New lights about Neanderthal extinction

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Introduction

Neanderthals are certainly the best known fossil hominid group. At the same time many aspects of their history are still misunderstood and especially their extinction and taxonomic relations with modern humans. There are two schools on this topic: **(1)** Neanderthals and modern humans were two distinct species or **(2)** they were considered as one single species, with or without two subspecies. Hypotheses about neanderthal extinction depend mostly on their taxonomic statut. If those two human populations belong to the same species, the extinction of the neanderthal morphology would be the result of neanderthal absorbtion by modern human. On the contrary, if they belong to two distinct species, the extinction of neanderthal morphology would be the result of a competition with modern human without interbreeding.

We will see above that Neanderthal extinction could be due to the speciation by distance which allows to use arguments from both schools

I.) A West to East morphological cline

Table 1 : Neanderthal cranial and mandibular characters

	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
The 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

Skull and postcranial characters as well as body proportions display a East to West cline (Tab. 1, 2 & 3). In others words, the more popolutions are westward, the more their neanderthal characters are prononced.

Table 2: Neanderthal post-cranial characters

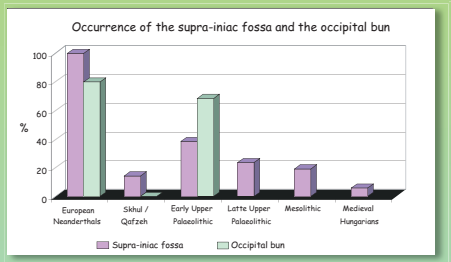
	West Europe	Near East	Modern human	Authors
Clavicle morphology	Two curvatures in dorsal view	Some clavicle show only one curvature in dorsal view, like modern humans	One curvature in dorsal view (the inferior one)	Voisin, 2000, 2001, 2004
Scapula: Axillary sulcus	Dorsal	Bisulcate or ventral	Ventral, sometimes bisulcate	Frayer, 1992; Nara, 1994; Voisin 2000
Radius shaft	High curvature	Slight curvature	Slight curvature	Hambücken, 1997; Arensburg and Belfer-Cohen, 1998
Pubic length relative to body size	Very long (outside modern range of variation)	Short (inside modern range of variation)	Short	Rosenberg (1998)

Table 3: Neanderthal body proportions

	West Europe	Near East	Modern human	Authors
Stature (for 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 Max = 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 Cold adapted body proportion	Shorter More Specialized	Longer Less specialized	Longer Less specialized	Trinkaus, 1981 Churchill, 1998

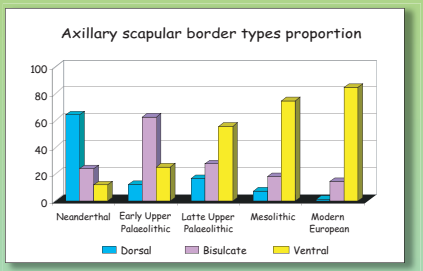
II.) Neanderthal charaters in post-Neanderthal populations

According to numerous authors, some morphological characters in early modern Europeans reflect a Neanderthal influence. These traits exhibit a higher frequency in early modern Europeans than in later Europeans and non-European Pleistocene samples (for exemples see graph. 1 & 2). This pattern, used to infer a Neanderthal contribution to early modern Europeans, is found only in post-Neanderthal populations of Eastern Europe, and no worker has demonstrated such a contribution to Western European populations.



Graphic 1: Occurrence (in %) of the supra-iniac fossa and the occipital bun (from Frayer, 1992 & Smith et al., *2005)*

Neanderthal characters in early modern humans display also a West to East cline. These traits exhibit a high frequency in modern human from central Europe and are absent from western Europe populations of modern human. Smith *et al.* (1989) summary it in writting: "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 modern human condition".



Graphic 2: % of axillary scapular border types (from Frayer, 1992)

III.) What about DNA?

Observed differences between Neanderthal and modern human mtDNA should be enough to consider that this two human groups are two distinct species.

However, differences may be due to numerous other factors

§ Introgression : replacement of all or a part of a genome by an another one inside a population (Monoulou, 1989)

§ Between mtDNA and nuclear DNA trees strong incongruence may exist (Sota & Vogler, 2001)

§ Diagenesis and DNA amplification could enhance artificially differences between fossils and modern taxons (Hofreiter *et al.*, 2001)

Moreover, observed differences between this two human groups are less important than between two chimpanzees subspecies (Barriel & Tillier, 2002).

IV.) Spéciation by distance, an new way for understanding this morpholgical cline ?

1°) A particular speciation by distance: the ring species.

In central Siberia, two distinct forms of *Greenish warblers* (fig. 1), *Ph. tr. viridanus* and *Ph. tr. plumbeitarsus,* are sympatric without interbreeding (fig. 2). These two forms are nevertheless connected by a chain of interbreeding populations encircling the Tibetan plateau to the south, and traits change gradually in consecutive populations (Irwin *et al.*, 2001).

Figure 1 : Phyloscopus trochiloides viridanus *(greenish warblers) (Irwin et al., 2001)*

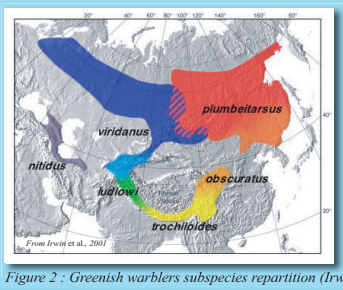


Figure 2 : Greenish warblers subspecies repartition (Irwin et al., 2001)

Two populations located at the exetremities of a species repartition area, and connected by a gene flow, could display phenotypic and genetical differences, strong enough to impende hybridations.

2°) Speciation by distance and relation modern humans / Neanderthals

To explain the morphological cline in neanderthal population as well as the distribution of neanderthal traits in first modern human in Europe, three steps are needed (fig. 3):

1°) Settlement in Europe of the first human metapopulation (whatever the species).

2°) Clinal differentiation of this first species where each consecutive population was linked by gene flow. Hence, from Western Europe to 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.

3°) Spread of modern human into Europe with hybridisation possibility in the Near-East and central Europe (shown by neanderthal characters in post-neanderthal populations) and without any hybridisation in western Europe (no neanderthal traits in first modern human population).

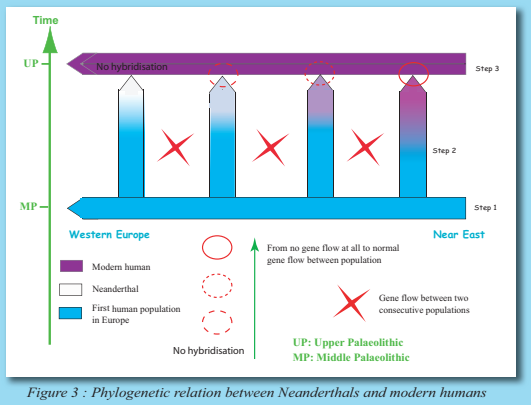


Figure 3 : Phylogenetic relation between Neanderthals and modern humans

Conclusion

Speciation by distance allows to explain the Neanderthal morphological variation along an East/West axis as well as the presence of neanderthal traits in some modern human populations and the absence in others. Neanderthal disparition would be the result of an absorption by hybridisation in the Near East and central Europe and, in west Europe, neanderthal would have been replaced by modern human. The evolution would have been reticulate (often in primates (Holliday, in press)) and not dichotomic.