

Neanderthals, *Homo sapiens*, and the question of species in paleoanthropology

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Summary - *Species boundaries in the fossil record are frustratingly elusive to recognize, largely because of the untidy way in which biological diversity is “packaged”. Accepting that species are most fundamentally “individuals,” with origins, births, and extinctions, rather than essentialist collections of traits, means also accepting that neither qualitative nor quantitative assessments of morphology will provide an infallible guide to species status. Beyond a certain level of differentiation the problem ceases, however, and this level is comfortably exceeded by *Homo neanderthalensis*. What is more, the Neanderthals appear not simply to constitute a separate species lineage, but to form part of a larger endemic European clade to which such distinctive forms as the Sima de los Huesos and Steinheim fossils also belong. This clade has a contemporary occurrence in Europe with the larger and more cosmopolitan species *Homo heidelbergensis* (exemplified by specimens such as those from Arago, Petralona, Kabwe, and Bodo, and probably also Dali and Jinniushan), showing that hominid history in this region is more complex than simply that of a single lineage evolving toward the terminal species *Homo neanderthalensis*.*

Keywords - *Neanderthals, European hominids, *Homo neanderthalensis*, *Homo heidelbergensis*, Human evolution, Species recognition.*

Introduction

No problem in paleoanthropology is more fraught than that of recognizing species in the hominid fossil record. How to apportion the large mass of hominid fossils now known into biologically meaningful units has been debated endlessly, and seems set to splinter paleoanthropology for years to come. The negative consequences of this lack of consensus are severe, not least because this failure to agree on our basic evolutionary units deprives our discipline of a common terminology. This is bad enough among colleagues who know more or less what their professional counterparts believe; but it is nothing short of disastrous when it comes to communicating our science to the public that supports us.

There are many reasons for this discord on

the matter of species and their recognition in the hominid record; but perhaps the unfortunate state of affairs just described is above all a matter of unrealistic expectations. The reductionist human mind is most comfortable operating in an environment where boundaries are sharp and can be taken for granted; gray areas are always problematic. But while species are the basic units into which groups of individuals are “packaged” amid the rampant diversity of Nature, such packaging is not necessarily neat. And it is precisely the lack of tidiness so evident in the packaging of Nature that is reflected in the huge variety of species definitions currently on offer. Indeed, there are currently so many definitions of species to choose from (at least 25 according to Coyne & Orr, 2004) that to make them usable they have in turn been subdivided into categories: inclusionary,

exclusionary, evolutionary, and so forth. All of these definitions have their attractions, all have their failings; but not one of them usefully applies to all cases in the real world. Indeed it appears that, in our ongoing search for a better way of defining species in the abstract, we end up pleasing nobody in the attempt to please everybody.

Perhaps, then, it is time to step back and view the problem from another angle. Species are the end products of speciation, and almost every species definition available takes for granted that the processes of speciation, by which species originate, must produce a basically uniform outcome. Yet the reality is that species, which are best viewed as the products of speciation rather than as a definable category in themselves, are far from consistent in their characteristics. For speciation is *not* a unitary mechanism, and species are best viewed as a *result* that is only visible in retrospect and that may come about through a whole raft of causes. Speciation may be associated with major developmental changes in a population; or it may be associated with tiny external morphological cues, or even with subtle shifts in behavioral preferences. The only thing that all potential agents of speciation (at levels ranging from point mutations to chromosomal rearrangements to developmental cascades) need have in common is that they result in the establishment of a population as an *effectively* independent historical entity. Michael Ghiselin (1974) pinpointed the crux of the matter when he described species as individuals; and he was wise not to tout this characterization as a definition.

The notion of species as individuals places species in the same category as pornography, at least insofar as it acknowledges that the entity concerned defies absolute definition, and thus poses problems essentially of recognition. It also means that the kind of problem that alpha taxonomists face is not unique. Judges share it. And judges, who claim to know pornography when they see it even if they cannot satisfactorily define it, have long decided such cases on the preponderance of the evidence. Perhaps this is how paleoanthropologists should also proceed, and cease worrying about whether long-extinct

populations, now known only from fossils, could potentially have “exchanged genes” with others or not – something that is essentially unknowable. And it is also, to a large extent, irrelevant. Species are not like absolutely watertight containers: they are dynamic and more or less cohesive entities which, to misappropriate with apologies a term from Niles Eldredge (2003), resemble a “sloshing bucket,” in which gene frequencies swill back and forth within the containing walls, the occasional overflow being effectively lost (Tattersall, in press).

The key attribute of species is that they maintain their historical identity over sustained periods of time, regardless of any incidental gene inflow or outflow at the edges. In which case, the essential question that has to be decided on the balance of the evidence is not whether a morphologically or otherwise diagnosable population can and/or did exchange genes with close relatives; it is whether this population is or was a fully individuated historical entity, with a unique history. If we can show reasonable cause to believe that such an entity is or was beyond the point of reticulation, we are justified in naming it a distinct species, and in regarding it as a fully individuated actor in the evolutionary play. Lines of evidence available to enter into this evaluation are numerous, and all are embedded in one or another of the many species definitions to hand. But it is important to appreciate that, short of the total inability to form zygotes, all of these lines of evidence, whether they involve morphology, hybridization, behavior, or whatever, are *indirect*. Among fossil forms – and among living ones with any degree whatever of interbreeding capacity – there is, quite simply, no “silver bullet” that will infallibly tell you that you are dealing with an historically individuated entity. And this is why we are obliged to look at the preponderance of the evidence, limited in this contribution to the strictly biological.

***Homo neanderthalensis*: morphological distinctiveness**

From the very beginning there have been two opposing views on how to classify the large-

brained fossil hominids we know informally as Neanderthals. In the tradition established by Schaaffhausen (1859) and Huxley (1863) shortly after the discovery of the Feldhofer type fossil, many paleoanthropologists today continue to regard the Neanderthals as a variant of *Homo sapiens*, *H. s. neanderthalensis* (e.g., Trinkaus, 1983; Wolpoff *et al.*, 2004). On the other hand, many incline to the almost equally venerable view, first articulated by William King in 1864, that the Neanderthals constitute their own species, *Homo neanderthalensis* (Tattersall, 1986; Stringer & Gamble, 1993, Rak, 1998). It is important to note that this is not an issue that will ever be settled by compromise between these extremes: either the Neanderthals constituted an individuated historic entity, or they did not, although there is no way to know *a priori* how such individuation might be expressed in the record.

Interestingly, there has never been any really significant debate over whether or not the Neanderthals form a diagnosible entity. In recent decades suggestions have occasionally been made that one or another fossil reflects some degree of hybridization between Neanderthal and modern populations (e.g. Wolpoff, 1980; Duarte *et al.*, 1999); but none of them has withstood close scrutiny, and none impinges on core Neanderthal distinctiveness as reflected by these hominids' well-entrenched informal name. Indeed, Jeffrey Schwartz and I have argued that in terms of morphology alone the Neanderthals constitute the most clearly demarcated extinct group of extinct hominids known (Tattersall & Schwartz, 2000, 2006; Schwartz & Tattersall, 2002, 2005). Whether a particular fossil is or is not a Neanderthal has rather rarely been an issue; and indeed, the boundaries of Neanderthal-ness have tended to become somewhat sacrosanct, as witness the allocation by Arsuaga *et al.* (1997) of the Atapuerca/Sima hominids to the species *Homo heidelbergensis*, despite the fact that they exhibit a host of apomorphies in common with Neanderthals – and few, if any, with the other fossils more conventionally ascribed to *Homo heidelbergensis*.

Among the features traditionally cited as Neanderthal apomorphies (see, for example,

Hublin, 1978, 1988; Santa Luca, 1978; Vandermeersch, 1981; Stringer *et al.*, 1984; Schwartz and Tattersall, 1996a,b, 2005; Rak & Hylander, 2003) are the rounded and double-arched supraorbital tori; inferomedially truncated orbits; narrow lower face with sharply retreating zygomatics; medial projections anteriorly in the large nasal fossa with a clearly delineated prenasal fossa below; “puffiness” of the midface reflecting the presence of large maxillary sinuses; an angling along the anterior squamosal suture that divides the temporal fossa into clearly demarcated anterior and posterior portions; the ovoid (“en bombe”) coronal cranial profile; the pitted suprainiac fossa that lies above an “occipital torus” that is really only properly demarcated below; highly pneumatized petrosal; long, narrow and ovoid foramen magnum; sigmoid notches of mandible deepest in front of a low-set condyle; obliquely truncated gonial angles; sigmoid notch crests that terminate close to the lateral ends of the condyles; relatively thin bone across the base of the symphysis. The molars have relatively complex but constricted occlusal surfaces, with centroconids/centrocones and inwardly sloping sides. Additional dental apomorphies are noted by Bailey (2002, 2004) and Bailey & Lynch (2005); and CT studies by Spoor *et al.* (2003), among others, have suggested that the labyrinth of the middle ear of Neanderthals is so distinct from that of modern humans as to suggest “differences in locomotor behaviour and the kinematic properties of the head and neck” (Spoor *et al.*, 2003: 141).

Cranially, then, there is an unmistakable Neanderthal *Gestalt*: one that contrasts dramatically with that of *Homo sapiens*, which represents another theme entirely.

This observation holds equally for the postcranial skeleton. Sawyer and Maley (2005) not long ago described a complete composite Neanderthal skeleton confected from the remains of six incomplete skeletons from sites in four different countries. It has long been known that Neanderthals exhibited a whole variety of distinctive characteristics of the bones of the postcranial skeleton, including such features as thick-walled long bones with restricted

medullary cavities and expanded articular surfaces; long scapulae with expanded rotator-cuff attachment areas and long and narrow glenoid fossae; long clavicae with relatively flattened shafts; pelvises with flaring iliac blades and long, attenuated pubic rami; and the large carpal tunnels, the expanded pollical and ulnar distal phalangeal tuberosities, and the generally accentuated muscle attachment areas in the hand skeleton (see descriptions in Trinkaus, 1983). What is remarkable about the new reconstructed Neanderthal skeleton, however, is the degree to which it departs from *Homo sapiens* in the overall proportions of the thoracic and pelvic regions (see Fig. 1). In contrast to the barrel-shaped human rib cage, which tapers slightly inwards not only at the top, but also at the bottom to match the narrow pelvis, the Neanderthal rib cage is extremely narrow at the top – despite broad shoulders defined by the long clavicae – and flares dramatically out and down to match the very wide pelvic basin. Additionally, the mobile vertebral column is set against a rather more inferiorly positioned sacrum, substantially reducing the effective vertical length of the waist (Sawyer and Maley, 2005).

It is important to note that the Neanderthals were not unique in many of those features that distinguish their skeletons from that of *Homo sapiens*. Both cranially and postcranially, many of them are shared with certain earlier extinct hominids from Europe. Foremost among such fossils are those from Steinheim in Germany, and the Sima de los Huesos at Atapuerca, in Spain. The Steinheim cranium, uncertainly dated but probably marginally earlier in time than anything claimed with any certainty to be a Neanderthal, shares with Neanderthals certain features of the face (for example, supraorbital and orbital morphology, presence of a prenasal fossa) and of the cranial rear (e.g. suprainiac fossa, horizontal occipital “torus” that is only fully defined below). Yet it is distinctive in its tall coronal profile, broad zygomas, and a variety of other features (Schwartz & Tattersall, 2005; Tattersall & Schwartz, 2006). Few have cared to call this

specimen a Neanderthal, and indeed there is little evident reason to do so; instead, it seems most rational to allocate the Steinheim specimen to a sister taxon, allied to the Neanderthals but nonetheless distinct from them. A similar conclusion applies to the 500,000 year-old fossils from the Sima de los Huesos. These, too, share features of the cranium with the Neanderthals, but fewer than in the case of Steinheim. Postcranially, the Sima remains are equally interesting, in that they also show the robustness of the postcranial skeleton and the flaring of the pelvis that is so well documented in the Neanderthals (Tattersall & Schwartz, 2006). Taken together, these fossils suggest the existence in the Middle Pleistocene of Europe of an endemic hominid clade, consisting on present evidence of Neanderthals+Steinheim, with Sima as the immediate outgroup, to which all of these hominids belonged. On chronological grounds it might just be argued that the Sima (500 kyr), Steinheim (ca. 225 kyr) and Neanderthal (<160-200 kyr) fossils might form a transformational sequence, but if this was so the rate of transformation was far from smooth, and on current evidence this interpretation seems like special pleading.

The emerging picture of systematic complexity in the Middle Pleistocene of Europe is enhanced by the dating of the Sima hominids as penecontemporaneous with the morphologically very distinct hominids of Arago, in southern France (Bischoff *et al.*, 2003). Dental, and to a certain extent mandibular, evidence allies the Arago fossils with the Mauer type mandible of *Homo heidelbergensis*, and both the cranial and dental fossils from Arago show clear morphological distinctions from hominids of the Neanderthal-group, while allying them with other European fossils such as the poorly-dated Petralona cranium from Greece and with the Bodo and Kabwe specimens from Africa. And although it is not inconceivable that the rather older (600 kyr) and more plesiomorphic Bodo specimen might in a broad sense represent the general stock from which the Neanderthal group as well as hominids of Arago type emerged, the Petralona specimen shows massive cranial

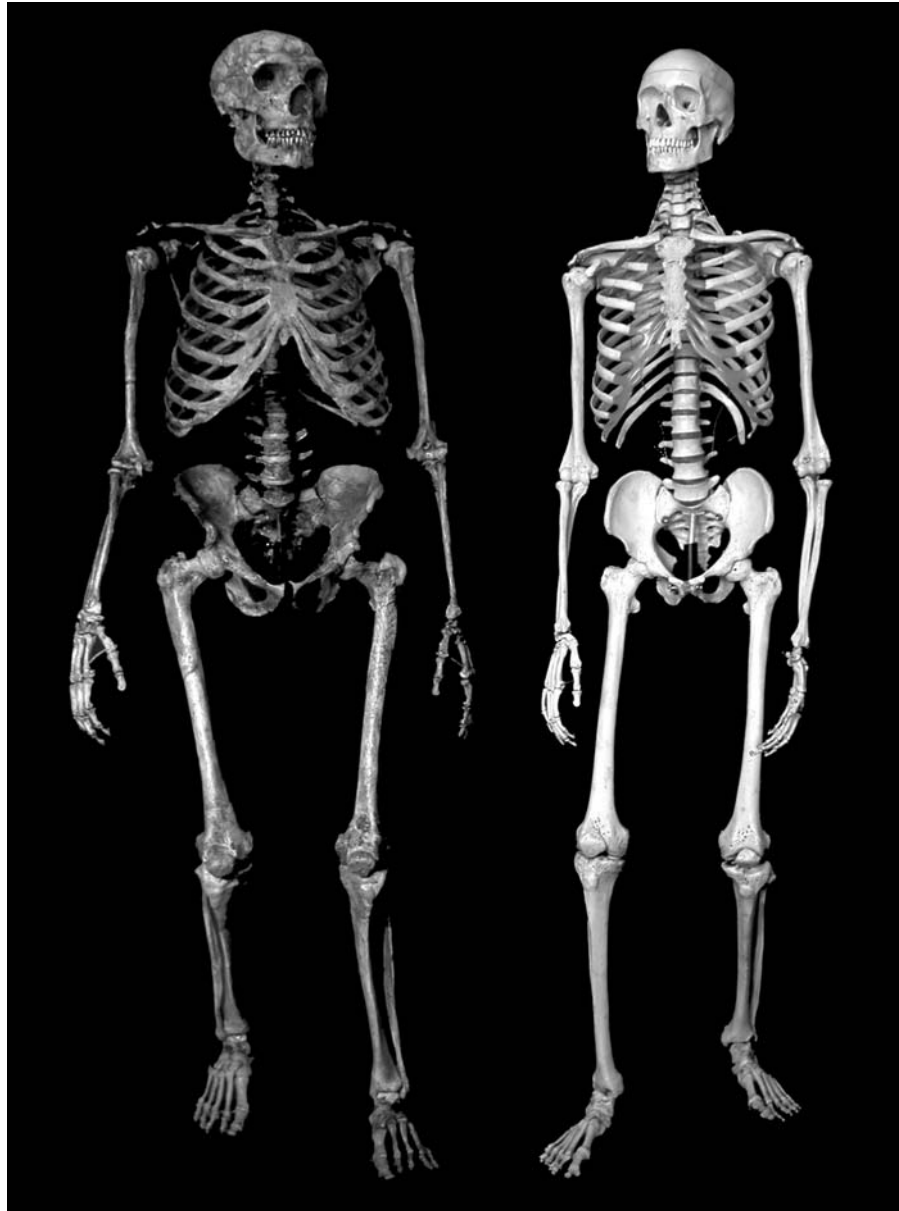


Fig. 1 - Front view of the composite Neanderthal skeleton (Sawyer and Maley, 2005) compared with a skeleton of a modern Homo sapiens male of similar stature. Photo courtesy of Ken Mowbray.

pneumatization that clearly excludes it from membership in any pre-Neanderthal lineage. Evidently, more than one lineage of hominid existed concurrently in Middle Pleistocene

Europe, and specimens such as those from Bilzingsleben and Vérteszöllös hint tantalizingly at more systematic complexity yet (Schwartz and Tattersall, 2005; Tattersall & Schwartz, 2006).

***Homo neanderthalensis*:
a fully individuated species?**

Against the background just sketched, *Homo sapiens* appears highly distinctive. Indeed, with its gracile and retracted face, tall, short braincase, bipartite brow ridges, unique chin structure, and a host of other features, anatomic *Homo sapiens* does not pair comfortably with anything else yet known (Schwartz & Tattersall, 2005), and appears as the outlier among all known late Middle and Late Pleistocene species of *Homo*. The Neanderthals, on the other hand, fall securely within a wider hominid clade. Thus, by the simple geometry of systematic relationships, it is barely credible that Neanderthals and modern humans could fall within the same species – which would necessarily have to be expanded to include such forms as the Sima hominids and even possibly the Mauer/Arago group. What is more, the sheer scale of the morphological differences between the Neanderthals and *Homo sapiens* makes it vanishingly implausible that both could fall within the envelope of morphological variation within a single species. I have pointed out elsewhere (Tattersall, 1986, 1993) that osteodental differences between primate species classified within the same genus are typically subtle, and that among mammals in general bony distinctions on the order of those that separate Neanderthals and modern humans are commonly associated with different genera. It is fairly fruitless to argue about exactly where in quantifiable terms it is reasonable to draw the morphological line among hominid species, but it is clear that in this case that limit has been abundantly exceeded.

Interestingly, the new Neanderthal skeletal reconstruction, as well as the studies of the Neanderthal pelvis by Rak (1990) and of inner ear morphology by Spoor *et al.* (2003), suggest that differences in gait existed between Neanderthals and modern humans. In particular, the very broad and short waist would have imparted a “stiffness” to Neanderthal movement that would have made them cut a very distinctive figure on the landscape. The consequent distinctive behavioral signal further reduces the probability

that the two kinds of hominid would have shared any elements of a specific mate recognition system, and that any biologically significant level of gene exchange ever occurred between them. This conclusion of genetic separateness has recently also been bolstered by molecular evidence (e.g., Krings *et al.*, 1997; Caramelli *et al.*, 2003; Lalueza-Fox *et al.*, 2005). There is some heterogeneity among the samples of Neanderthal mtDNA that have been isolated – just as there is morphologically among Neanderthals from different sites and times – but all analyses show the Neanderthal population to be a substantial outlier to all modern human populations; and Currat and Excoffier (2004) have calculated that even on optimistic assumptions the maximum interbreeding rate between the populations following the Cro-Magnon incursion into Europe would have been below 0.1%, indicating effective intersterility. Once again, the evidence is strongly in favor of the inference that the two kinds of hominid were fully individuated.

Conclusion

In recognizing species in the fossil record there is, as pointed out above, no “silver bullet” that will ever demonstrate absolutely definitively that two closely related lineages are historically individuated, as species must be. In principle, then, no claim of this kind – or indeed, to the contrary – can ever be “proven.” But science is fortunately not about proof (Tattersall, 2002); and the “preponderance of the evidence” approach advocated here makes ineluctible the conclusion that *Homo sapiens* and *Homo neanderthalensis* are properly regarded as separate species. Much more difficult will be the task of properly distinguishing species within the wider Neanderthal clade. Since in the case of modern humans vs Neanderthals we are facing an either/or dichotomy (one species, or two?), the conclusion that the two kinds of hominid represent entities fully individuated from each other is extremely robust. This is because the evidence in favor of separate specific status is overwhelming, yet all

that is required is to move beyond the point of balance. For the moment, at least, we can be confident in dignifying *Homo neanderthalensis* with its own individual identity: an identity that is well deserved, but that has too often been denied.

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