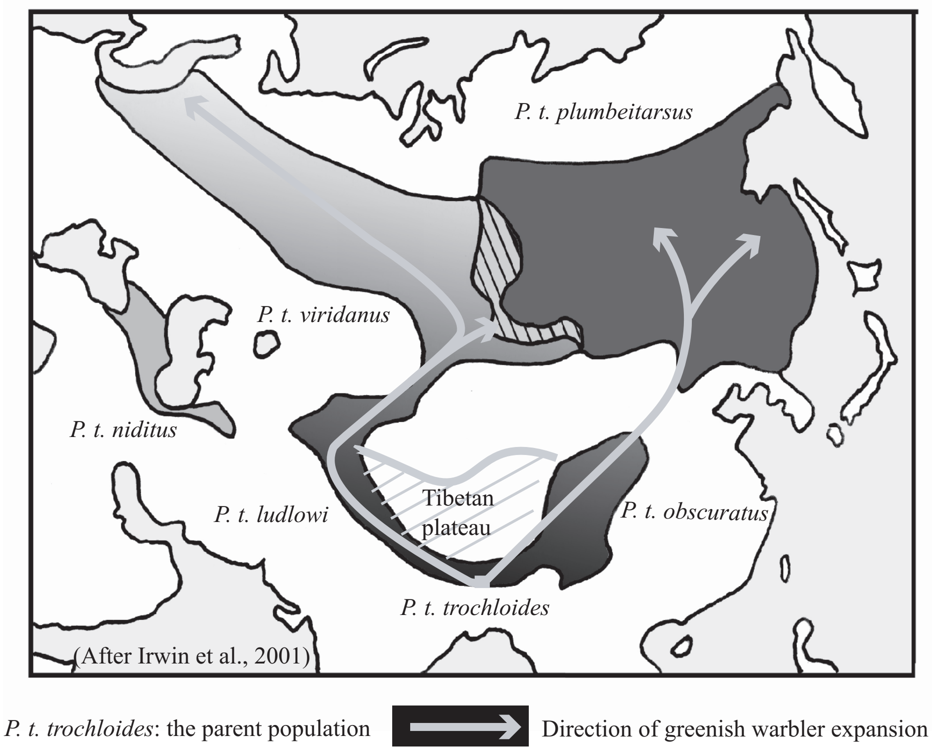

Figure 1. The greenish Warblers (*Phylloscopus trochiloides*) ring species. The break in the population in west China is inferred to be recent and caused by deforestation (after Irwin et al., 2001).

human populations throughout Europe and the Near East, more or less connected by gene flow (the gene flow rate would have varied as the ice sheets expanded and receded). When modern humans migrated westwards into Europe, they met more and more Neanderthal-like human populations. In Western Europe they encountered classic Neanderthals and were no longer able to interbreed with them, except in rare instances (see below).

In other words, the meeting of the two populations took place in two steps (Figure 2): (1) The spread of the first human populations into Europe, involved a clinal differentiation of this species, where each consecutive population was 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 became more and more marked from east to west; (2) In Western European Neanderthal populations, differentiation reached a level that did not allow interbreeding with modern humans. In Central Europe, gene flow was still possible, as shown by the persistence of Neanderthal features in post-Neanderthal populations (Smith, 1991; Smith and Trinkaus, 1991; Stringer, 1992; Frayer, 1992, 1997; Wolpoff and Caspari, 1996; Ahern et al., 2004; Wolpoff et al. 2004). This scenario is analogous to the sympatric populations of Greenish Warbler (*P. t. viridanus* and *P. t. plumbeitarsus*) to the north of the Tibetan plateau in Siberia. The two human populations in Western Europe were morphologically too different to allow admixture between them.

What Was the Level of Genetic Separation Between Western Neanderthals and Modern Humans?

The very low frequency or lack of admixture in Western Europe could have arisen in

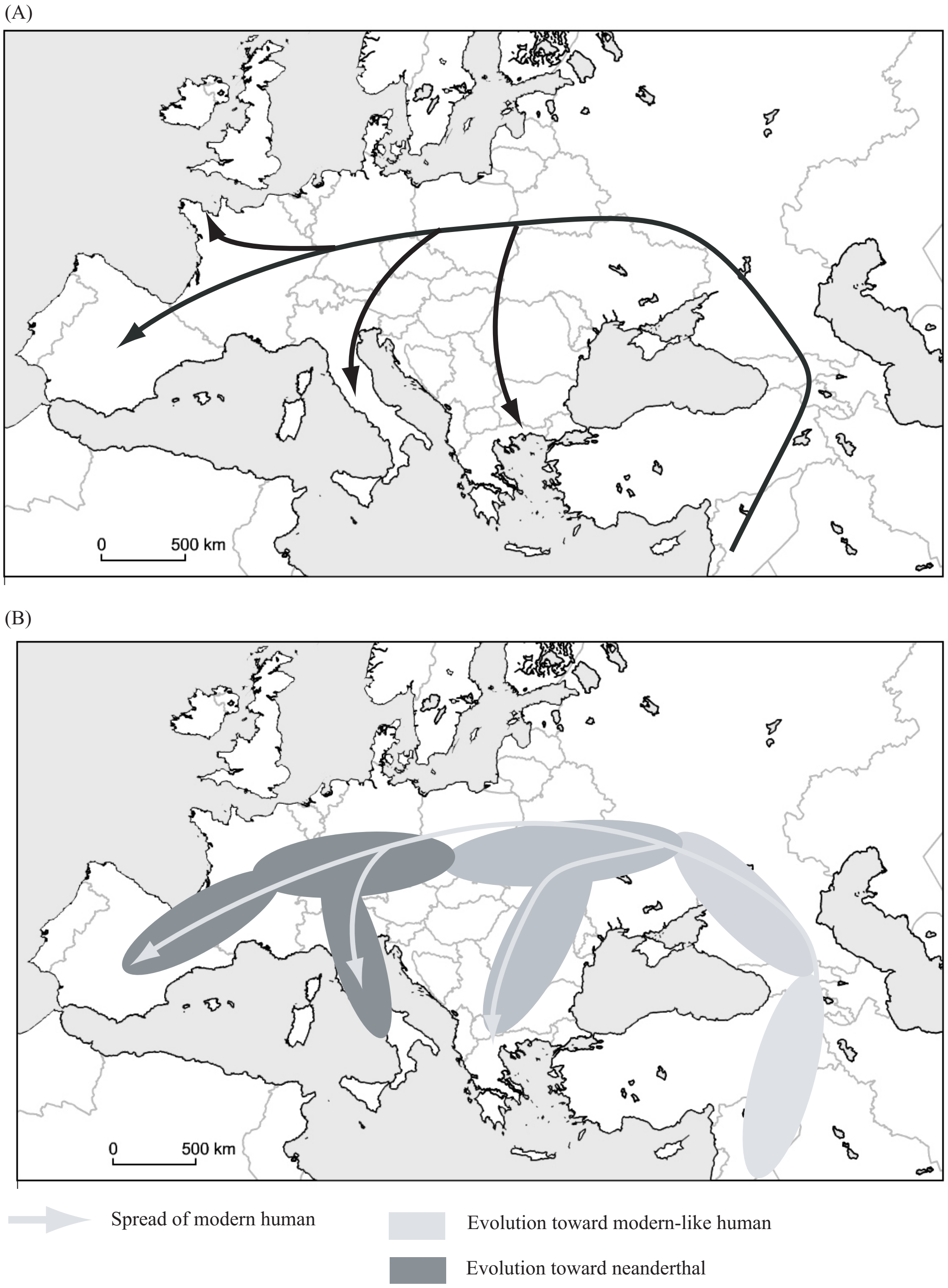

Figure 2. (A) the spread of the first human population into Europe. (B) differentiation of human populations, producing less Neanderthal-like people in the east (light grey), increasingly more Neanderthal-like in Eastern Europe, and classical Neanderthals in Western Europe (dark grey). Bright grey arrows symbolise the rapid spread of the first wave of modern humans into Europe.

numerous ways. The best-known mechanism is pre-zygotic isolation (genetic incompatibility and/or no mating between individuals of the two populations). However, other biological forces can create reproductive isolation, whereby hybrids are sterile or have a low fitness (i.e., the Lagar Velho child, see below for a discussion). In this latter case, hybrid individuals would not participate in gene flow between the two populations. Post-zygotic isolation between modern humans and western Neanderthals could have taken several forms (Ridley, 2004): (1) vanishing or low fitness of the male (Haldane's rule); (2) increased level of isolation between two populations by natural selection (reinforcement); and (3) interactions among several gene loci by epistasis (Dobzhansky-Muller theory).

Post-zygotic isolation would allow some degree of admixture between the two human groups, but it would have resulted in limited gene flow. Moreover, in humans, culture can also effectively contribute to reproductive isolation, with groups rejecting people with different behaviors. It is likely that cultural and biological factors worked together to limit gene flow between the two human groups.

Pre-zygotic isolation fits well with a classic view of the biological species concept, but often the distinction between closely related species is not so clear-cut. There are numerous ways of reaching genetic incompatibility (Schilthuizen, 2001; Ridley, 2004), and species level differences could exist prior to genetic incompatability. The time necessary to attain incompatibility is variable and can be very long; up to 4 myrs in some primates (see Holliday, this volume). Thus, in Western Europe, differences between the two human groups could have reached the species level without also reaching pre-zygotic isolation. This hypothesis excludes any large genetic contribution by Neanderthals to early modern human in Europe, which fits well with the DNA evidence (Caramelli et al., 2003; Serre et al., 2004; Serre and Pääbo, this volume).

In this way, is it possible to resolve the debate about the Lagar Velho child and its peculiar characters? Duarte et al. (1999) contend that it is a modern human-Neanderthal hybrid, while Tattersall and Schwartz (1999) regard it as a modern human without any admixture. However, if one considers the Lagar Velho child as a hybrid, it might be possible to infer that it had a lower fitness than Neanderthals and modern humans, as it died before reaching reproductive age. More fossils from this time period are needed to test this hypothesis.

It will never be possible, based on the fossil evidence alone, to establish beyond a doubt if there was post- or pre-zygotic isolation, but we can infer what is most probable. The morphological evidence implies that Neanderthals and modern humans in Western Europe may have behaved as two distinct species, most probably by post-zygotic isolation. In Eastern Europe and the Near East, the separation between the two human groups was apparently less clear-cut and some level of admixture was possible.

Neanderthal Evolution and Migration

The hypothesis of speciation by distance and temporal overlap between modern humans and Neanderthals implies that the ancestors of Neanderthals arrived and evolved in Europe, a geographical dead end, and that gene flow between Western and Eastern European populations was limited. Moreover, the effect of gene flow would have been more important in the eastern than in the western part of Europe because of the low density of Neanderthal populations (Mellars, 1998) and the asymmetric distribution of hunter-gatherer populations (Demars, 1996). Hence, Near Eastern Neanderthals should not be interpreted as the result of migrations of Neanderthal populations toward the East, but as a continuum in space and time. This interpretation allows us to explain why Near Eastern Neanderthals display such marked differences from Western European Neanderthals. It is also more consistent with the archaeological evidence (i.e., a lack of evidence of European cultural intrusion) than the notion that Neanderthals migrated into the Near East (Ahern, personal communication).

Conclusion

The evidence presented here indicates that there was a morphological cline (in skull form, postcranial skeleton, and stature) from west to east in Neanderthal populations. The farther those populations lived to the west, the more they displayed pronounced Neanderthal characters. Moreover, Neanderthal features seem to persist in Central Europe and Near East post-Neanderthal populations.

Ancient DNA studies do not settle the debate about the relationship of Neanderthals and modern humans because several alternative explanations may account for the observed differences; not only replacement of one population by the other. These explanations could be: (1) that mtDNA and nuclear DNA trees are not always congruent because of differences in selection pressures; (2) introgression; and (3) problems with ancient DNA conservation and extraction that introduce artificial differences between the two human populations.

In order to explain the peculiar distribution of characters in Neanderthals, as well as in post-Neanderthal populations, a two-phase model is proposed. First, an initial spread of human populations into Europe, followed by a clinal differentiation. This led to a succession of populations distributed from the Near East to Western Europe in which, over time, Neanderthal characters became increasingly

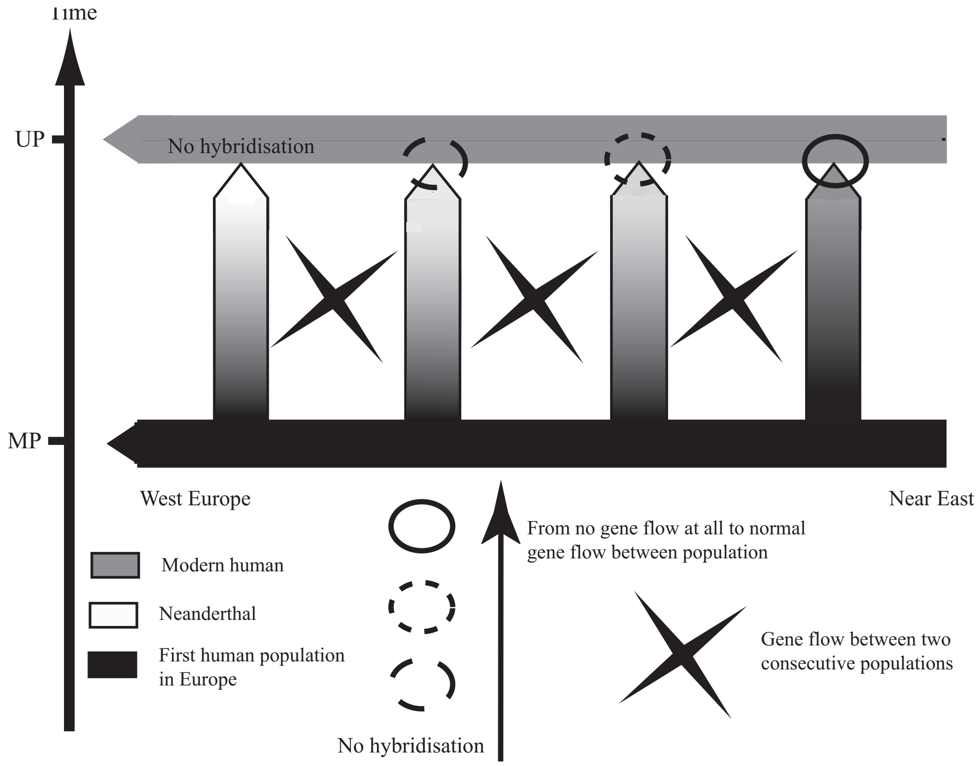

Figure 3. Gene flow between Neanderthal and modern human populations. UP: Upper Palaeolithic and MP: Middle Palaeolithic.

more marked from east to west. In other words, a speciation by distance could have occurred within the first European inhabitants. Second, when modern human spread into Europe at around 40,000 years ago, they met populations with more and more pronounced Neanderthal characters as they moved westward. Admixture was probably still possible in the Near East and in Central Europe, but in Western Europe differentiation between the two human groups reached such a level that admixture was no longer possible as a result of pre- or post-zygotic isolation (Figure 3).

Isolation between modern humans and Western Neanderthals would probably not have been achieved at this time. In other words, only post-zygotic isolation would have existed between the two human populations, and occasional admixture may still have occurred, although hybrids may have had a low fitness. The main basis for this assumption is the long time that is usually needed to attain pre-zygotic isolation in primates.

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