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Program and Abstracts



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Conveners: SILVANA CONDEMI & WINFRIED HENKE

Respondent: PATRICIA SMITH

After 150 years studying of Neanderthals, what do we really know about them? Which of their anatomical traits permit us to recognize and define them? What do we know about their growth and development? Do their morphological features result from adaptation to the particular climate of the middle Pleistocene? Does the Neanderthal pattern indicate long-term isolation in Europe or even speciation? The Neanderthals inhabited a vast geographic area extending from Portugal to Uzbekistan, and from northern Europe to the Near East. This raises the question concerning the homogeneity of the Neanderthal population. Is it possible to identify local variations in such a large areas? Can one recognize sub-groups?

Neanderthal as another humankind: where are we now?

JEAN-JAQUES HUBLIN

Department of Human Evolution, Max-Planck-Institut für Evolutionäre Anthropologie, Deutscher Platz 6, 04103 Leipzig (hublin@eva.mpg.de)

A century and a half of investigation in Europe and in the Middle East has resulted in the collection of a large sample, allowing us to study many aspects of the biology and behaviour of the Neanderthals. One main interest of this late Middle-early Upper Pleistocene fossil hominin group results from its peculiar situation in the hominin phylogenetic tree. It likely represents our sister species, i.e. the last diverging branch before the emergence of modern humans. Because of this proximity, assessing the anatomical differences between the two groups and their evolutionary significance has provided ground for discussions about how to define fossil species within the Pleistocene hominins.

During the twentieth century, the possibility of an ancestor-to-descendant relationship between the two groups was rejected by many scholars, especially in Europe. The "Wurmian Neanderthals" were too close in time and too different to be ancestral to the modern Europeans (e.g. Piveteau, 1957). Among these authors, disagreements centred primarily upon the timing of the separation between the two groups. For the supporters of the "pre-sapiens model", best expressed by Vallois (Boule and Vallois, 1952; Vallois, 1958), the modern human ancestors had long existed in Europe or in Asia and eventually replaced the Neanderthals. For the supporters of the "pre-Neanderthal model" such as Sergi (1953), the features of the two groups were present in variable proportions in the European and Near-Eastern fossil record until the last interglacial, and the separation occurred only later. Authors such as Le Gros Clark (1955)

and Howell (1957) did not express very divergent views. Alternatively, scholars such as A. Hrdlicka (1927) and F. Weidenreich (1947), later followed by L. Brace (1964), supported a direct ancestral relationship between the Neanderthals and the modern Europeans. Following a somewhat different line of thought, the views of Weidenreich according to which modern "races" were rooted, in the form of identifiable regional lineages, in this stage and even before, flourished with the works by C. Coon (1962) and other supporters of the "regional continuity" model Wolpoff *et al.* (1984). During the same period, a re-examination of the European and Near Eastern fossil evidence occurred. This led to a much clearer definition of Neanderthal morphology (Stringer, 1974; Hublin, 1978; Santa Luca, 1978; Trinkaus, 1981, 1983) and confirmed the diverging nature of the Neanderthal lineage from the middle of the Middle Pleistocene Hublin (Hublin, 1980; 1988a,b). These analyses, mostly influenced by cladism, have led us to propose an "accretion model" (Hublin, 1998), which argues that most of the Neanderthal morphology was established in the late Middle Pleistocene, on specimens as old as Isotopic Stage 7 such as Biache (Rougier, 2003). This establishment results from an increase in the frequency of features mostly already present in the spectrum of variability of the earlier Middle Pleistocene European hominids. When considering the African lineage leading to modern origins, similar questions arise. Some authors (Braüer, 1984) have proposed a model of gradual emergence of the *Homo sapiens* phenotype through an accretion process quite comparable to what we proposed for the Neanderthal lineage. Alternatively, it is possible that a different process would have resulted into a speciation event resulting in the emergence of *Homo sapiens* 160-180 ky ago in Africa. To date, the scarcity of the material as well as the uncertainties surrounding the ages of many specimens leaves this question open. It is difficult, however, to draw a clear-cut line between "fully modern" and "archaic" morphologies.

Features' Significance

A continuing discussion addresses what can be seen as plesiomorphic retentions or derived features in Neandertals and modern humans. Although Neandertals do display some derived conditions and possibly unique features, some have argued (Trinkaus, in press) that they display more primitive conditions than do late modern humans. Similarities in some aspects of the Neandertal morphology with the pattern observed in the common ancestors of Neandertals and modern humans, together with the distinct morphological distance observed between Neandertals and modern humans, actually reinforce the notion that *Homo sapiens* is a recently developed species. Isolating and defining morphological features was central in the re-examination of the Neandertal anatomy, in particular, in a cladistic perspective.

It is also central to the problem of assessing the morphological distance that exists between Neandertals and modern humans, and how this compares with the modern variability and the morphological distance observed between species or subspecies of extant primates. One must say that this issue is far from being resolved, and it has led to a number of discussions (e.g., Trinkaus, 1990; Lieberman, 1995). When anatomical features are divided into sufficiently discrete elements, in most cases it is possible to sustain the view that these "features" are observed in both Neandertals and modern humans, but with different frequencies. In reality, the biological significance and validity of these features as independent traits, and often, their complete homology, are questionable. It remains that for virtually all single metric features used in osteological analyses, there is some overlap between Neandertals and modern humans. However, when combinations of metric or non-metric "features" are taken into consideration, a different picture emerges and the two groups appear to be quite distinct (Hublin, 1988a; Bailey, 2002; Harvati et al., 2004).

One main problem comes from the lack of understanding of the determining factors underlying many of the "features" used. Most cranio-mandibular and postcranial features are unclear in terms of evolutionary emergence (adaptation *versus* random drift), development (genetic *versus* epigenetic determinism) and independence. The development of these "features" depends partially on both behavioural and environmental factors during individual growth. In particular, this means that if significant behavioural changes occurred with the last Neandertals or with early modern humans, it might be difficult to discriminate between results of gene flow and the results of these behavioural changes (Hublin and Bailey, in press). It is, however, also to be noted that in some cases we are dealing with nonplastic

features which are therefore primarily determined by the genome and unlikely to be submitted to very significant behavioural or environmental influences. This is true for the morphology of the inner ear (Hublin et al., 1996; Spoor et al., 2003) and for dental non-metric traits (Bailey, 2002). Both of these are at least partly fixed before birth and display clear distinction between Neandertals and modern humans. Similarly, Ponce de León and Zollikofer (2001) have recognized that cranio-mandibular differences between Neandertals and modern humans are established following parallel but distinct growth trajectories.

Finally, another difficulty arises from the fact there is a certain level of integration of development within anatomical units, and that the definition of "independent features" can be quite problematic. However, in phylogenetic analysis, morphology is routinely split into elementary traits. As already stated, when combinations of features are used, for example as in 3D morphometrics analysis (Harvati, et al., 2004) or in analysis of nonmetric dental features (Bailey, 2002), Neandertals and modern humans unquestionably represent discrete morphological entities. Evidence for integration several aspects of the posterior portion of the brain case have been recently established by Gunz and Harvati (submitted).

Selection *versus* Drift

In the palaeoanthropological literature, adaptation by way of selection is implicitly considered the main phenomenon driving hominin evolution. However, direct evidence of this process is rarely provided when dealing with specific features routinely used in phylogenetic and taxonomic analyses. There is little doubt that features such as the body proportions in Neandertals might result from a climatic adaptation to the middle latitudes with an environment that was, most of the time, colder than in present-day conditions (Trinkaus, 1981; Holliday, 1997). However, similar interpretations regarding, for example, face pneumatization or nasal morphology failed to be demonstrated (Franciscus, 1999). In the accretion model as we proposed it in 1998, a major role is assigned to genetic drift in relation with distance and isolation. We have argued that this drift was partially driven by environmental changes, namely the "Middle Pleistocene Revolution" (Helmke et al., 2003). Changes in the periodicity and amplitude of the swing between glacial and temperate episodes resulted, for Western Eurasian populations, in periodic increases in isolation relative to Africa, and also in periodic demographic crashes. Under these conditions, non-metric features such as those observed in the Neandertal cranial vault (Hublin, 1998) or dentition (Bailey, 2002) would have been fixed by chance, and their frequency

would have increased without any significant selective pressure. It must be said that the adaptive advantage represented by the development of a suprainiac fossa on the occipital or a transverse trigonid crest on the lower molars is far from being obvious, unless we assume that these features are connected, by pleiotropic effects, to some unknown biological feature of great adaptive value. In support of this view is the fact that mitochondrial DNA variation within Neandertals is on the same order of magnitude as that observed in large modern groups of populations, and well below what is observed in great apes (Gagneux et al., 1999; Serre et al., 2004). For most geneticists, this would presumably result from the occurrence of bottlenecking events in humans (Neandertals or modern), contrasting with a more stable demographic history for the direct ancestors of extant hominoids. Recent work by Roseman and Weaver (2004) and Harvati and Weaver (in press) as suggested that cranial morphological features commonly used to assess the phylogenetic status of Pleistocene hominids vary in modern human populations in direct relation with genetic distance, and only in some instances with environmental parameters. In addressing more directly the issue of Neandertal/modern human divergence, Weaver *et al.* (submitted) have shown, by applying a series of statistical tests, that the emergence of Neandertal and modern cranial morphologies is likely related to random genetic drift. In particular, they have underlined how cranial linear measurements can compare to the neutral evolution of genetic structures such as microsatellites.

Taxonomic Status

Supposing that Neandertals and modern humans were rodents or antelopes, no vertebrate palaeontologist would hesitate in assigning them to different paleontological species. Indeed, they are humans that shared very similar technical and behavioural adaptations. In the past, this, among other things, has led many anthropologists to incorporate them into the same species as ourselves. In part, this is a product of anthropologists' characterization of humans as a unique entity characterized by Culture. In some extreme examples (Wolpoff and Caspari, 1996), all hominids post-dating 2 million years BP are incorporated into the species *Homo sapiens*, which is seen as a chronospatial network of populations connected by gene flow, and subject to the same general adaptive trends.

Neandertals identified as a late Middle and early Upper Pleistocene western Eurasian group of hominins are quite different from modern humans. In terms of shape distance, Neandertals and late Pleistocene modern humans are at least as different as some closely related species of apes,

such as bonobos and chimpanzees (Harvati *et al.*, 2004).

Whether these clear phenotypic and developmental differences imply that Neandertals and modern humans represented totally isolated biological species and/or whether or not there could have been some hybridization or gene flow between the two groups is a separate issue. In nature, there are abundant examples of hybridization between closely related extant species, including the production of fertile hybrid populations (Holliday, in press). From a morphological point of view and in a paleontological perspective, it makes sense to use different specific denominations for the two groups, i.e. *Homo neanderthalensis* and *Homo sapiens*, and these concepts are fully operational for the terminal portion of the two lineages. The separation is, of course, less clear-cut when moving back in time, closer to the splitting point between the two lineages. This situation is nothing new in palaeontology.

To date, more than fifteen Neandertal remains have provided mitochondrial sequences, among which ten or so have been published (Krings, et al., 1997; Ovchinnikov et al., 2000; Serre, et al., 2004; Lalueza-Fox et al., 2005). Specific motifs in the basic sequences are found systematically in these fossils and remain unknown in extant humans and in any fossil specimen demonstrable non-Neandertal. Unfortunately, mitochondrial DNA does not provide us with any kind of yardstick with which to address the issue of species definition and tells us more about relationships and time of divergence between lineages as well about their demographic history. Several attempts of modelling based on the palaeogenetic data have been made in order to assess the possibility of interbreeding between Neandertals and modern humans at the beginning of the Upper Palaeolithic in Europe. Modelling based on very conservative and simple assumptions by Serre *et al.* (2004) initially suggested that gene flow between Neandertals and modern humans could not be rejected based on the limited number of specimens available at the time of their analysis. However, even then, Neandertal genetic participation in the modern European gene pool could not have exceeded 25% without being visible. More recently, Currat and Excoffier (2004) refined the model taking into account the fact that the invasion of Europe by modern humans would result in the establishment of a moving front of potential hybridization. Their analysis of the data concludes a maximum introgression of Neandertal genes into the modern European gene pools at a level of 0.1%.

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Paleoanthropology applied to Neanderthals

ANNE-MARIE TILLIER

Laboratoire d'Anthropologie des Populations du Passé (UMR 5199-LAPP)
Université Bordeaux 1 avenue des Facultés
33405 Talence ; phone 0033 40008935;
fax 0033 40002545 (am.tillier@anthropologie.u-bordeaux.fr)

The fossil record from Europe documents morphology and ontogenetic patterns in Neanderthals and is essential for addressing the question of distinctive growth patterns relative to modern humans. Evolutionary studies of skeletal remains demonstrate that bone preservation and sampling limitations magnify the difficulties in the reconstruction of the skeletal biology of immature Neanderthals. Non-adult individuals represent no more than 25% of the overall Neanderthal sample, and given the preservation of the fossil record, some skeletal growth stages are less well documented than others. The specimens employed to document distinct developmental stages within the entire Neanderthal population originated from sites often separated by hundred (or thousands) of kilometres and thousands of years in time. Only a few European sites have a large enough sample size to evaluate individual variation or to permit a comparison between non-adult and adult skeletal morphologies within a single sample. Geographical and temporal variations, as well as lack of data, should not be neglected in the analysis of the fossil record and the reconstruction of maturation patterns.

Recent modern human samples used in comparative analyses are mostly originating from regional collections (some of them used in forensic medicine studies). Reference modern standards (e.g. enamel microstructure growth components, tooth calcification and erupting sequence, limb proportions, body size) may or may not be appropriate for the specimens under investigation. Examinations limited to individuals belonging to sedentarized and/or industrialised populations are, indeed, inadequate to define the contrasts in skeletal robusticity between Neanderthal and early modern children, or to discuss evidence of