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WHO WERE THE NEANDERTHALS?

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Abstract: The Neanderthals are commonly thought of as a bizarre variant of our own species *Homo sapiens*, even by many who do not consider them to represent a "stage" in our own ancestry. But careful scrutiny of the record indicates otherwise. Both fossil and molecular evidence suggests that Neanderthals and modern humans last shared an ancestor more than 500 kyr ago, and the enlarging European hominid fossil record suggests that *Homo neanderthalensis* is actually the last surviving species of a fairly diverse endemic clade that flourished in the subcontinent between that time and about 27 kyr ago. For the scattering of fossils making up this record, including the crania from Steinheim, Reilingen, and the Sima de los Huesos, all show some but not all of the Neanderthal cranial hallmarks. For example, Steinheim possesses many of the typical Neanderthal features of the cranial rear and upper face, but lacks the puffy and retreating midface, while the best Sima cranium has Neanderthal-like supraorbital morphology and pterygoid tubercles in the lower jaw, but lacks the typical Neanderthal medial nasal projections, the ovoid coronal profile of the cranium, and Neanderthal features of the cranial rear such as the strongly undercut occipital torus. The resulting cluster of morphologies strongly supports the notion not only that *Homo neanderthalensis* was indeed a distinctive species, but that it emerged from a local adaptive radiation that occurred subsequent to the first successful implantation of hominids in Europe at some time between about 1.0 and 0.5 myr ago. The distinctiveness of the Neanderthals is further underlined by a new composite reconstruction of an entire Neanderthal skeleton recently made at the American Museum of Natural History. Combining elements from a half-dozen skeletons from almost as many countries, this new reconstruction contains sufficient continuity of elements from a single individual (La Ferrassie 1) to impart considerable confidence as to the reliability of its body proportions as well as its morphologies. And it shows that Neanderthals would have cut a very distinctive figure on the landscape, particularly with its narrow-topped and wide-bottomed rib-cage that tapers out below to match its wide, flaring pelvis with virtually no waist. As to lifestyles, while it is clear that at least in pre-contact (with Cro-Magnons) times the lives of Neanderthals were largely symbol-free, it is less obvious that the Neanderthals exploited a different range of food resources than that used by their clearly symbolic successors. Indeed it has been argued recently that the major shift in hunting-gathering subsistence strategies took place in the early Holocene, rather than in the "transition" between Middle and Upper Paleolithic ways of economic life. The Neanderthals were clearly ecological opportunists, successfully coping with a wide variety of environments through flexibility of behavioral response. Yet equally clearly they did not perceive and interact with the world around them as we *Homo sapiens* do today. We do the Neanderthals no favors by classifying them as *Homo sapiens neanderthalensis* simply because they had big brains. Instead, we should be trying to understand these unique hominids as the unique and separate evolutionary entity they undoubtedly were.

Introduction

Whether you believe that the first discovery that we *Homo sapiens* possess extinct fossil relatives took place in Belgium in 1829, or in Gibraltar before 1848, or in Germany in 1856, that discovery was of a Neanderthal fossil. And this historical fact has had profound consequences for our interpretation of the species *Homo neanderthalensis*, placing this distinctive hominid at front and center in portrayals of the hominid evolutionary drama. Of course, in the very earliest days of paleoanthropology, when there was no compelling reason to suspect diversity in human evolution, it made sense to look upon the Neanderthals as a variant or precursor of ourselves. But over the past century or more the growing human fossil record has made such scenarios increasingly difficult to sustain, as it becomes impossible to ignore the fact that this record contains a signal of systematic as well as moprhological diversity.

Certainly, as befits the species that is both behaviorally and anatomically the best-known among all known extinct human relatives, the Neanderthals must occupy a very special niche in our efforts to understand humanity's historical context and its place in Nature. These remarkable hominids do indeed constite a unique mirror that helps us discern just what it is that makes us unique. But given the emerging nature of the fossil record, this fact can no longer be deployed to justify the interpretation of the Neanderthals as a mere variant of our species, or alternatively as part of a single lineage that was bracketed at the far end of the timescale by "pre-Neanderthals" or "proto-Neanderthals", and at the near one by evolution or absorption into *Homo sapiens*. Yet such interpretations linger in a number of different guises, and the reason that they do so relates much less to the morphological facts of the matter than it does to the persistance of a deeply-rooted mindset. For the concept of a lineage of this kind is not based only

on the received belief that Neanderthals need to be fitted somehow into the specific context of *Homo sapiens*. It has also flourished in the context of the fairly strictly linear notion of expected pattern in human evolution that became common wisdom in the second half of the twentieth century.

This perspective grew out of the wholesale capitulation of paleoanthropology to the gradualist notion of the evolutionary process that was espoused by the movement known as the Evolutionary Synthesis (see Tattersall 1995). Ultimately viewing evolutionary change as amounting to very little more than generation-by-generation change in gene frequencies within lineages, even in its least dogmatic forms the Synthesis suggested that *Homo neanderthalensis* was part of a single isolated or quasi-isolated European and western Asian lineage that somehow evolved directionally over a period of upwards of 500,000 years; and indeed, in his classic paper of 1950, the ornithologist Ernst Mayr, one of the the architects of the Synthesis and the one whose views were perhaps most influential among paleoanthropologists, concluded that the Neanderthals were no more than a "geographical race" of *Homo sapiens*. Still, in terms of general patterns of mammalian evolution this pattern would have been unusual indeed. Europe was virgin territory for hominids until a rather late date; and when a new type of mammal successfully enters an environment for the first time, what typically ensues is an adaptive radiation of new species, as the newcomers busily explore the new adaptive and ecological opportunities that are available to them.

The Phylogenetic Position of *Homo neanderthalensis*

Over the past several years my colleague Jeffrey Schwartz and I have been looking quite closely at the European and western Asian fossil records associated with the Neanderthals (see, e.g., Tattersall & Schwartz 2000). And because among the quite large array of hominid fossils known from Europe in the past several hundred thousand years there exist several forms that share some but not all of their features with the Neanderthals, we have concluded that in the fossil record of Pleistocene Europe we are indeed looking at a hominid adaptive radiation, rather than at a linear sequence that leads insensibly from a "primitive" ancestral form to the latest, "classic", Neanderthals. This is particularly evident because *Homo neanderthalensis* is highly apomorphic in numerous cranial features and is consequently a relatively easy morphological entity to define – remarkably, much easier than the differently autapomorphic *Homo sapiens* has turned out to be.

Fossil crania with full-blown ("classic") Neanderthal identity, all known from within the past 200,000 years or so, have brow ridges that roll back smoothly out of the orbital roofs and form a double arch over eye-sockets that have curiously cut-off lower middle corners as a result of major expansion of the maxillary sinuses. They also have a narrow lower face, a rather puffed-out but sharply laterally-retreating midface, and variably-developed "medial projections" just inside the lateral margins of the very large and broad nasal cavity (Schwartz & Tattersall 1996). In posterior view, the large but low braincase is squat and smoothly rounded at the sides, and at the back it bears a pitted suprainiac fossa in the midline of the occipital plane, which often projects in a "bun". Below the fossa there is a long and horizontal "occipital torus" that is defined beneath by a broad undercutting, but above only in the midline by the shallow and sometimes rather small suprainiac fossa. In the mandible are seen such features as a retromolar space, a sigmoid notch that is deepest posteriorly near the low-set condyle, a rather cut-off gonial angle, an elevation at the front of the anterior inferior margin of the corpus, and no formation in the midline of the external symphysis of the distinctive modern human chin (Schwartz & Tattersall 2000). Internally on the jaw there is a medial pterygoid tubercle; and among the teeth the molars are particularly distinctive, with relatively restricted and complex occlusal surfaces that are ringed by blunt crests.

Despite various claims to the contrary (e.g. Bermudez de Castro *et al*. 1997), it seems unlikely on morphological grounds that either of the earliest human fossil samples known from Europe, the 800 kyr-old Atapuerca Gran Dolina *Homo mauritanicus* fragments (see Hublin 2001; Schwartz & Tattersall in press) and the possibly even older Ceprano *Homo cepranensis* calvaria (Mallegni *et al*. 2003), represents a population that is ancestral to later European hominids. It is also hard to find apomophies that the specimens assigned by most authors to *Homo heidelbergensis* share with members of the Neanderthal group (and the extreme size of the intracranial sinuses in certain *Homo heidelbergensis* specimens, notably Petralona, tends to rule them out of the ancestry of the latter). It still seems most likely that the ancestry of both later *Homo sapiens* and *Homo neanderthalensis* lies somewhere within the mass of material from Eurasia and Africa that has been ascribed to *Homo heidelbergensis*; but specific links are still lacking, and the earliest European hominids that can be allied with the Neanderthals on the basis of clear cranial apomorphies are the 400 kyr-old Sima de los Huesos fossils from Atapuerca. These have been allocated by their describers (Arsuaga *et al*. 1997) to the species *Homo heidelbergensis*, but their possession of various cranial apomorphies seen also among Neanderthals contradicts this attribution, while at the same time they do not display the full Neanderthal apomorphy suite (see discussion below). The earliest claimants to fully Neanderthal status include some (but not all) of the Ehringsdorf fossils, probably over 200 kyr old, and the Swanscombe occipital, which may be even older; by the time of the approximately 175 kyr-old Biache partial cranium, Neanderthal morphology was apparently well-established, and non-Neanderthal hominid cranial morphologies are no longer found in Europe until the arrival of the Cro-Magnons some 40-35 kyr ago.

Various European fossil hominids show some, but not all, of the characteristics that typify Neanderthals. Thus, the famous cranium from the German site of Steinheim, perhaps about 225,000 years old, has Neanderthal features of the supraorbital and orbital areas. It also has a large nasal cavity that shows a hint of a medial projection, and it shows various other Neanderthal hallmarks that include long, horizontal parietomastoid and anterior lambdoid sutures and a (faint)

suprainiac depression. However, this specimen also lacks the puffy and markedly retreating Neanderthal midface, and it is not usually considered to be a Neanderthal. Instead, among known forms, it appears to represent the "sister-taxon", the closest known relative, of the Neanderthals. Similar observations can be made of the partial braincase from the German site of Reilingen. This is at least 125,000 years old and perhaps as much as 225,000 years old, and it has several of the features that are found in both the Neanderthals and Steinheim. These include expanded petrosal pneumatization; a suprainiac depression; a horizontal occipital torus that is only fully delineated below; incomplete lateral ossification of the ectotympanic tube, and the rounded posterior profile of the braincase. On the basis of these similarities it is possible to interpret this specimen as belonging to a sister taxon to the one that includes both the Neanderthals and Steinheim.

Moving outwards, as already suggested the 400,000-plus-years-old hominids from Spain's Sima de los Huesos also have some but not all of the typical Neanderthal characters. Features that these fossils share with *Homo neanderthalensis* include: orbital and brow-ridge shape; a large nasal aperture that shows some forward extension of the frontal processes; a long, horizontal parietomastoid suture; and a pitted suprainiac depression. There are medial pterygoid tubercles in the lower jaw. However, the nasal fossa lacks a medial projection (instead, there is a clear conchal crest); the braincase rear profile shows much more vertical sides than in Neanderthals, together with a central peaking at the top; there is no well-undercut occipital torus; and the midface is not puffy and does not retreat sharply. Thus, while the possession of several "Neanderthal" apomorphies clearly excludes the Sima hominids from the species *Homo heidelbergensis* to which they were allocated by Arsuaga *et al*. (1997), they are equally clearly not Neanderthals, and nobody has ever claimed that they are. Again, it seems that these hominids are best interpreted as representing the sister group of those already mentioned.

It should be emphasized that the Neanderthal, Steinheim, Reilingen and Sima "morphs" I have just characterized are simply morphological groupings, and no claim is made that all of them necessarily represent distinct species in the biological sense – although some of them doubtless do. But what they do appear to provide evidence for is an *in situ* European hominid radiation. Certainly, the morphologies of these fossils – and others like them – do not form a neat transformation series that would suggest a linear pattern of evolution within a single Neanderthal lineage (even though the task of forcing them into such a structure is facilitated by generally poor dating). Instead, this apparent nesting of European hominids of the past 400,000 years or so can be interpreted as reflecting a major evolutionary exploration over this period of the ecological possibilities offered by the new lands of Europe. Rather than constituting the end-product of a single lineage that steadily evolved toward the morphology we see in the so-called "classic" Neanderthals of the last Ice Age in Western Europe, the distinctive *Homo neanderthalensis* actually formed part of a wider local radiation of hominids over this period. This signal in the European hominid fossil record of diversity rather than of linearity actually makes a great deal of sense given the wildly fluctuating environmental conditions that reigned in Ice Age Europe. For the climatic oscillations of the later Pleistocene evidently led to the frequent abandonment and recolonization by hominids of wide swaths of the subcontinent, even as the correlated fluctuations in sea levels played havoc with its geography. The emerging pattern of the European hominid fossil record suggests that *Homo neanderthalensis* was simply the most successful species, and the latest survivor, of an endemic European hominid radiation. And this, intriguingly, suggests that the Neanderthals may have done to their own closest relatives exactly what *Homo sapiens* would later do to them when, in the form of the Cro-Magnons, our own species arrived in Europe towards the end of the last Ice Age.

Neanderthals as an Individuated Species

Phylogenetically, then, the Neanderthals were simply members of an endemic hominid radiation in Europe with its roots perhaps half a million years ago. But exactly what kind of beings were they? As already noted, for historical reasons as well as because they had brains as large as ours, they have often been viewed in recent years simply as a bizarre variant of our own species, *Homo sapiens*. But they differed from us anatomically in numerous ways, and I have been convinced for decades now that they are to be understood properly only as an entirely independent evolutionary entity, that is to say, as their own species *Homo neanderthalensis* (see Tattersall 1986). I am convinced more than ever of this by the reconstruction of an entire Neanderthal skeleton recently completed by my American Museum of Natural History colleagues Gary Sawyer and Blaine Maley. Due to the fact that these hominids at least occasionally buried their dead, partial skeletons of quite a lot of Neanderthals are known. But all of them are very far from complete, and Sawyer and Maley had to combine casts of bones from half a dozen Neanderthal skeletons, from France, Israel, Belgium and Germany, to reconstruct the skeleton illustrated in figure 1.

Seeing the entire being in front of you like this is very different from looking at individual bones, or even at lists of characteristics in a monograph. And I must say I had a really visceral reaction when I first saw this skeleton fully assembled. Because, for the first time, I felt that I had truly *met* a Neanderthal. And, moreover, that I had met a creature truly unlike ourselves. Reviewing lists of differences between *Homo sapiens* and *Homo neanderthalensis* skeletal elements in a monograph, or even directly comparing the bones, lacks the *Gestalt* impact of a full-size reconstruction. This composite skeleton will be described in detail elsewhere (Sawyer & Maley in press), but even a superficial comparison (such as that shown in figure 2) between the composite Neanderthal and a modern individual of comparable height (approximately 164 cm) shows some remarkable differences in proportioning of the major body elements. In this connection it is important to note that we can have considerable confidence in the accuracy of the reconstructed body proportions because, in all major body areas, the reconstruction has continuity in elements from a single individual: the La Ferrassie 1 Neanderthal.

Figure 1. Front and side views of the composite Neanderthal skeleton reconstructed by G.J. Sawyer and Blaine Maley. Photograph by Denis Finnin, courtesy of the American Museum of Natural History.

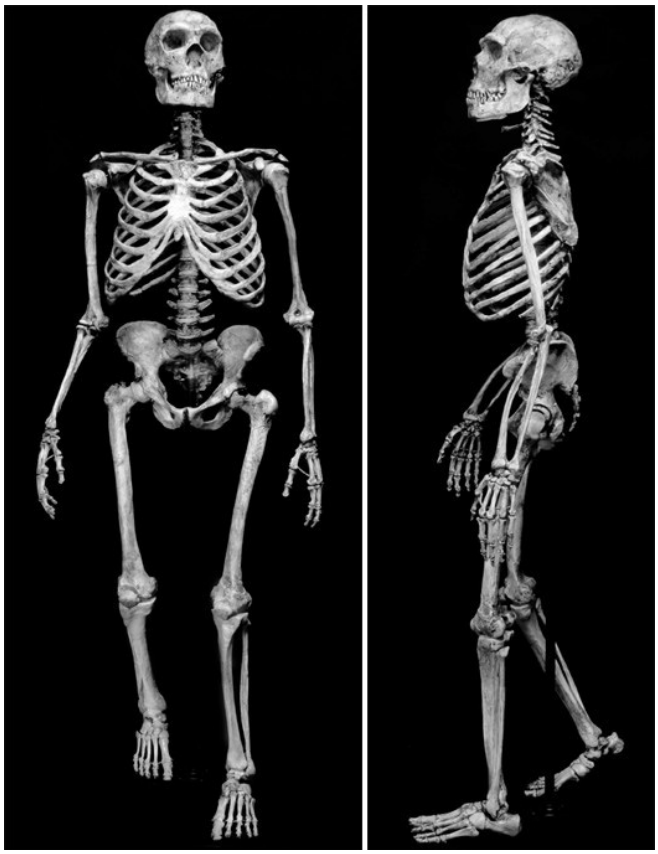

Figure 2. Comparative front views of the composite Neanderthal skeleton (left) and a modern *Homo sapiens* of the same stature. Photograph by Ken Mowbray.

Particularly striking are the extreme differences between the *Homo neanderthalensis* and *Homo sapiens* skeletons in the form of the thorax. The conical Neanderthal rib cage shows a dramatic upward tapering, from the the widely flaring waist area up to its narrow top; and in this characteristic it closely resembles the rib cages of both the "Lucy" (NME AL288-1, *Australopithecus afarensis*, ca. 3.2 Ma) and the "Turkana Boy" (KNM-WT 15000, *Homo ergaster*, ca. 1.6 Ma) specimens, the only even tolerably complete such specimens from earlier in the record. The broad inferior sweep of the rib cage in the Neanderthal is matched by the remarkable width of the broadly flaring ilia of its pelvis, and a similar conformation is found in the Lucy and Turkana Boy specimens (albeit attenuated in the latter by its immaturity). In contrast to what can thus apparently be regarded as the primitive hominid pelvic and thoracic proportions, the *Homo sapiens* skeleton seen in figure 2 appears strikingly derived, with its parallel-sided, barrel-shaped thorax and narrow pelvis. Taken together with the laundry-list of detailed osteological differences between Neanderthals and modern humans in the skull and the postcranial skeleton reviewed, among many others, by Stringer and Gamble (1995) and Tattersall & Schwartz (2000), the proportional differences just pointed out present an unassailable morphological case for distinguishing between the species *Homo neanderthalensis* and *Homo sapiens*. Indeed, in many other mammal groups species presenting morphological differences on this scale might well be classified in different genera without raising any eyebrows.

Neanderthals on the Landscape

It is thus fairly certain that when the first Cro-Magnons arrived in Europe, some 40,000 years ago, they would have recognized in the Neanderthals creatures very different from themselves. How the two kinds of hominid would have interacted is material for a separate discussion, and I will just say here that I find it hardly credible that there was any biologically significant exchange of genes between the two populations. And this would, of course, be entirely unsurprising when one considers that both molecular and morphological evidence suggests that the two hominid lineages were probably separated by at least a half million years of independent evolution (Krings 1997; Tattersall & Schwartz 2000).

This message of biological distinctness is fully consistent with the behavioral one that I derive from looking at the archaeological record the Neanderthals left behind. Admittedly, from the economic point of view the picture is a bit murky. In Europe the Mousterian and Upper Paleolithic tool kits of the Neanderthals and early modern people are for the most part easily distinguishable; but this had not been not true of *Homo neanderthalensis* and *Homo sapiens* many millennia earlier in Israel, where both species are found in Mousterian associations. And Ofer Bar-Yosef (2004), among others, has recently argued that the evidence is equivocal for any major economic restructuring as the Mousterian

gave way to the Upper Paleolithic. Instead, Bar-Yosef sees a truly innovative general change in extractive habits only in the very latest phases of the Old Stone Age. The implied basic similarity in the structure of Neanderthal and modern diets in Ice Age Europe is supported by analyses of food remains left by *Homo neanderthalensis* and *Homo sapiens* at late Pleistocene European habitation sites; these show, overall, a general similarity in composition (Stewart 2004). The few available stable-isotope and dental-wear studies of Neanderthals agree in suggesting that Neanderthal diets were generally rich in meat (see review by Drucker & Bocherens 2004); but detailed studies of animal food remains at Neanderthal sites suggest also that the strategies used by these hominids to obtain such resources varied substantially in space as well as in time (e.g., Stiner 1994). It thus seems eminently reasonable for Bar-Yosef (2004) to caution us that, whatever the hominid, later Pleistocene foraging strategies must have been largely governed by what was seasonally available in the local environment. The environments that the Neanderthals faced varied enormously, both locally and over time, and the animal and plant resources offered by these environments differed equally dramatically. Hence it seems entirely fair to conclude that Neanderthals were behaviorally opportunistic and highly flexible in the way in which they made their living, in a diversity of often extremely difficult environments.

Yet while in the beginning, at least, the overall economic portraits presented by the Neanderthals and the Cro-Magnons may not have differed too dramatically, it seems a reasonable inference that the Neanderthals were non-symbolic and non-linguistic, at least in the way in which we understand these things today (see discussion by Tattersall 2004). This is because, at least before the arrival of the Cro-Magnons in their European homeland, the very abundant material record of the Neanderthals contains nothing very compelling in the way of symbolic objects. In dramatic contrast, the record luxuriantly attests that the lives of the Cro-Magnons were, from the beginning, drenched in symbol. Socially and cognitively, here were two entirely different entities, despite some late hints that the Neanderthals, always facile imitators, might have picked up some behavioral traits from the invaders. And the cognitive contrast that the symbolic record suggests existed between the two hominid species strongly implies that, despite the fact that both necessarily exploited the same economic resources, the Neanderthals perceived, related to, and interacted with the world around them in ways that were very different from the Cro-Magnons' – and from our own.

So what does this mean for our understanding of the Neanderthals? It is no denigration of a tough, resourceful and behaviorally flexible hominid species to say that it did business differently from us, and it is clear that we are doing the Neanderthals no favors by classifying them as *Homo sapiens neanderthalensis* simply because they had big brains. We need to stop writing them off as a bizarre and by implication inferior version of ourselves, and to focus on understanding these remarkable hominids as the unique and separate evolutionary entity that they undoubtedly were. Which is something we can only do if we concede *Homo neanderthalensis* its own identity: an identity entirely separate and distinct from our own.

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