Neanderthals Revisited: New Approaches and Perspectives

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This volume is dedicated to the memory of W.W. Howells (1908–2005) for his remarkable and pioneering contributions to the study of human evolution, especially his role in the greater understanding and appreciation of the Neanderthals. He was mentor and source of inspiration to generations of anthropologists, and his work continues to be a tremendous resource for research in human variation and evolution.

1. Neanderthals revisited

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Abstract

Neanderthals are the best represented and most studied group in the fossil human record. The relatively large number of Neanderthal fossils and their good preservation offers the possibility of robust inferences about their evolution and paleobiology. Nevertheless, debate still continues on important issues, and this suggests that deeper theoretical and methodological differences lie at the root of the lack of consensus. Such disagreements are not likely to be resolved by additional fossil findings, but rather require critical re-evaluation of the evidence at hand and the application of novel techniques and perspectives. This is the premise and main goal of this volume. The major debates in Neanderthal research are re-examined with the use of innovative state-of-the art methods and exciting new theoretical and conceptual approaches. The diverse contributions presented here offer fresh insights and advances that move us closer to reaching a consensus.

As the contributions to this volume illustrate, the Neanderthals are the best represented, most comprehensively studied, and most thoroughly understood group of fossil hominins. The wealth of specimens currently available to the scientific community, including dozens of relatively complete crania and partial skeletons from across a broad geographic range, affords scholars the opportunity to develop well-informed and robust inferences about the anatomy, phylogenetic relationships, taxonomy, and paleobiology of the Neanderthals. Equally importantly, we know a great deal about their archaeology, paleoecology, paleoenvironment, and zoogeography, all of which offer key evidence for interpreting their paleobiology in a broader environmental, behavioral, and phylogenetic context. Paleoanthropologists studying earlier parts of the human fossil record are less fortunate,

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having to work with taxa that are much more poorly represented, and in some cases known only by a few fragmentary specimens. It is certainly an enviable position to be in, one in which most vertebrate paleontologists, who universally lament the shortcomings of the fossil record as an impediment to resolving key problems, would be most content to find themselves.

Nevertheless, despite the quality and weight of the evidence, there continue to be major debates (that have lasted for 150 years) about a number of contentious issues, especially whether or not Neanderthals should be included in the same species as anatomically modern humans, and what is the precise phylogenetic relationship between these two forms. Our inability to agree on these fundamental questions is a matter of serious concern for paleoanthropologists: it leads to the inevitable conclusion that if we are unable to come to a decision about the nature of the relationship between Neanderthals and modern humans, how can we have confidence in our ability to resolve relationships in the earlier, much more scanty, fossil human record. However, the lack of unanimity is unrelated to the quality of the material. It is more a consequence of deeper theoretical and conceptual issues that relate to how different researchers analyze and interpret the anatomical and genetic evidence, and to the manner in which these are ultimately situated in the broader context of how biological systems operate in the natural world. If this is the case, then it will take some time before a consensus can be reached, regardless of the amount of fossil material available for study. One way forward is to explore new methods and theoretical approaches in order to better understand the paleobiology and phylogenetic relationships of Neanderthals.

The main theme of this volume is to revisit the major debates concerning the place of Neanderthals in human evolution. How morphologically distinct are the Neanderthals from modern humans, and what do these distinctions mean in terms of their paleobiology and phylogeny? How genetically distinct are Neanderthals from modern humans, and what does this mean for interpreting the population dynamics, taxonomy and phylogenetic structure of Late Pleistocene hominins in Europe? Were Neanderthals and modern humans capable of interbreeding, and can they be considered the same or different species? What were the paleoenvironmental and paleoecological contexts of Neanderthals, and how did this impact on their paleobiology, evolution, and extinction? All of these issues are tackled head-on in this volume. By presenting new evidence, using innovative and state-of-the art techniques and methods, and exploring exciting new theoretical and conceptual approaches, the contributors gain fresh insights into these issues, and ultimately succeed in edging the debate closer to a consensus. However, we leave it up to the reader to decide just how far we still have to go in order to attain a satisfactory solution to some of these long-term problems.

As editors of this volume, our aim was to assemble a collection of papers written by leading international researchers who have tackled many of these important questions using a variety of novel approaches. Equally importantly, as can be discerned from the chapter titles and the content of this volume, we have also tried to accommodate a diversity of opinions and perspectives that reflect the plurality of viewpoints among contemporary scholars. The range of topics covered include phylogeny, taxonomy, speciation, development, lifeways and adaptation, population genetics, extinction, paleoecology and archaeology, while the methods adopted include morphological analyses (i.e., traditional comparative morphology, dental anthropology, developmental biology, unilinear measurements, and three-dimensional geometric morphometrics), genetics (i.e., mtDNA, microsatellite data), experimental modeling, and computer imaging.

This volume is not organized in formal sections, but rather it follows the logic of the

general themes addressed by the contributors. It starts with the Middle-Late Pleistocene human fossil record and the evolution of the Neanderthal morphotype; continues with an examination of Neanderthal and modern human ontogeny, bioenergetics, and paleobiology, and their implications for inferring behavior; followed by genetic perspectives on Neanderthals and the utility of mtDNA and cranial morphological data in reconstructing phylogeny, the possibility of Neanderthal-modern human interbreeding and its taxonomic implications; and concludes with a review of the factors that may have contributed to the extinction of the Neanderthals.

In the opening chapter, Tattersall and Schwartz (Chapter 2) review the abundant morphological and genetic evidence supporting the distinctiveness of Neanderthals from modern humans, but also from earlier Middle Pleistocene hominins. To them, this evidence clearly confirms the status of Neanderthals as a separate clade. Does this mean that they are a different species? This is a difficult, perhaps even impossible, question to settle, because as Tattersall and Schwartz highlight, nature does not come neatly packaged and there are no absolute criteria by which to recognize species, especially in the fossil record. Nevertheless, Tattersall and Schwartz make the crucial observation (echoed by other authors in the volume) that Neanderthals as a group constitute a clear-cut morphologically and historically individuated entity, evidently equivalent to those commonly recognized today as species. They further point out that the morphological variability in the European Middle Pleistocene is little understood, and provocatively propose that several hominin clades might have been contemporaries in Europe during this period. This chapter sets the stage for the subsequent discussion of both the taxonomic position of Neanderthals and the tempo and mode of their evolution.

The next two chapters address the appearance of the Neanderthal morphotype and its evolution. Bruner and Manzi (Chapter 3) reassess the Saccopastore 1 cranium, which is correlated with oxygen isotope stage (OIS) 5, and is commonly considered to be an "early Neanderthal". Even though the specimen has been known since 1929, Bruner and Manzi are able to gain new insights into the endocranial morphology of the specimen using computer tomography. Their observations on cranial capacity, degree of pneumatization, and inner ear morphology support previous conclusions that this specimen exhibits a Neanderthal-like morphology despite its small size, thereby pinpointing the appearance of this morphotype to at least 130–100 ka. The authors suggest that the demographic impact of OIS 6 was probably catalytic in the evolution of full-blown Neanderthal features through genetic drift. Rosas, Bastir, Martínez-Maza, García-Tabernero and Lalueza-Fox (Chapter 4) propose the "organismic model" for Neanderthal evolution as an alternative hypothesis to the widely accepted "accretion model," drawing insight from their work on the extensive Spanish Middle and Late Pleistocene material. The authors postulate a two-phase evolutionary process in the European Middle-Late Pleistocene fossil record. The first phase is proposed to involve an increase in body size, greater postcranial robusticity, and increased midfacial prognathism. The second phase in turn would represent a true speciation event at about 300–250 ka, corresponding with a major re-organization of cranial architecture in Neanderthals relative to their Middle Pleistocene precursors. Their hypotheses point to a promising direction of research in the study of human evolution in Europe in the Middle Pleistocene.

Chapters 5 and 6 compare Neanderthal and modern human ontogeny from several different viewpoints. Ponce de León and Zollikofer (Chapter 5) obtain three-dimensional data from computer tomography scans and analyze them using geometric morphometric methods, in order to compare the ontogenetic trajectories of two sets of sister taxa: Neanderthals and modern humans, as opposed to chimpanzees and bonobos. Their analysis indicates

that the two human taxa share a common ontogenetic trajectory, but have different perinatal morphologies resulting from differences in prenatal growth. The two species of *Pan*, although overall more similar in shape to each other than the human groups, differ not only in the length of their ontogeny, but also in the direction. As Ponce de León and Zollikofer observe in their concluding comments, one of the most important findings of their study is that "spatial and temporal differences in growth and development not only generate distinct adult morphologies, but also give rise to taxon-specific life histories". This will surely be a very fruitful avenue of future research that will dramatically improve our understanding of the phylogenetic relationships and paleobiology of fossil hominins. In the following chapter, Zollikofer and Ponce de León (Chapter 6) use computer modeling of their 3-D data to simulate cranial growth under diverse conditions. This approach allows them to explore the ways in which a simple developmental system can be modified to produce different outcomes. Their results demonstrate the complexity of developmental processes, with intricate patterns potentially arising from simple changes and vice versa. The differences in the developmental pattern between Neanderthals and modern humans suggest that a change in the initial conditions may result in subsequent differences in their developmental trajectories.

Various aspects of Neanderthal anatomy, and their implications for understanding Neanderthal behavior, are explored in the next four chapters. Churchill (Chapter 7) applies a bioenergetics approach, coupled with experimental modeling of the Neanderthal body form. His innovative analysis indicates that the capacious Neanderthal ribcage may have been related to heat production, rather than to heat retention, as is commonly postulated under Bergmann's rule. Churchill's results also suggest a very high-caloric diet, with important implications for Neanderthal hunting abilities, ranging behavior, and demographics. Even though Neanderthals appear to have had bodies better adapted to generate and conserve heat than early modern Europeans and modern-day cold-adapted populations, the finding that Neanderthals occupied sites with warmer winter temperatures than early modern humans, suggests that they were less able to tolerate extreme glacial conditions. This may reflect a greater capability by early modern humans to capture sufficient calories for sustaining adequate heat generation or the use of clothing or shelters with higher insulative values. Pearson, Cordero and Busby (Chapter 8) re-assess Neanderthal habitual activities, commonly thought (based on anatomical differences) to differ markedly from those of modern humans in their extreme activity levels and foraging inefficiency. They compare Neanderthal upper and lower limb robusticity to those from several recent human foraging groups, and conclude that Neanderthals do not appear unique, but instead are quite similar to modern foraging peoples that exploit limited territories. The authors conclude that these results, far from indicating foraging inefficiency, may instead imply a more intensive form of foraging.

Niewoehner (Chapter 9) uses three-dimensional geometric morphometric methods to evaluate Neanderthal hand morphology compared to that of Early and Late Upper Paleolithic modern humans. He relates the observed shape differences to differences in inferred habitual grip positions, possibly suggesting differences in hafting technology and preference for wood as a raw material. In contrast, Upper Paleolithic human hand morphology is consistent with the archaeologically observed expansion of the technological repertoire that would have required increased emphasis on precision handling and shifts in manipulative postures. His results suggest a gradual transition in hand morphology from the Middle to the Late Paleolithic. Bailey and Hublin (Chapter 10) re-examine the isolated dental remains associated with the

Châtelperronian levels of the Grotte du Renne (Arcy-sur-Cure) site in France. These were previously considered taxonomically unidentifiable, but using a new dental scoring method developed by Bailey, the authors are able to establish the Neanderthal identity of the dental assemblage from this site. Their findings substantiate earlier inferences that Neanderthals are associated with the Châtelperronian industry in Western Europe, and that they were most likely the makers of these archaeological assemblages. Equally importantly, the recognition that isolated teeth from Late Pleistocene sites can be identified taxonomically opens up the possibility of investigating the mode and tempo of human evolution in Europe with much better sampling and a finer-grained temporal resolution than was previously possible.

Chapters eleven and twelve consider aspects of Neanderthal and modern human genetics. Serre and Pääbo (Chapter 11) present a new method for ancient DNA recovery. This resolves the problem of contamination by modern human DNA, which leads to the inability to detect modern-human like genetic material from fossil humans. Among the specimens examined under this protocol, all Neanderthals yielded Neanderthal-like mtDNA sequences, while all early modern Europeans yielded only modern human like mtDNA. The authors interpret their findings as indicating a minimal degree of possible Neanderthal contribution to the modern human gene pool. They also show that major demographic changes occurred in Late Pleistocene mammal species that coincide temporally with the extinction of Neanderthals. Such analyses highlight the importance of the study of population history for understanding Neanderthal evolution, and for providing important clues as to the timing and causes of their extinction. In the next chapter, Hawks (Chapter 12) critically re-examines the conclusions derived from mtDNA evidence about the phylogenetic relationships between Neanderthals and modern humans. In particular, he questions whether previous models predicated on the assumption of selective neutrality are valid, and proposes an alternative hypothesis that human mtDNA may have recently undergone a "selective sweep," possibly related to climate adaptation. Hawks suggests that it was positive selection rather than population replacement that explains the disappearance of archaic mtDNA variants. In this case, the observed differences between the mtDNA in Neanderthals and modern humans would be rendered phylogenetically uninformative.

The relationship between genetics and morphology in modern humans is explored further in chapter thirteen. Harvati and Weaver (Chapter 13) evaluate the usefulness of different cranial regions (i.e., face, vault, and temporal bone) in reconstructing the phylogenetic placement of Neanderthals. They assess the degree to which morphological differences (represented by three-dimensional geometric morphometric data) among recent human populations correspond to known neutral genetic differences (as represented by microsatellite data) and/or to climatic differences. Although facial morphology alone shows a relationship with climate, both vault and temporal bone morphology track neutral genetics, with the temporal bone tracking older events more successfully. The authors conclude that temporal bone morphology may be most appropriate for reconstructing the phylogeny of Neanderthals and early modern humans. Their analysis does not support a unique phylogenetic link between Neanderthals and early modern Europeans.

The issue of Neanderthal-modern human relationships, and the possibility of interbreeding between these populations, is taken up in greater detail in chapters fourteen and fifteen, with conflicting opinions expressed. Ahern (Chapter 14) addresses the question of whether Neanderthals and Upper Paleolithic Europeans differ in a significantly greater number of distinct morphological traits than do two modern human populations: a "replacing" (European Americans) and "replaced"

(Native Americans) group. The author is unable to reject the hypothesis that Neanderthals and modern humans were conspecific for most of the features used, although he does add a note of caution by acknowledging that additional traits or combinations of features might eventually falsify the single morphospecies hypothesis. Bräuer, Broeg and Stringer (Chapter 15) address the same question by re-examining the most complete crania from Mladeč in the Czech Republic. These are among the earliest modern European specimens known and they have often been suggested to exhibit Neanderthal-like features. However, the univariate and multivariate statistical analyses of frontal bone metric data presented by Bräuer and his colleagues offer no support for the claim that the Mladeč individuals might represent hybrids.

Further discussion of the concepts of speciation and interbreeding is explored by Holliday and Voisin in the next two chapters. These contributions draw on studies of other vertebrates to reframe the species question in a broader comparative perspective. Holliday (Chapter 16) reviews the literature on hybridization among mammal species, and applies it to the Neanderthal-early modern human case. He demonstrates that among interbreeding mammal species, those that have diverged as recently as these two human taxa are still able to produce fertile hybrids. He concludes from this evidence that Neanderthal-modern human hybridization was possible in all likelihood, even though there is no evidence from the genetic data or the fossil record to confirm that it actually took place. Building on ideas and concepts developed in previous work by Clifford Jolly, Holliday argues that Neanderthals and modern humans are perhaps best considered "allotaxa," good morphological species that may still have been able to interbreed. He invokes the concept of syngameon – that closely related interbreeding species can be grouped into larger taxa – as a useful model for interpreting Late Pleistocene European hominins. As a flip side to this study, it would be interesting to examine how many non-reproducing pairs of large mammal species have diverged in the past 700 ka. We suspect that it would be very few; a finding that would serve to underscore just how rapidly Neanderthals and modern humans diverged. Neanderthals are evidently autapomorphic, but it needs to be recalled that much of the distinction between Neanderthals and modern humans stem from the highly autapomorphic nature of modern humans.

Voisin (Chapter 17) extends this approach by adding a broader comparative dimension using recent models of speciation in birds. In particular, he focuses on the ring species *Phylloscopus trochiloides* (greenish warbler) from central Asia as an analogy for European hominin migration and evolution. His model of speciation by distance and temporal overlap is offered to explain the East-West morphological cline observed in Neanderthals, as well as the possible intermediate morphology of some Central European Upper Paleolithic modern humans. Voisin suggests that modern humans arriving in Eurasia during the Late Pleistocene were able to interbreed to some degree with the less derived Neanderthals in Western Asia and Central Europe, but hybridization was not possible or was extremely limited with the more highly derived Neanderthal populations at the furthest extreme of the morphological cline in Western Europe. In other words, Neanderthals and modern humans behaved as two distinct biological species in Western Europe, but not elsewhere.

Finally, Stringer (Chapter 18) presents new data on the chronology of the appearance of modern humans in Europe and the extinction of the Neanderthals. Current paleoclimatic evidence indicates a much harsher and increasingly unstable climate during the period of Neanderthal extinction (OIS 3). Stringer shows that the greatest climatic stress would have been experienced around 30 ka, and he argues that this stress probably played a key role in the demise of the Neanderthals. Stringer's contribution

highlights the challenge of integrating the diverse kinds of data that are becoming increasingly available to fully test hypotheses of Neanderthal and early modern human population histories.

The contributors to this volume provide important new insights that help us to better appreciate and understand the evolution and paleobiology of the Neanderthals. These advances have been brought about not through the discovery of startling new fossil finds, but through the application of exciting new methods and technologies, and a critical questioning of established theoretical and conceptual paradigms. This is certainly the way forward, and we echo Chris Stringer's concluding remarks that we undoubtedly have some exciting years ahead of us in Neanderthal and modern human origins research. Finally, although this volume is devoted entirely to the study of Neanderthals, it should not be overlooked that it is through comparisons with them that we are able to recognize and reflect on the uniqueness and remarkable peculiarities of our own evolutionary history.