Neanderthals Revisited

Vertebrate Paleobiology and Paleoanthropology

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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.

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Preface

The question of modern human origins and the role of Neanderthals in human evolution have fascinated paleoanthropologists and the public alike for more than a century. Recent years have witnessed important scientific breakthroughs in these areas of investigation as a result of ancient DNA studies, the application of new imaging and analytical tools in the study of morphology, and novel theoretical and conceptual approaches in evolutionary biology. These exciting and important developments have transformed our understanding and appreciation of the paleobiology, environmental adaptations, evolutionary relationships, and extinction of the Neanderthals. Although a number of influential edited volumes have previously dealt with these questions, there have been no recent compendia on the subject that have allowed leading international scholars specializing in Neanderthal research to present their latest ideas and to explore new methods and approaches to these long-standing problems.

With the 150th anniversary of the discovery of the first Neanderthal specimen drawing near, and while Katerina Harvati was still an Assistant Professor at the Anthropology Department at New York University (NYU), we conceived of a conference that would provide an opportunity for those scientists actively involved in all aspects of Neanderthal research to present their latest findings and to discuss the implications of these advances for understanding the evolutionary history of Neanderthals. The "*Neanderthals Revisited: New Approaches and Perspectives*" conference was held at NYU on January 27–29, 2005. An important aim was to unite researchers in the early stages of their careers with more established authorities, thereby encouraging a fresh look at some enduring problems using innovative new methods and perspectives. We invited some 35 scholars from the USA, Europe and the Near East to present their research or to act as discussants, most of who were able to attend. This edited volume is the outcome of that conference, and it presents, in more detailed fashion, the cutting-edge research that was showcased in New York. From the close of the conference to submitting the final manuscript to the Press has taken just slightly more than one year, so we are confident that the collection of papers included in this volume present up-to-date research and current ideas on Neanderthals.

The conference program included two days of presentations and discussions open to the academic community and to the public, followed by a half-day workshop restricted to conference participants. Contributions ranged from the re-evaluation of Neanderthal and modern human anatomy, inferred Neanderthal adaptations and habitual activities, developmental patterns, phylogenetic relationships, and Neanderthal extinction. Participants also applied new methods, including computer tomography, 3D geometric morphometrics, experimental growth studies, genetic and paleogenetic analyses, and presented new perspectives and approaches, including dental analysis, cladistic methodologies, bioenergetics, and broader comparative analyses. One of the most remarkable aspects of this gathering was that the venue provided an opportunity for researchers to present contrasting views on modern human origins without the rancour that has characterized much of this debate in past years. At the close of the conference there was general agreement that we were close to reaching a consensus on the critical issue of the Neanderthal-modern human relationship, while other key questions, such as the relationship of development with morphological change, the relationship between genetics and morphology, and the

re-evaluation of presumed Neanderthal adaptations, were given closer critical scrutiny.

We would like to thank all the contributors to this volume for participating in the "*Neanderthals Revisited*" conference and for providing us with uniformly outstanding papers. We are also grateful to the invited discussants at the conference: Susan Antón, Jean-Jacques Hublin, Clifford Jolly, Giorgio Manzi and Milford Wolpoff, as well as Alison Brooks and Randy White. They all provided insightful comments and initiated lively discussion during the meeting. Bob Franciscus, Yoel Rak, and Mark Stoneking participated in the conference, but were unable to contribute to this volume due to other pressing professional commitments. Special thanks go to Jen LeClair, Jennie Tichenor, Myriam Haas, and Allison Cleveland for their invaluable help in organizing the conference, creating the conference poster, and formatting the manuscripts. Several NYU students graciously volunteered their time to help with the smooth running of the conference, thereby ensuring a minimum of technical and organizational hiccups. Among these, Tom Rein, Maja Seselj, Connie Fellmann, Tim Cavaretta, Joe Califf, Andres Link, Gisselle Garcia, Laura Gaydosh, Deena Emera, and Ilana Soloman deserve special mention.

Finally, we are grateful to all the colleagues, students, members of the press, and public at large who attended the conference in large numbers and showed their remarkable enthusiasm for all things Neanderthal.

Financial support for the conference was provided by the Center for the Study of Human Origins at NYU, the Department of Human Evolution of the Max-Planck-Institute for Evolutionary Anthropology, and the Dean for Social Sciences at NYU. Fred Myers, Richard Foley, Jean-Jacques Hublin and Eric Delson were especially supportive and instrumental in the realization of both the conference and the volume. We are very grateful to Springer and to the editors of the Vertebrate Paleobiology and Paleoanthropology series, Eric Delson and Ross MacPhee, for agreeing to publish this volume, and to all the colleagues who devoted their time to reviewing the manuscripts and providing helpful input. Finally, we owe the greatest gratitude to our families, and particularly to our spouses, Elias and Terri, for their support and encouragement in this and all endeavors.

Katerina Harvati
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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.

2. The distinctiveness and systematic context of *Homo neanderthalensis*

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Abstract

The "packaging" of the diverse living world is untidy, with the result that there are no absolute criteria for recognizing in all contexts the bounded historical entities we call species. However, there is no doubt whatsoever that *Homo neanderthalensis* is as clear-cut a morphological entity as any in the hominid fossil record: one that is characterized by a whole host of cranial apomorphies. Further, a recent full-skeleton reconstruction further emphasizes just how different Neanderthal body structure was from that of *Homo sapiens*, not simply in numerous anatomical details, but in the proportions of the thorax and its relation to the pelvic region. These bodily proportions would have given these extinct hominids a very distinctive appearance on the landscape, and enhance the likelihood that we are dealing here with a reproductively differentiated entity. Still, *Homo neanderthalensis* is not unique in all those features that distinguish it from *Homo sapiens*. Many "Neanderthal" cranial features are shared with various middle Pleistocene European hominids, notably the Steinheim specimen and, to a lesser extent, the Sima de los Huesos hominids from Atapuerca. Indeed, it appears that, far from being an isolated phenomenon, *Homo neanderthalensis* formed part of a larger endemic European hominid clade. This clade seems to have existed contemporaneously in Europe with at least one other hominid lineage or clade, exemplified by the *Homo heidelbergensis* fossils from Mauer, Arago and Petralona.

Introduction

Over the century and a half since the first description of a Neanderthal fossil, an impressive record of these extinct hominids has accumulated. Indeed, not only has the morphological distinctiveness of *Homo neanderthalensis* for long been vastly better documented than that of any other of our fossil relatives (Tattersall, 1986), but we are also in a better position than in the case of any other extinct hominid to appreciate the morphological

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variations (around a very distinctive mean) that are shown by the various populations of this form over time and space (Tattersall and Schwartz, 2000). Yet many paleoanthropologists continue to equivocate over the question of whether the Neanderthals actually constitute a bounded historical entity (Ghiselin, 1974) of the kind that warrants recognition as a species. Since this problem appears to be related, at least partly, to more general difficulties of species definition and recognition, it seems appropriate to begin our discussion of the status of the Neanderthals with a brief consideration of the nature of the boundaries that exist in the living world.

Species as Bounded Historical Entities

It must be very clear to anyone concerned with the luxuriant variety of living organisms that at some level Nature is "packaged." The biosphere is composed of a mass of discrete (but nested) units. At higher taxonomic levels there is no problem distinguishing these units: all horses are distinct from all whales by any definition. But as we approach finer degrees of distinction, particularly at intrageneric levels, difficulties proliferate. These difficulties are reflected in the extraordinary plethora of definitions of the species, by practice and by common consent the basic systematic unit, that is currently on offer. As Hey (2001) observed, literally dozens of new such definitions have been proposed in recent decades. This is not the place to trawl yet again through this lengthening list, but perhaps it is appropriate to point out that it is vanishingly unlikely that any single definition of the term "species" will ever fit all cases. This is not only because any universal definition would have to fit both living and extinct species, which offer us different information sets; it is also because speciation, the process by which individuated, non-reticulating units come about, is not a unitary mechanism. It is not, for example, simply an inevitable, passive, consequence of the morphological differentiation of populations over time (though this routine if poorly understood process certainly furnishes the basis for the morphological differences by which species may often be distinguished). Instead, speciation is a *result* (individuation, expressed most essentially among living populations as reproductive independence, but always seen *a posteriori*: Tattersall, 1994), which may eventuate from shifts in developmental regulation at many different levels (Schwartz, 2005).

Human beings are instinctively reductionist creatures; but for all these reasons, and more, we may be unrealistic in expecting Nature to be *neatly* packaged. Ultimately, the boundaries defining historically (evolutionarily) independent units must lie in their (effective or absolute) reproductive isolation. But even reproductive behaviors may not provide us with a golden bullet. The studies of Clifford Jolly and his colleagues (e.g. Jolly, 2001) have shown that evidence of quite extensive hybridization between adjacent populations of baboons that are sometimes well differentiated to the eye may often be readily observed; yet evidence is still lacking that such behaviors are necessarily associated with the progressive integration of what evidently continue to be distinctive gene pools. Jolly (2001: 17) has, indeed, penetratingly observed that baboon allotaxa may at one and the same time be " 'phylogenetic' species, but 'biological' subspecies." And if this is truly the case, from a historical (evolutionary) perspective morphological differentiation becomes much the most significant factor to consider. Still, this hardly simplifies matters much. For, from the phenotypic standpoint, remarkable amounts of geographically (or artificially) maintained morphological variety may accumulate within a species without the disruption of reproductive continuity – although, at the same time, the latter can occur in the absence of readily detectable phenotypic change. Indeed, Schwartz (1999) has emphasized that there are

no biological reasons whatever for expecting that morphological change, deriving ultimately from changes in communication at the molecular level, should be associated with reproductive incompatibility unless it specifically affects such factors as protein recognition between sperm and ova, gametic or zygotic viability, or reproductive organ morphology. Nonetheless, in the fossil record morphological characteristics are almost invariably all we have to go on.

Given these awkward realities, we have to accept the unfortunate fact that even among sympatric or parapatric living forms, whose natural behaviors we can directly observe, it will sometimes never be certain whether two close relatives are "biologically" specifically distinct or not. And the difficulties only multiply when fossils are involved, for no specifiable or quantifiable degree of morphological differentiation can be associated with speciation; and in almost all cases fossils can offer us only morphology as a basis for making species judgments. It might be argued that the Neanderthals are actually a partial exception to this, given that fragments of their (distinctive) mitochondrial genome are now available (Krings et al., 1997, 2000; Ovchinnikov et al., 2000; Schmitz et al., 2002); but while the large mtDNA differences between available Neanderthal samples and all living *Homo sapiens* populations tested are indeed strongly suggestive, it nonetheless remains true that DNA differences suffer from analogous limitations to morphology in the context of assessing "species" status.

How, then, do we determine whether two clearly related forms represent independent (individual) entities? It has recently become fashionable to argue that species are most usefully or practically equated with "basal (smallest) clusters of diagnosably distinct populations" (Cracraft, 2002: 130). But while this approach may have its possibly Siren attractions for the working systematist, it still leaves paleontologists in a quandary. Because while systematists studying living populations will often already know from direct evidence what the geographical boundaries (and the morphological variation occurring within those boundaries) of their populations happen to be, the paleontologist has to work backwards, inferentially, from morphology alone. Moreover, distinctive morphologies frequently characterize geographic variants that are not reproductively/historically individuated. Given this constraint, it would appear appropriate for paleontologists to exercise caution, and to err on the side of inclusivity when using morphological differentiation as a basis for inferring the existence of reproductively and historically independent entities. Where, then, do the Neanderthals fit within this perspective?

Homo neanderthalensis as a Morphologically and Historically Individuated Entity

There has been remarkably little debate over which hominid fossils are Neanderthal or not Neanderthal (as witnessed, for example, by the remarkable unanimity on this question, at least, among the very heterogeneous assortment of contributors to the classic volume edited by Smith and Spencer [1984]). Only at the fringes has there been any significant discussion, but this has usually focused upon whether or not a particular fossil was somehow related to the Neanderthals, as a precursor or otherwise, rather than on the matter of its inclusion within the group itself (see historical account in Tattersall, 1995). This is largely because, among all extinct hominid entities, the Neanderthal group appears by far the most clearly delimited morphologically. Instructively, of all other fossil hominids only *Homo erectus* is comparably well represented in the record, yet no end is in sight to the debate over which specimens should or should not be attributed to this

species (compare, e.g., Wolpoff et al. [1994] to Schwartz and Tattersall [2000] and Antón [2003]).

Traditional cranial characters that are commonly cited as typical of Neanderthals (see e.g., Hublin, 1978, 1998; Santa Luca, 1978; Vandermeersch, 1981; Stringer et al., 1984; Schwartz and Tattersall, 1996a, b, 2005; Rak and Hylander, 2003) are numerous and include: double-arched supraorbital ridges whose surfaces roll smoothly upward from the orbital roofs and onto the frontal squama; orbits that are obliquely truncated inferomedially; a narrow lower face and a sharply retreating midface; medial projections emerging above a spinoturbinal crest that delineates a prenasal fossa lying just within the very large nasal aperture; very long and typically thin zygomatic arches; a "puffy" midface that reflects the presence internally of expanded maxillary sinuses that swell out the infraorbital and medial orbital regions; an angulation along the anterior squamosal suture, delineating distinct anterior and posterior temporal fossae; a smoothly rounded ("en bombe") cranial profile in rear view; a pitted suprainiac fossa that lies above a superior nuchal line that is undercut by the nuchal plane but poorly delineated above; a long and more or less straight parietomastoid suture that flows directly behind into an anterior lambdoid suture; widespread pneumatization within the petrosal; incomplete ossification of the ectotympanic tube laterally; and a long, narrow, ovoid foramen magnum. A useful table published by Hublin (1998, Table 1) lists several others in addition. A particularly interesting new source of cranial information has been provided by CT studies (e.g., Hublin et al., 1996; Spoor et al., 2003) showing that the bony labyrinth of the inner ear in Neanderthals is distinguished in numerous derived features from that of *Homo sapiens* (and of *Homo erectus*). In the most comprehensive such study to date, Spoor et al. (2003: 141) suggested that such differences reflected a distinctive pattern of head movements possibly related to "aspects of locomotor behaviour and the kinematic properties of their head and neck."

In the Neanderthal mandible are seen retromolar spaces; sigmoid notches that are deepest posteriorly, in front of low-set condyles, and sigmoid notch crests that terminate medial to the lateral extremities of the condyles; obliquely truncated gonial angles; symphyseal bone that, when viewed from below, is thinner from side to side than the bone distal to it. In the dentition the molars have relatively complex occlusal surfaces, with centroconids and centrocones present on the lower and upper molars respectively, and distinct talonid and trigonid basins in the relatively long and narrow lower molars. The molar occlusal surfaces are well defined peripherally by blunt crests, and are constricted in area by their inwardly sloping sides. Additional apomorphies of the Neanderthal upper and lower cheek dentitions have recently been cited by Bailey (2002, 2004) and Bailey and Lynch (2005).

Unsurprisingly, not all these and other craniodental characters typical of Neanderthals are equally strongly expressed in all unarguably Neanderthal specimens that preserve them; and indeed it is evident that, in any widely distributed group that is as close-knit phylogenetically as the genus *Homo*, there is bound to be some overlap among differentiated populations in the frequency and extent of expression, as well as in the presence/absence of particular traits. Thus, among the large assemblage of unquestionably Neanderthal fossils individuals vary, sometimes substantially, in features such as the degree of bunning of the occiput, the size of the suprainiac fossa, the length of the retromolar space, the presence or absence of a distinct postorbital plane behind the brow ridges, the prominence of the medial projections in the nasal fossa, the extent of cheektooth taurodontism, the depth of the zygomatic arches, and so forth. But it is abundantly clear – and almost universally

acknowledged – that, despite their manifest individual and geographic variation, the Neanderthals represent an unusually coherent and readily recognizable group. Certain authors (e.g., Wolpoff, 1980; Frayer, 1984) have suggested that the relatively restrained expression of some of these characters in certain Neanderthals of late date indicates a degree of intermediacy with *Homo sapiens*, but there are numerous reasons for rejecting this notion (Tattersall and Schwartz, 2000).

Still, as impressive as the list of craniodental apomorphies of the Neanderthals undoubtedly is, the extent to which these hominids are distinguished morphologically from *Homo sapiens* is made particularly evident by the full-skeleton reconstruction (Figures 1, 2) recently reported by Sawyer and Maley (2005). Reconstituted from the remains of a half-dozen partial skeletons from four countries, this postcranial reconstruction draws attention to the classically Neanderthal characteristics of the postcranial skeleton that have already been exhaustively documented by numerous authors (e.g., Boule, 1911–1913; McCown and Keith, 1939; Straus and Cave, 1957; Trinkaus, 1983).

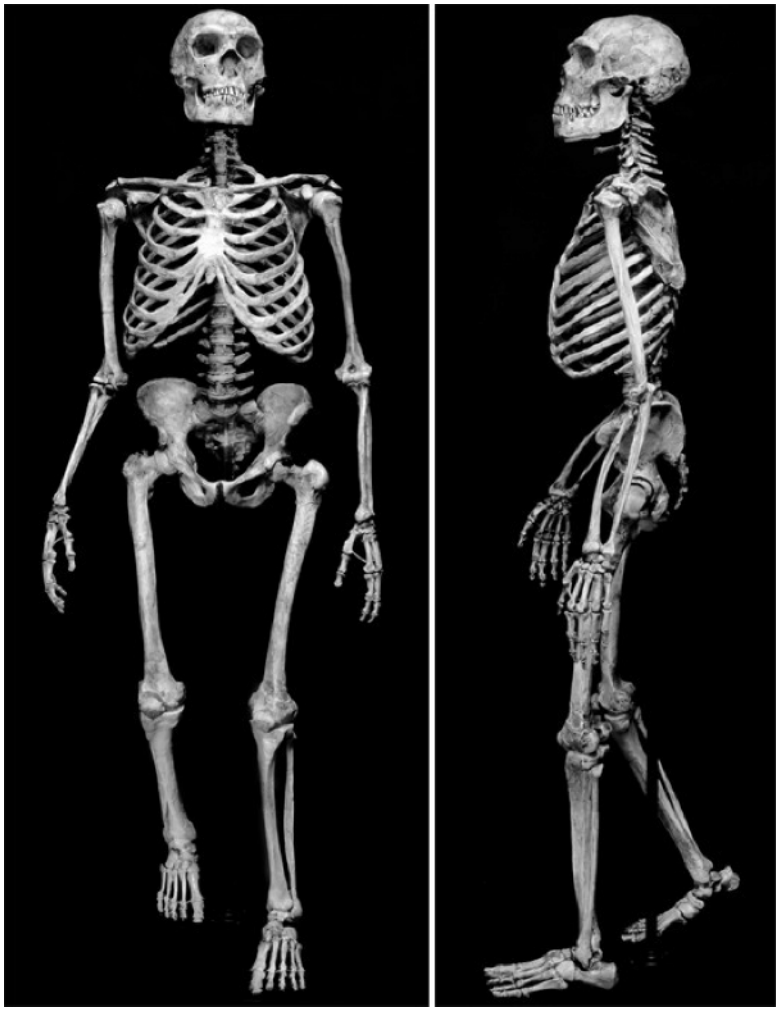

Figure 1. Front and lateral views of a complete Neanderthal skeleton as reconstructed, using elements from five partial skeletons (principally La Ferrassie 1 and Kebara 2), by G. J. Sawyer and B. Maley. Photo courtesy of Ken Mowbray.

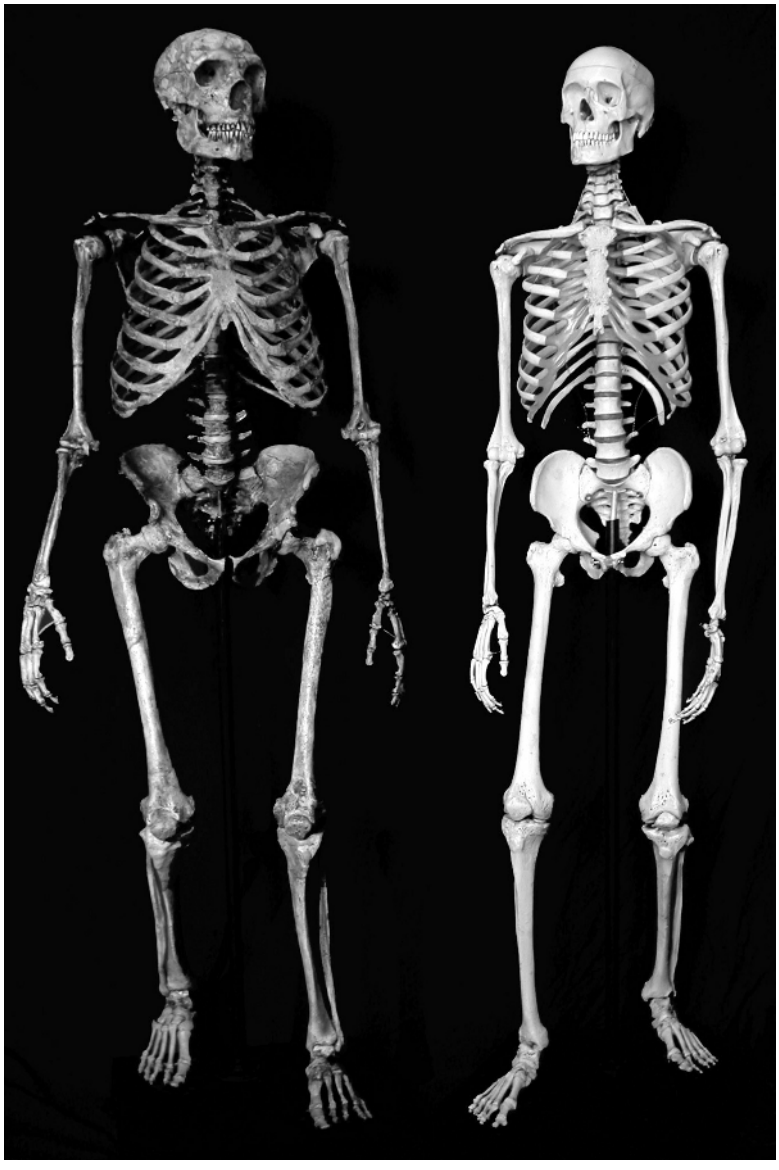

Figure 2. Front view of reconstructed Neanderthal skeleton compared with a skeleton of a modern *Homo sapiens* male of similar stature. Photo courtesy of Ken Mowbray.

Among the long-noted apomorphies that are also especially apparent from individual skeletal elements are, of course, the large limb articular surfaces, the flaring iliac blades and long, thin pubic rami of the pelvis; but the reconstruction also dramatically underlines the proportional differences in the thorax and its relationship to adjacent regions that emerge when Neanderthals and modern humans are compared (Figure 2). In the Neanderthal the rib cage is constricted above and flares dramatically out and down to match the broad pelvic bowl below. This conformation contrasts dramatically with the typical "barrel-shaped" *Homo sapiens* condition in which the thorax tapers up and also down to match a narrower pelvis. Further, as Sawyer and Maley also remark, the base of the Neanderthal vertebral column "sit[s] much lower in the pelvic basin than is the case among modern humans"

(Sawyer and Maley, 2005: 30), contributing to an extreme shortness of the waist in the former that, in limiting thoracic torsion, would have had significant consequences for gait, as well as for appearance. Altogether, this reconstruction makes it abundantly evident that in life the Neanderthals would have cut a very different figure on the landscape from *Homo sapiens*.

This major *Gestalt* difference adds, of course, to the existing morphological basis for surmising that the two kinds of hominid were significantly differentiated reproductively as well as morphologically. And, while not demonstrating this conclusively, from the perspective of "inclusive," rather than "exclusive," species concepts it also adds weight to the inference that specific mate recognition systems would have differed significantly between the two. This does not, of course, eliminate the possibility that occasional instances of coupling might have occurred when the two kinds of hominids came into contact; but it does very strongly buttress the already substantial reasons furnished by the fossil record for inferring that no significant integration of the two populations ever took place. Overwhemingly, then, the probability must be that the two kinds of hominid, Neanderthal and modern, were/are independent historical as well as morphological entities. In which case, we are fully justified, under virtually any set of criteria, in regarding the former as constituting the species *Homo neanderthalensis* (see also Harvati et al., 2004).

Neanderthals in Wider Systematic Context

The morphological distinctiveness of *Homo neanderthalensis* is hardly surprising when one considers that both molecular (Krings et al., 1997, 2000) and paleontological (e.g., Stringer and Gamble, 1993; Hublin, 1998; Tattersall and Schwartz, 2000) studies suggest that this species last shared a common ancestor with *Homo sapiens* at least a half-million years ago. For close to a century now paleoanthropologists have sought the roots of the Neanderthals far back in time, and in one guise or another many have discerned evidence in Europe for what Hublin (1998: 297) has recently termed a "Neandertalization Process," linking forms from the early Middle Pleistocene (Mauer, Tautavel, etc.) to the latest (stages 5–3) "classical" Neanderthals, via "Holstein-Hoxnian" (Bilzingsleben, Sima de los Huesos, etc.) and "Saalian" (Biache-Saint-Vaast, Ehringsdorf, etc.) intermediates. Still, if *Homo neanderthalensis* really was the end product of a steady course of phyletic modification, as this notion of a process implies, what is perhaps most surprising is how clearly the morphological boundaries of the species *Homo neanderthalensis* actually appear to be drawn.

Hublin himself finds it difficult as a matter of logic to exclude any of the "specimens involved in the Neandertalization process" from *Homo neanderthalensis*, "even if they display only a few derived Neandertal features" (Hublin 1998: 302). But from our own examination of the fossils concerned, what seems most remarkable in the longer-established record is that in strictly morphological terms there is really only one potentially questionable case of attribution to *Homo neanderthalensis*, apart from such apparently permanently inscrutable specimens as the Fontéchevade fragments (see Vallois, 1949; Trinkaus, 1973). This is the rather fragmentary assemblage from Ehringsdorf which, despite its limited size, shows unusual variation in morphology (Vlček, 1993; Schwartz and Tattersall, 2005). Thus, one occipital (Ehr H9 1032/69) lacks a suprainiac fossa, and shows instead twinned depressions both below and above the occipital "torus," while the Ehr H3 1026/69 parietal is also atypical for a Neanderthal in showing a "tent-shaped" coronal profile in rear view. And the temporal Ehr H3 1026/69 shows the straight and long

parietomastoid suture of a Neanderthal, but uncharacteristically for this group the posterior root of its zygomatic arch diverges strongly from the cranial wall. Still, if we provisionally regard this material as early Neanderthal, it serves to emphasize the relative homogeneity of the rest of the Neanderthal hypodigm.

None of this is to say, however, that all "Neanderthal" characteristics of the kind we listed in the last section are confined to the large group of fossils that we may comfortably regard as belonging to *Homo neanderthalensis*. This is because in the middle Pleistocene of Europe we can indeed, like Hublin and most others, identify a variety of hominid fossils displaying some, but not all, of the features that typify Neanderthals (Hublin, 1998; Schwartz and Tattersall, 2005). Perhaps most notable among these is the Steinheim cranium (probably stage 7, around 225 ka), which possesses a fairly standard Neanderthal-like morphology of the upper face, with separately arching and smoothly rolled supraciliary ridges over orbits that have truncated inferomedial margins. The large nasal fossa and the presence of a prenasal fossa between well defined lateral and spinoturbinal crests are characteristics shared with Neanderthals, as are the angulation apparent along the anterior squamous suture, the long, straightish parietomastoid and anterior lambdoid sutures, the (rather faint) suprainiac depression, the horizontal occipital "torus" that is only fully defined below, and the rather rounded posterior profile of the braincase. There are even the rudiments of a vertically oriented medial projection faintly evident within the nasal cavity. On the other hand, the puffy midface of the Neanderthals is absent from the Steinheim specimen, as are the sharply retreating zygomas, with their laterally rising anterior roots, that give Neanderthal faces their highly characteristic allure. The poorly inflated Steinheim braincase departs from the Neanderthal condition in having fairly vertical side walls in coronal section and in showing a smoothly rounded lateral profile at the rear. As a result, despite the many Neanderthal resemblances of this specimen, it has been more or less universally regarded (see reviews by Day, 1986; Schwartz and Tattersall, 2002) as an example of "archaic *Homo sapiens*" rather than as of Neanderthal affinity. Few have ever called Steinheim a Neanderthal, and it would certainly be inaccurate to do so. However, based on the constellation of characters it exhibits, it would seem entirely reasonable to consider the Steinheim specimen as representative of the sister taxon to *Homo neanderthalensis*. Conceivably this taxon was directly ancestral to the Neanderthals; but to make that claim would involve a variety of assumptions that we would prefer to avoid here (see discussion by Tattersall and Eldredge, 1977).

Another German specimen with many of the characteristic Neanderthal cranial traits is the frustratingly incomplete partial calvaria from Reilingen, which is possibly penecontemporaneous with that from Steinheim (Ziegler and Dean, 1998). Early analyses resulted in attributions to *Homo erectus* (Czarnetzki, 1989) or to "archaic *Homo sapiens*" (Adam, 1989, Schott, 1990), but more recent contributions have focused on the Neanderthal affinities of this specimen (e.g., Condemi, 1996; Dean et al., 1998). Like Neanderthals, this fossil possesses expanded petrosal pneumatization; an occipital "torus" that is fully delineated only below, with a suprainiac depression above; an *en bombe* coronal profile of the expansive braincase; and incomplete lateral ossification of the ectotympanic tube. As in Steinheim, though, the sagittal profile of the occiput is quite rounded, and the weakly undercut occiput is fairly narrow, though the cranial vault itself appears considerably flatter and more Neanderthal-like than that of Steinheim. This specimen exemplifies the difficulty of categorizing members of this wider group strictly on characters of the cranial rear, though it is abundantly clear that Reilingen is either *Homo neanderthalensis* or a close relative.

The impressive assemblage of hominid fossils from the Sima de los Huesos at Atapuerca in Spain, now thought to be around 400 ka or possibly more (Bischoff et al., 2003), appears to be relatively homogeneous. All of this material has been referred by its describers (e.g., Arsuaga et al., 1997) to the species *Homo heidelbergensis*. This species is, however, based on the Mauer jaw, a specimen to which none of the mandibles known from the Sima appears to bear notable similarities. At the same time, Arsuaga and colleagues have noted that various features of the Sima fossils are "transitional" to Neanderthal morphology, and have concluded that these hominids are early members of the Neanderthal lineage, as well as simultaneously linked to other European middle Pleistocene fossils (Arsuaga et al., 1997). And certainly, while the Sima hominids do show fewer components of the Neanderthal character constellation than Steinheim does, the number of apparent Neanderthal synapomorphies that they possess is nonetheless quite extensive. Cranially, such resemblances to *Homo neanderthalensis* include: bilaterally arced supraorbital tori with tall and evenly rounded anterior surfaces; orbits with obliquely truncated inferomedial corners; a large nasal aperture showing a distinct prenasal fossa with a continuous internal margin; some projection of the frontal processes around the nasal aperture; an angulation along the anterior squamous suture; a long, straight parietomastoid suture; incompletely laterally ossified ectotympanic tubes; and a pitted suprainiac depression. Like those of Neanderthals, the Sima mandibles display medial pterygoid tubercles on the inner surface of the ramus, and have sigmoid notch crests that terminate just lateral to the midline of the condyle.

At the same time, however, the Sima hominids are cranially less derived and quite distinct from *Homo neanderthalensis*. In the structure of the face, differences from the latter include: an uninflated infraorbital region; horizontal conchal crests just within the aperture of the nasal cavity in lieu of vertical medial projections; no sharply retreating and inferiorly tapering midface; and anterior zygomatic roots that angle out more sharply laterally. Farther posteriorly, the Sima hominid shows deep zygomatic arches, a very short anterior lambdoid suture, and there is no clearly undercut occipital "torus." In sagittal profile the braincase is smoothly rounded, and in coronal profile it has parallel sides and a sagittal peak. Postcranially the robust Sima pelvis shows greatly flaring iliac blades, long pubic rami and a capacious pelvic canal. These pelvic features recall the Neanderthals; but they are likely to represent the primitive condition for the genus *Homo*, or at least for the subclade that contains both the Neanderthals and the Sima hominids.

Based purely on the material discussed up to this point, it might (just) be possible to argue that this "Neanderthal clade," fairly well defined in terms of synapomorphies, included a chronological succession of taxa of which *Homo neanderthalensis* was the terminal outcome. But from the evidence presented below, it is evident that the larger story of middle Pleistocene hominid evolution in Europe was more complex than the notion of a single evolving lineage can accommodate.

For the conclusion that hominid evolution in Europe prior to the abrupt arrival of *Homo sapiens* was *not* an essentially unilineal affair is dramatically reinforced by a survey of the entire variety of hominid fossils known from Europe in the period centering on 400 ka. Such fossils include the specimens from Swanscombe, in England (about 400 ka: Stringer and Hublin, 1999), the Arago hominids from southern France (perhaps 450 ka: Iacumin et al., 1996); the German Mauer jaw (around 500 ka: Cook et al., 1982); the Bilzingsleben hominids, also from Germany (300–400 ka: Schwarcz et al., 1988), and possibly the Vérteszöllös occipital from Hungary which might be as old as 350–250 ka (Cherdyntsev, 1971) though Schwarcz and Latham (1990) consider it younger.

Morphologically there is strong justification for associating the Greek Petralona cranium with the Arago hominids (Schwartz and Tattersall, 2005), although Grün (1996) concluded that this exceptionally poorly dated fossil most likely derives from significantly later in time, around 250–150 ka.

The committee that was originally convened to evaluate the two first-found elements of the Swanscombe cranial rear emphasized metrical comparisons to both *Homo sapiens* and Steinheim (Morant, 1938), and influential later contributions (e.g., Howell, 1960; Stringer et al., 1984) continued an essentially "presapiens" assignment. However, following the lead of Santa Luca (1978), most workers have moved toward comparisons with *Homo neanderthalensis* (see Stringer and Gamble, 1993; Stringer and Hublin, 1999). And, indeed, Swanscombe clearly does sort into the Neanderthal clade, although it does not seem to represent a typical Neanderthal, and in some ways it more closely resembles its counterparts from the Sima de los Huesos, for instance in having a relatively narrow and weakly undercut occipital "torus" and a poorly defined suprainiac fossa. Still, while having more vertical cranial walls than is usual for Neanderthals, it does also show a more rounded coronal cranial contour than is seen in the Spanish material and it does possess a fairly large, ovoid foramen magnum.

The Vértesöllös occipital was initially announced as a representative of *Homo erectus* (Vértes, 1965) – in hindsight a virtually meaningless attribution in the European context – and was subsequently moved to "archaic *Homo sapiens*" by Stringer et al. (1979) at a time when the Petralona cranium was similarly classified. The two hominids share a long and very horizontal occipital "torus," but otherwise the Vértesöllös specimen remains fairly enigmatic. Also rather inscrutable are the Bilzingsleben hominids, which have been ascribed to *Homo erectus* by their finders (e.g., Mania, 1983; Vlček and Mania, 1987). Stringer et al. (1984) found these fossils to be the "most *erectus*-like and the least Neanderthal or modern-like" of the "archaic *Homo sapiens*" group, a conclusion later sustained by Stringer (1989) through comparisons with the Saldanha calotte. The two Bilzingsleben crania are both fragmentary, but awkwardly they appear to display differences from one another (Schwartz and Tattersall, 2005) that are substantial enough at least to raise the question of whether they belonged to a single population. The affinities of neither are clearly evident, but there is little reason to associate all of the material with the Neanderthal clade and the net effect is to add to the growing impression of hominid diversity in the European middle Pleistocene.

The Arago and Petralona crania are nowadays widely accepted as classic European exemplars of the species *Homo heidelbergensis*, originally founded solely on the basis of the Mauer mandible. It is fortunate that the existence of both mandibles and crania in the Arago collection allows this attribution to be substantiated (Schwartz and Tattersall, 2005). There is a substantial *Gestalt* difference between the Mauer jaw and the two better preserved Arago mandibles because the latter are more gracile than the former, and lack its remarkable ramal length. However, both the Mauer and Arago 13 mandibles show a common configuration of the anteroinferior margins of the jaw. They also share excavated and rounded gonial regions, anteroposteriorly long coronoid bases, posteriorly decreasing corporal height, and tall but shallow infracondylar sulci that lie along the posterior margins of the rami. More striking, though, are the dental similarities. Notably, the anterior teeth in both mandibles were large, and the molars long and ovoid; the P_1s are obliquely truncated mesiodistally along their lingual surfaces, and are hence more mesiodistally tapering and elongate than the short, buccolingually wide and more ovoid P_2s; the protoconids on both the P_1s and P_2s are centrally placed; on P_1 the

low lingual swelling lies opposite the protoconid, while on P_2 the metaconid is mesially situated relative to the protoconid, and on both premolars the lingual swelling or cusp is bounded by a very small fovea mesially and a much deeper fovea distally. In the molars M_2 is larger than both M_1 and M_3; the protoconids and metaconids are situated very mesially on the crowns, and in the same mutual relationship; M_1 shows evidence of a tiny trigonid basin, while this basin is more pronounced on $M_{2–3}$. On all molars the hypoconulid lies just buccal to the crown midline, and the talonid basin is or was quite long mesiodistally and truncated buccolingually, with some evidence of enamel wrinkling.

If we can allocate the Mauer and Arago lower jaws to the same species, then it appears permissible to regard the well-preserved Arago 21 fossil as the classic exemplar of the face of *Homo heidelbergensis*. In turn, we can associate with this species the more complete and potentially much more recent Petralona cranium, which shares with Arago 21 a massive and broad lower face that lies below hugely developed and superoinferiorly tall supraorbital margins that attain their maximum thickness around mid-orbit. In both fossils, the superior margin of the orbit bears a blunt edge that demarcates the anterosuperiorly twisting front surface of the torus from the shallow posttoral sulcus behind. The same features unite these European specimens with others from Africa (Bodo, Kabwe, Saldanha) and Asia (Dali, Jinniushan). Interestingly, while there is also a fair amount of variation in other features of the cranium among this cosmopolitan group (see discussion by Schwartz and Tattersall, 2005), that variation does not appear to be geographically organized in any clear-cut manner. In the present context, however, it is important to note that the upper facial features of *Homo heidelbergensis* noted above distinguish this species absolutely from *Homo neanderthalensis* as well as from broadly contemporaneous members of the latter's clade such as the Sima hominids.

Conclusion

Homo neanderthalensis is an unambiguously demarcated morphospecies, recognizable on a host of cranial and postcranial characters, that was also, as definitely as such things can be known in the fossil record, a fully individuated historical entity. Its identity did not shade into that of any other known hominid, and certainly not into that of the species *Homo sapiens* that entered its European and western Asian zone of distribution some 40 kyr ago and entirely displaced it within about a dozen millennia. Further, it clearly emerges from the evidence just adumbrated that the larger Neanderthal clade, if not the species *Homo neanderthalensis* itself, was already in existence in the period centering on 400 ka.

Inadequate specimens or poor dating make it hard to be sure whether or not multiple kinds of hominid belonging to this "Neanderthal clade" coexisted at this juncture, although the probability may lie in that direction. On the other hand, the new datings make it evident that at around this same time point there also existed in Europe at least one other hominid lineage, represented by *Homo heidelbergensis* (as defined by the Mauer/Arago fossils). This species is clearly demarcated from all members of the equally derived Neanderthal/Steinheim/ Sima clade in which this cranial region is known by the apparently derived structure of its upper face (among other features). It is beyond the scope of our discussion here to broach the many problems of apparently geography-independent morphological variation in the larger group to which the species name *Homo heidelbergensis* has been applied in recent years (e.g., Rightmire, 1990; Stringer and McKie, 1996; Schwartz and Tattersall, 2005). But it is already evident that this species, as broadly defined, somehow shared the European habitat with the Neanderthals and/or their relatives, potentially over a period of several hundred thousand years if the late dating of Petralona turns out to be accurate.