

## Neanderthals Revisited: New Approaches and Perspectives

Katerina Harvati and Terry Harrison (editors)

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Any book on the Neanderthals has the potential to attract a great deal of interest among both professional and popular audiences. Neanderthals have been the subject of palaeoanthropological investigation and debate for some 150 years and still attract a great deal of scientific and popular attention. *Neanderthals Revisited: New Approaches and Perspectives* (2<sup>nd</sup> printing, 2008) is the result of a conference held at New York University in January 2005, which provided a forum “in all aspects of Neanderthal research” (p. xiii), particularly including new technological and conceptual approaches to interpreting the Neanderthal fossil record. As such, this volume presents a stimulating survey of current perspectives on Neanderthal issues, ranging from species concepts and systematics, to dental morphology and developmental studies, to molecular approaches and morphological analyses. If not entirely balanced, the volume highlights a diversity of current research, and its wide-ranging scope would foster a great deal of discussion in any graduate-level seminar course.

In their introductory chapter, the editors comment that Neanderthals are the “best represented, most comprehensively studied, and most thoroughly understood group of fossil hominids” (p. 1), yet controversies concerning Neanderthal systematics, morphology, and behaviour continue to stimulate robust debate whenever they are raised. This absence of consensus may result from “deeper theoretical and conceptual issues” (p. 2) relating to methods of analysis, interpretation, and contextualization of research and its results, and resolving these issues will take yet more time.

In general, research on differing aspects of Neanderthal paleobiology is framed in the context of the modern human origins debate. The essential questions seem to be—are the observable differences in “Feature X”: a) distinctive enough that Neanderthals should be viewed as an independent species/lineage in relation to modern *Homo sapiens*?; or, b) relevant in some way to Neanderthal extinction? As a “Plio-Pleistocene Man” myself, this over-riding theme can be tiresome. This volume presents thought-provoking research in diverse areas, but is it really the case that hand morphology, thorax capacity, associated archaeology, temporal bone morphology, developmental patterns, brain size, and more, can be best understood in the context of the disappearance of Neanderthals from the fossil record? If so, it is amazing that they ever managed to evolve at all!

Within the diversity of research in this volume, the two traditional interpretations of the Neanderthal-modern

human relationship are, of course, represented: a) those favouring the view that Neanderthals are a (morphologically, genetically, behaviourally) distinct species representing a separate evolutionary lineage (i.e., Replacement, mostly); and, b) those which do not, or may not, or are still working on another idea (i.e., various degrees of Continuity).

The overview by Tattersall and Schwartz (Chapter 2) unsurprisingly falls into the first group, summarizing information on Neanderthal morphology and the issues arising on Neanderthal systematics. They have compiled a comprehensive list of Neanderthal craniodental and postcranial apomorphies, and conclude that Neanderthals are “an unusually coherent and readily recognizable group” (p. 13), and that Neanderthals and modern humans “were/are independent historical as well as morphological entities” (p. 15); Neanderthals, they say, “would have cut a very different figure on the landscape from *Homo sapiens*” (p. 15). It is very difficult to argue against the position that Neanderthals were morphologically distinct, but if the systematics were really this cut and dry, there would be no need for volumes like this, not to mention the long-standing debate over such fundamental questions.

Tattersall and Schwartz have emphasized the distinctiveness of Neanderthals, but other reconstructions over time have emphasised aspects of their similarity to modern humans. This latter perspective can be traced back to Coon’s 1930s reconstruction of a Neanderthal, benefiting from a shave and haircut, and riding unnoticed on the New York subway. Always at odds, these alternating interpretations are like a “mini-skirt” of Neanderthal fashion—they keep coming back, but this line of argument obscures issues of more evolutionary significance. In my view, these perspectives probably reflect more about the personal viewpoints of modern paleoanthropologists than they do about our scientific understanding of Neanderthal paleobiology.

Other contributions present taxonomic and phylogenetic interpretations based on various distinctive Neanderthal traits. Bruner and Manzi (Chapter 3) present a CT-based analysis of the Saccopastore 1 cranium, concluding that this specimen represents “the earliest record of full Neanderthal identity” (p. 32), despite its small brain size and other differences. Bailey and Hublin (Chapter 10) provide a detailed and well-illustrated summary of Neanderthal dental traits, and identify isolated teeth associated with a Châtelperronian assemblage from Arcy-sur-Cure as Neanderthals, reinforcing their view that Neanderthal and modern human cultural associations are not mixed. Harvati and

Weaver (Chapter 13) argue that traits from most regions of the skull are phylogenetically uninformative because of adaptive and functional influences on morphology; in their analysis, the temporal bone is an exception, and morphological distances derived from this region illustrate Neanderthal distinctiveness. Brauer and colleagues (Chapter 15) employ a variety of statistical techniques to demonstrate the distinctiveness of Neanderthal fronto-facial morphology compared to the Mladeč early European modern human sample, and thus to reject the hypothesis of continuity between these populations.

These papers all support a common conclusion—Neanderthals are a morphologically distinct species and/or lineage. Given close consideration, however, the arguments and methods among studies are not all consistent. The latter two papers provide an example—the first paper warns that morphological data from some cranial regions, such as the face, are not phylogenetically informative, then the second paper presents an analysis of fronto-facial morphology expressly to make a phylogenetic argument. Obviously, this conflict is a side effect of compiling diverse independent contributions—the two papers are not collaborative—but how should the student or non-specialist interpret such complex (and unresolved) issues in a biologically meaningful way?

With less focus on phylogeny, another group of papers evaluate the physiological, behavioral and developmental implications of Neanderthal morphology. From a bioenergetic perspective, Churchill (Chapter 7) tested different explanations for increased Neanderthal thoracic volume (and thus body surface area), concluding that heat production cost, not heat retention (Bergman's Rule) was the limiting factor for Neanderthal energy budgets. Pearson and colleagues (Chapter 8) compared patterns of postcranial robusticity to evaluate differences in mechanical loading patterns relating to different subsistence behaviours. Their results “de-emphasize the distinctiveness of Neanderthals” (p. 151) compared to a variety of recent modern human groups, but suggest that some early modern humans (e.g., Skhul-Qafzeh) were distinct. Niewoehner (Chapter 9) analyzed the morphology of Neanderthal hand bones compared to other Late Pleistocene humans, finding considerable variability in features relating to grip strength and manipulative postures relating to tool use. Of particular interest is the finding that some Early Upper Palaeolithic samples demonstrate similarities with Neanderthal hand bones, particularly in features relating to the transmission of high levels of force at the base of the thumb. These anatomical patterns suggest that the transition from Mousterian to Upper Paleolithic for related tool using and manufacturing behaviours “was slow and gradual rather than abrupt” (pp. 184–185).

What I appreciate about this group of papers is that they actually do improve our understanding about “being a Neanderthal,” and focus much less on questions of phylogeny compared to other papers. While Neanderthals are still viewed as a distinctive hominid, these studies also characterise other geographic and/or temporal “groups”

of hominids by various features. In particular, some “early modern humans” can be distinguished from “recent modern humans,” which suggests that “distinctiveness” is relative, and that concepts of “modernity” regrettably still require re-evaluation and clarification.

The papers by Rosas and colleagues on craniofacial development models (Chapter 4), Ponce de Leon and Zollikofer comparing Neanderthal-modern human growth differences to those in chimps and bonobos (Chapter 5), and Zollikofer and Ponce de Leon discussing heterochronic and heterotopic effects in Neanderthal ontogeny (Chapter 6), involve complex but intriguing discussions of the potential sources of developmental—and thus, morphological—variation between Neanderthals and modern humans. While these papers are generally theoretical in scope, they attempt to clarify the connections between developmental and evolutionary mechanisms that might have produced the distinctive Neanderthal morphology. It remains to be seen how such ideas can be tested with “hard data” and whether they will shed light on issues such as the evolutionary significance of Neanderthal and modern human morphological variation—are they developmentally distinct lineages, or just developmentally variable populations?

The majority of recent ancient DNA studies involving Neanderthal samples are usually characterised to strongly support, if not convincingly prove, that the species *Homo neanderthalensis* was replaced by *Homo sapiens*. Serre and Paabo have been involved in much of the important genetic research on Neanderthals, and in this volume (Chapter 11) they analyse additional Neanderthal and early modern human mtDNA samples. As in previous studies, they again find no evidence for, and argue rigorously against, any significant gene flow between these groups—but also again, they are not able to rule it out completely on statistical grounds. However, the most noteworthy comments from this paper are that: a) these results describe *population* history and “do not necessitate reproductive isolation or any other biological criterion that can be used to define species” (p. 217); and, b) the concept of a “genetic ancestor” (for a specific segment of DNA, not an organism) differs from that of a “paleontological ancestor,” because they do not occur in every past generation, but are identified as the last common ancestor sharing a specific genetic sequence with two contemporary individuals. It is probably safe to conclude that paleoanthropologists (and probably some geneticists) have not fully incorporated these genetic concepts in recent (and largely simplistic) formulations of Neanderthal-modern human evolutionary models.

Continuing the genetics focus, Hawks (Chapter 12) presents a detailed argument, along five different lines of evidence, that positive selection resulted in the replacement of Neanderthal mtDNA variation. Hawks also points out that positive selection renders Neanderthal mtDNA variation phylogenetically uninformative. If selection for mtDNA is not neutral, one of the fundamental assumptions of the Replacement model fails, and other lines of evidence (nuclear genomic variation, and anatomical and archaeo-

logical interpretations, some of which are represented in this volume) support arguments for some degree of continuity.

Ultimately, interpretations about Neanderthal morphological variation, behavioral adaptations, hybridization, and genetic variation relates to the “species question;” a few papers in this volume address this issue explicitly. Given that non-metric trait variation is a matter of frequency differences, Ahern (Chapter 14) analysed trait frequencies for non-metric craniodental variables in an Amerindian-Euroamerican sample compared to Neanderthals and Upper Paleolithic modern humans. The differences between the fossil samples were no greater than observed between the fossil samples, suggesting admixture and that Neanderthal-modern human patterns are consistent with intra-, not inter-, specific variation.

Holliday (Chapter 16) evaluated the concept of a syngameon—a group of freely hybridising taxa, usually applied to plants—to more usefully describe the Neanderthal-modern human phylogenetic relationship. In this assessment, the ability to interbreed can be retained by two sister taxa as a plesiomorphic character. Holliday presents documentation of mammalian back-crossed individuals that demonstrate no phenotypic evidence of hybridization—a confounding observation for paleontologists attempting to identify Neanderthal-modern human hybrids in the fossil record. Based on available data for molecular divergence times and interfertility data for extant mammalian species, his analysis suggests that Neanderthal-human divergence is consistent with that among mammals that maintain interfertility.

Voisin (Chapter 17) presents a model of speciation by distance, using data from “ring species” in other vertebrates, and including elements of both Replacement (in Western Europe) and Continuity (in Eastern Europe and the Near East, where gene flow/interbreeding is inferred from morphological patterns). Neanderthals and modern humans are portrayed as distinct populations, not species, and the taxonomic question is ultimately left open.

The ideas presented in these papers—concerning different taxonomic levels—are not necessarily new, but the analyses here test the models with available data, and openly consider different views concerning Neanderthal taxonomic status. The issue is far from resolved, and as reviewed in Holliday’s contribution, any assessment of Neanderthal systematics is still challenged by numerous and conflicting views of species.

Stringer (Chapter 18) discusses the Neanderthal-modern human interface in Eurasia, an important region in either Replacement or Continuity models. As always, Stringer considers Neanderthals and modern humans as separate evolving lineages—and grants modern humans “inherent superiority” (p. 319), but concedes that “it may be safer” (p.

317) to consider them as allotaxa, after Jolly’s baboon model. Stringer’s recent climatological reconstructions involve great complexity, suggesting that Neanderthal-modern human interactions involved many factors which should be considered at population levels, including local extinction, replacement, and “even hybridization” (p. 321) over a long time period, not just at the endpoint of the Neanderthal temporal range.

To sum up, this volume is a very worthwhile addition to one’s bookshelf, presenting a diverse collection of current and stimulating research papers. Regarding consensus, I believe that most readers will take what they want from the contributions presented depending on their already-defined points of view, but the book on the whole offers little clarity—in fact, it raises many questions, controversies, and conflicting viewpoints. However, I think that this accurately reflects the state of the field (still), and not just the research presented in this volume.

There are some signs of hope—most authors acknowledge a shift from “species” to “population,” even if they continue to support the same old viewpoints clothed in new terminology. The terms (and concepts) of Replacement and Continuity are both extremely well-developed, argued, and presented at this stage, yet so obviously inadequate in resolving the issues surrounding Neanderthal and modern human evolution. A real innovation would be to come up with a truly new idea with which to replace the old models.

The issues raised in this volume alone should stimulate a great deal of future research, but it seems imperative to find some consensus on a variety of terms and concepts first. For example, the language of taxonomy is changing, and researchers are now writing of populations rather than species, allotaxa and syngameons—how do these various taxonomic “groups” impact on ideas such as Replacement and Continuity? Is hybridization (between species) the same as interbreeding (between populations)? If Neanderthal populations were replaced in some regions, but interbred (or hybridized) with modern humans in others, is either traditional model an appropriate summary of these events? Finally, there is perhaps too much fine focus on the Neanderthal-modern human issues—given that Neanderthals were a regional population of hominids, they could all have gone extinct without making any contribution to the modern human gene pool, and this alone would not actually support the Replacement Model as an explanation of a much broader evolutionary phenomenon. Most of these same controversies about the Neanderthal-modern human relationship would also apply to populations in other geographic regions, including Africa, where the morphological distinctions among populations are less discernable. But those are other issues, and this is, after all, a book about Neanderthals.