

Chapter 2

One Hundred Fifty Years of Neanderthal Discoveries: Continuity and Discontinuity

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The original Neanderthal fossil was discovered in Mettmann near Düsseldorf, Germany, in 1856 and the present volume is based on the conference that I had the honor of organizing in July 2006 with Professors Wighart von Koenigswald and Thomas Litt to commemorate the 150th anniversary of this discovery. It is in Bonn, at the Rheinisches Landesmuseum that the holotype of the Neanderthal taxon is kept, and it was at the Rheinische Friedrich-Wilhelms Universität in that same city that the conference was held.

The five symposia into which the conference was divided are the basis of two volumes. This first volume brings together the reworked versions of the papers and posters presented in three of these symposia (numbers 1, 4 and 5) on human paleontology (paleoanthropology in the European sense), which dealt with the origin, evolution and disappearance of the Neanderthal population.¹ The second volume, organized by N. Conard and J. Richter, assembles the papers presented in the two other symposia (numbers 3 and 4), concerning the way of life, the culture and the environment of this extinct population.

The purpose of this conference was to present the state of our knowledge concerning this fossil group, to examine questions that it raises in the present, and to evoke perspectives for future research.

If we compare the results of this conference with the centenary conference held 50 years ago in Germany, it becomes immediately apparent, not only that our understanding of

the Neanderthal population has changed, but also that this change is closely interrelated with more general modifications in our conceptions of humanity since then. We also perceive that the geographical focus of research on this population has been greatly enlarged, corresponding to a shift in scientific paradigms. Europe was the focal point of interest during the first 100 years of study of this fossil, coinciding with the first century of paleoanthropology as a discipline, even when discoveries were made outside of the European continent. Investigations were carried out in relation to the European Neanderthals, since Europe was the pivotal axis around which paleoanthropological concerns in general turned. By contrast, the significance of Europe in paleoanthropology has clearly diminished over the past 50 years. Thanks to fossil discoveries throughout the ancient world and to developments in our methods of dating and of investigating fauna and industry, Europe has lost its primary place, and it is rather in light of discoveries in Africa and Asia that European fossils, in particular Neanderthals, are now interpreted.

In this introduction I will briefly summarize the principal moments that led to modifications in our view of Neanderthals and then, in the section that follows, present the different chapters included in this volume. These chapters clearly illustrate the changes in methods and techniques of contemporary research and the state of our knowledge regarding this fossil population.

An examination of studies published during the first 50 years following the discovery of Neanderthal brings to light an important change in our idea of the evolutionary history of humanity. After the initial discovery, the first researchers had to convince the scientific community that this specimen was not simply the remains of a pathological individual. They had to characterize its principal traits, while attributing to it a phylogenetic status and placing it, and Neanderthal discoveries that followed, in the theoretical framework of Darwinian evolution. In the scientific perspective of the second half of the nineteenth century, this *Homo neanderthalensis* (King, 1864) represented a chronological moment in the evolutionary history of humanity, a ring in the larger chain which the discovery of Cro-Magnon in 1868 and *Pithecanthropus* in 1891 would further elaborate. From the standpoint of its anatomy,

¹ Symposium 1: "Outside Europe and Neanderthal Origins", conveners: S. Condemi and F. Schrenk; Symposium 2: "Neanderthal Palaeoenvironment", conveners: W.v. Koenigswald and T. Litt; Symposium 3: "Neanderthal Lifeways, Subsistence and Technology", conveners: N. Conard and J. Richter; Symposium 4: "Neanderthal Anatomy, Growth, Adaptation and Physical Variations", conveners: S. Condemi and W. Henke; Symposium 5: "Neanderthals and Modern Humans", conveners: G.-C. Weniger and J. Orschiedt.

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its cognitive capacities and technical ability, Neanderthal was considered to be an “intermediary” being or “missing link”. Interpreted in this manner, the geographical distribution of Neanderthals was taken to be quite vast since, as representative of the evolutionary history of humanity as a whole, it was considered to have been present throughout the ancient world.

Up until the Second World War, this approach to the Neanderthals and to their place in human evolution remained predominant (with the exception of the so-called theory of the “pre-sapiens”). Moreover, it is this perspective that we still encounter in the book *Hundert Jahre Neanderthaler* (von Koenigswald 1958), assembling the papers presented at the centennial Neanderthal conference in 1956. Indeed, in this book, papers dealing with European fossils which are still considered to be Neanderthal today (for example, Monte Circeo, Pech de l’Azé, or Spy) are presented alongside others from outside of Europe that we no longer take to be Neanderthals, such as the so-called Rhodesian fossils or the Solo fossils from Java – both defined in that conference as “tropical” Neanderthals – or the north African fossils (for example, Jebel Irhoud) – considered to be “Neanderthaloid”.

At the same time, parallel to the 1956 centennial conference, a number of articles published in the 1950s already announced a more nuanced scientific perspective in which researchers entertained a less linear and more complex idea of human evolutionary history than that which had predominated since the initial discovery of the Neanderthal specimen. For example, the 1951 article of F. Clark Howell, “The Place of Neanderthal Man in Human Evolution”, presents a synthetic approach to the Neanderthal fossils in which the attempt to understand their evolution includes analysis of their environmental and climatic context. Moreover, the multiplication of fossil discoveries, not only in Europe but throughout the ancient world (*Australopithecus* in Africa is a noteworthy example) portrays a much longer chronological range and an evolutionary history in which there are clear differences according to the continent in which the discovery was made.

It is during the 1960s, in a favorable political context, that a large number of excavations were undertaken in the Middle East, which were the source of numerous original studies. Here, too, we must remember the pioneering work of F. Clark Howell, notably in his article “Upper Pleistocene Stratigraphy and Early Man in the Levant” of 1959, which had a decisive impact on the scientific community. In his analysis, the author raised important questions concerning the Mousterian sites of the Levant, and regarding the phylogenetic status of certain fossils which had been found in these sites during the 1930s. In addition, a series of excavations undertaken in sites in the Middle East during the 1960s (beginning with those of R.S. Solecki at Shanidar, H. Suzuki at Amud, B. Vandermeersch at Qafzeh and A. Jelinek at Tabun) and a considerable number

of studies on fossils, fauna, lithic industry, habitats, as well as dates from these sites have all been of particular significance for our present-day knowledge concerning Neanderthals. They have brought us to completely modify previous conceptions of Neanderthal as an intermediate fossil from the standpoint of anatomy, culture and chronology. Following these changes, new dating methods (TL, ESR) have led us to understand the need for a thorough revision of the idea of a succession of populations as it had been interpreted on the basis of the European model.

Beginning in the 1960s, these studies demonstrated that the geographic situation of Europe, a peninsula of Eurasia exhibiting particular environmental and climatic conditions, led to the differentiation of Neanderthals which, in overall evolutionary history, constituted a singular and marginal population. In addition, the multiplication throughout the 1960s and 1970s of fossil discoveries in Africa (for example, the different discoveries of *Australopithecus*, *Homo habilis*, etc.) brought to an end the Europocentric viewpoint in paleoanthropology stemming from the pre-war period. The whole series of these discoveries led to a still longer view of the evolutionary history of humanity and to a more differentiated perspective on human development according to the continents in which it occurred.

During the decades of the 1970s and 1980s, a number of paleoanthropological studies inaugurated an important shift in the approach to the Neanderthal fossil population. The quantification of anatomical traits, which had attained ever greater precision during the first century following the discovery of Neanderthal, was complemented during these decades with new kinds of approach to anatomical variability and to adaptive features among Neanderthals. The analysis of variation among modern human populations began to play a major role in Neanderthal studies, as the attempt was made to situate the data corresponding to Neanderthal specimens in a broader populational framework. It is in this scientific context that the Neanderthals were taken to represent a human fossil population, named *Homo sapiens neanderthalensis*, placed within the scale of variability of modern human populations.

Over the course of the 1980s, the multiplication of these anatomical studies of fossil populations, in particular of Neanderthals, accompanied by new methods of investigation such as cladistic analysis, and new tools such as the CT scan, led once again to a modification in approaches to the evolutionary history of the Neanderthal population. These anthropological studies, and those undertaken by prehistorians, aimed to better comprehend the way of life of this fossil population through investigation of the habitability of sites, the means and strategies of subsistence, or their paleo-environment. They have permitted us to clarify the question regarding not only the particularities of this population and its differences in regard to *Homo sapiens*, but also in relation to

fossils that preceded them in Europe and throughout the ancient world. Thus, over the course of the 1980s the singularity of this population was placed ever more clearly in the forefront.

Moreover, from the very beginning of the 1980s the idea of the singularity of Europe concerned not only the Neanderthals, but the totality of European peopling since its origin. According to this viewpoint, *Homo erectus* had never been present in Europe although it existed in the other parts of the ancient world, or at least in Asia. This indicated a great difference in the entire evolutionary history of Europe in relation to that of Asia and Africa. Here again, at the “First Congress of Human Paleontology” held in Nice in 1982, it was F. Clark Howell who defended this position. In spite of the fact that part of the Congress was devoted to what the discoverers of the putative *Homo erectus* of Arago (including numerous comparative studies with “other” European *Homo erectus* specimens), Clark Howell (1986) supported the idea concerning the singularity of Europe from the most ancient periods onward!

At the end of the 1980s a number of researchers working on Neanderthals adopted the idea of the singularity of Europe since the most ancient available traces of its peopling, and they elaborated on the implications of this idea for the evolutionary schema. They focused on the evolutionary consequences of the marginal geographical position of Europe, on the particular evolutionary pattern of Neanderthals, and on their probable speciation. By the end of the 1980s researchers once again considered Neanderthals to represent a species different from their contemporaries in the rest of the ancient world. The name *Homo neanderthalensis* was reintroduced to characterize these fossils belonging to Europe. Although the point of view which attributes to Neanderthals the status of a species is not shared by all paleoanthropologists, certain chapters included in this volume support this position, which DNA studies since 1997 have tended to corroborate.

This brief historical survey permits us to appreciate the important modifications that have marked the study of Neanderthals. If, as we have noted, these changes have depended above all on fossil discoveries, they have also been due to new methods of study and investigation, not only in paleoanthropology, but also in disciplines which work in close collaboration with it.

It is in this broad context that the conference marking the 150th anniversary of the discovery of Neanderthal was held in 2006. In illustrating the contemporary state of our knowledge, we may also ask how long the view of Neanderthals presented here will retain its validity. We can anticipate certain technological and methodological developments in the future, such as those depending on the extraction of DNA which is well preserved in the crystal aggregates of fossil bones, and we can also expect new developments in research, above all in

relation to the origin of the oldest European populations. It is nonetheless difficult to predict in any comprehensive way how Neanderthal studies will develop over the course of the next 50 years. Our brief historical investigation illustrates the primary importance of new fossil discoveries which may well overturn our current hypotheses. We may predict with high probability that research will develop extensively in areas which are not well known today, such as in certain regions of Africa and Asia. It is likely that the privileged and, indeed, nearly “exclusive” conception of relations and exchanges in peopling between Europe and Africa will be complemented, if not replaced, by the idea of relations and exchanges between Europe and Asia. If I have not dealt in any detail with the changes in our methods of study, it is clear that they have changed considerably over the past 50 years, which have witnessed the emergence of areas of investigation which could not previously have been imagined. Hence, although the helical structure of DNA had just been determined, during the commemorative Neanderthal conference in 1956, it would have seemed fantastic to imagine the possibility of extracting DNA from the fossil bones of Neanderthals! There is an increasing tendency for studies of this population to gravitate from paleoanthropology to the field of paleobiology. It therefore seems certain that a different vision of the Neanderthals will emerge over the next 50 years.

F. Clark Howell presented the opening address to the conference in Bonn in 2006. This eminent researcher, who also participated in the centenary anniversary of the Neanderthal discovery in Düsseldorf, promised to provide us with a written text for this volume. His sudden death several months after the Bonn conference prevented him from completing this text. We therefore present in this volume a transcription of his oral talk.

In his opening address F. Clark Howell recalls the stages of his scientific development that we have briefly noted above. He places in relief the scientific context of the post-World War II period and the burgeoning of ideas that has been characterized as the “modern evolutionary synthesis” which fortified the Darwinian basis of natural selection in the process of evolution and led to a paradigm change in our general scientific outlook. At the same time, Howell indicates the change in the focus of scientific interest from Europe toward Africa. The narrative of his intellectual autobiography recalls changes that have marked our discipline, brought about not only through scientific influences but also through political developments over the past 50 years. It is fortunate that Clark Howell, animated as he was by an intense intellectual curiosity, was able to communicate his experience and his profound understanding to those around him. On a personal note, I remember with gratitude his kindness in permitting me, as a very young student, to use his large personal library, and his readiness to engage in discussions with me on the evolution of Neanderthals and on the relations

between European Neanderthals and those of the Middle East. In recognition of his important contribution to our discipline, this book is dedicated to his memory.

Following this introduction, 24 other chapters make up this volume. It is not divided into sections as was the conference itself. The editors have preferred to present the chapters according to their thematic order in relation to the origin, evolution and disappearance of Neanderthals. In presenting contemporary responses to questions that have arisen in these areas, we have aimed to place in relief the debates these responses have fueled and the further questions they have raised. It is for this reason that more synthetically oriented chapters are found in this volume alongside other chapters which address a particular problem or topic. The broader interest of the latter type of chapter lies in its exposition of methods and techniques of analysis that are current in our disciplines.

At the beginning of the volume, six chapters focus on questions regarding classification, Neanderthal origins and the origin of the fossil populations that were contemporary to them, as well as on cultural and faunal changes that characterized their world. Thus, in Chap. 3, W. Henke and T. Hardt discuss the evolution and origin of 'early' *Homo* and they illustrate the difficulty of species recognition in paleoanthropological research. In the chapter which follows, Chap. 4, I. Tattersall likewise deals with the difficulty of species recognition, but in a perspective more directly centered on the European fossils. This author places in question the nomen *Homo heidelbergensis* as it is applied today in European Middle Pleistocene hominid systematics and also the use of the "accretion model" applied to Neanderthal evolution.

In Chap. 5, F. Mallegni also deals with the question of the origin of Neanderthals on the basis of a study of the fossil from Ceprano (Italy). Through cladistic analysis of the skull, he suggests that this fossil might represent an archaic species, different from *Homo antecessor* which he defines as *Homo cepranensis*. For Mallegni, the Italian specimen represents the holotype of this species, and Ceprano belonged to a population that gave rise to the European *Homo neanderthalensis*. This assumption regarding the oldest fossils of Europe is somewhat different from the interpretation of Bermudez de Castro et al. In Chap. 6, these authors, on the basis of a revision of features observed on the oldest Spanish fossils in Atapuerca, formulate a different hypothesis. For them, either a phylogenetic continuity exists between these archaic fossils, called *Homo antecessor*, and Neanderthals, or else both species shared a common ancestor.

Since researchers working on European specimens often refer to fossils found outside of this continent, we asked Wu Liu and Xiujie Wu to present the Chinese hominids. In Chap. 7, the authors summarize research advances made in recent years, including the discovery of new hominid fossil sites, and they examine studies related to these discoveries.

Their data brings to light the significance of this recent work and the potential of China as a source of important fossils and insight into the relationship between Europe and Asia in years to come.

This first part of the volume concludes with two chapters which do not deal with particular fossil specimens, but with the dispersal of fossil populations, both toward and within Europe. In Chap. 8, N. Goren-Inbar focuses mainly on the geographical meeting point provided by the Levantine Corridor and places in relief the evolutionary and cultural background of Neanderthals. She argues that an understanding of the material culture and behavioral traits of this population requires the examination of earlier periods which form the background to Neanderthal abilities and productive capacity. Through her analysis of the Levantine culture, the author shows that particular aspects of the technologies characteristic of the Neanderthal era first emerged in the Lower Paleolithic.

In Chap. 9, W. von Koenigswald focuses on Pleistocene faunal exchange during the Middle and Late Pleistocene in Europe. He examines the impact of climate change and faunal turnover on human populations and concludes that migration as a result of such changes may account for morphological differences distinguishing various human fossils known from the Middle Pleistocene of Germany.

These last two chapters concerning the dispersal of fossil populations serve as a transition toward the second part of this volume, consisting of 13 chapters which deal with the anatomy and the diversity of the Neanderthal population. B. Vandermeersch and M. D. Garralda, in Chap. 10, summarize the data available for the principal human fossils in the European Middle and early Late Pleistocene. The authors illustrate the importance of Levantine fossils for the understanding of Neanderthals. Over the past 30 years, B. Vandermeersch has defended the thesis that there was a gradual evolution from the oldest European fossils to the Neanderthals (later called the accretion model). In this chapter, the authors do not exclude the possibility of gene-flow from groups of Asian or African origin, above all in view of the breadth of their geographic dispersal and the diversity of environments to which they adapted.

This question of variability of the Neanderthal population is also the theme of the chapter by J.-L. Voisin. In Chap. 11, he examines the variability of Neanderthals by applying to them the concept of "speciation by distance". Since the differentiation of Neanderthals occurred in Western Europe, this hypothesis accounts for the morphological cline among Neanderthals, from the west (displaying more pronounced Neanderthal features) to the east. For Voisin, the shoulder girdle reflects this morphological cline, but only for architectural and not for functional features.

The particularities and variability of Neanderthals are also examined in this volume in terms of ontogenetic and growth patterns among this fossil population. Three studies

deal with this theme. In the first, Chap. 12, A.-M. Tillier provides a synthetic view of difficulties we face in the effort to document distinct developmental stages among specimens originating from sites separated by vast distances or by large stretches in time. In spite of this limitation, the author illustrates the way in which comparative analyses may provide accurate information regarding the ontogenetic appearance of several diagnostic Neanderthal characteristics and reveal similarities and contrasts between Neanderthals and early modern children.

The two other studies on ontogenetic and growth patterns of Neanderthals are based on an examination of teeth. T. Smith et al., in Chap. 13, observe that studies of dental development have attained conflicting results regarding the similarity of Neanderthal growth and development to that of modern humans. Long-period lines on tooth crowns (perikymata) and roots (periradicular bands) are quantified, and crown formation, root development, and age at death are estimated. The authors show that Neanderthal dental development overlaps with the low end of modern human populations, and demonstrates a greater range of variation in Middle Paleolithic hominins than previously reported. On the basis of a different methodology, P. Smith et al. also examine Neanderthal growth patterns in relation to teeth. In Chap. 14, they consider tooth formation and the successive phases of dental development as a source of insight into ontogenetic processes. Using a three dimensional model to quantify developmental features, this study indicates that the characteristic features of Neanderthal teeth, expressed in intercusp distances and proportions, thin enamel and taurodont roots, represent a different partitioning of cell division and differentiation from that observed in *Homo sapiens sapiens*.

These studies are followed by further analyses of features found on Neanderthals which are open to debate. Their topics and methods permit us to gain a unique view of new approaches to the Neanderthal population.

The chapter by V. Volpato et al. (Chap. 15) employs synchrotron radiation microtomography (SR- μ CT) to investigate the shaft length and the cross-sectional geometric properties of the humeri of the Regourdou 1 Neanderthal. The authors support the previous conclusion that Regourdou 1 was right-handed by only a modest degree of right dominance, which characterizes this individual with respect to the available Neanderthal data.

In Chap. 16, K. Harvati et al. explore mandibular traits that differentiate Neanderthals from modern humans (greater robusticity, a receding symphysis, a large retromolar space, a rounder gonial area, an asymmetric mandibular notch and a posteriorly positioned mental foramen). Using a morphological integration approach, their study assesses the effects of allometry and evaluates the influence of masticatory and paramasticatory activities on mandibular shape.

Following this chapter, Chap. 17 by P. Gunz and K. Harvati deals with the occipital bun, which is considered by some authors to be a derived Neanderthal trait and, therefore, it is often cited as evidence for admixture between Neanderthals and anatomically modern humans. On the basis of geometric-morphometric analysis, the authors suggest that the occurrence of “hemibuns” should not be used as evidence for admixture, since this morphology is not an independent trait, but a predictable correlate of the relative position of the temporal bone.

In Chap. 18, U. Witzel examines the relationship between skull function and skull shape by means of an application of Wolff’s law through a deductive technique of structure synthesis. It aims to present a new method that can be used to test hypotheses regarding the relationship between structure and function during skull evolution.

D. Caramelli et al., in Chap. 20, and L. Orlando and C. Hänni, in Chap. 21, each give a review of current knowledge concerning Neanderthal DNA sequences and anticipate future challenges related to Neanderthal genomics. The authors illustrate that advances in ancient DNA technology have made possible a better understanding of the evolution of the Neanderthal gene pool and have permitted us to address the long-standing question of a possible genetic admixture with modern humans.

Chapter 19 presents the paleogeneticist’s point of view according to which Neanderthals display a particular mtDNA sequence. In this new study of mtDNA, presented in this volume by J. L. Arsuaga et al., the sequence that the authors present is very short (52 bp), but it contains substitutions common to all Neanderthals. There is also one substitution (16,243) that may to some degree vary with geological age. The authors conclude that the recovery of this short mtDNA fragment can be used as a diagnostic tool for taxonomic classification in European Late Pleistocene fossil human specimens.

The theme of the transition between Neanderthal and modern humans is analyzed in the third part of this volume comprising five chapters. Chapter 22 by O. Jöris et al. gives a critical review of the radiocarbon record available at the time of the demise of the last Neanderthals and the first appearance of anatomically modern humans in Europe. This paper provides a useful examination of the European radiocarbon-based chronometric record for the period between ca. 40.0 and 30.0 ka ^{14}C with reference to the stratigraphic evidence. From the point of view of dating, this chapter demonstrates how complex this period of transition is. It is here that the problem arises regarding the role of Neanderthals in the peopling of the Upper Paleolithic and the question of whether they were replaced by modern humans.

This question is developed in Chap. 23 by I. Jankovic et al. These authors place the genomic study of the fossil of Vindija in a larger context, which includes paleontological and archeological data for this site. The authors support the

hypothesis of possible population interaction patterns between Neandertals and early modern humans in Europe.

A similar point of view is shared by E. Trinkaus in Chap. 24. On the basis of analysis of fossils originating in eastern Europe, the author argues that the later European Middle Upper Paleolithic (Gravettian) sample exhibits persistence of some of these and other Neanderthal/archaic features. He stresses the conclusion that simple models of an abrupt behavioral and phylogenetic transition for this period in Europe should be abandoned.

This conclusion is shared by J. Zilhao in Chap. 25. In opposition to the positions of a number of current researchers, the author supports the idea that, contrary to the “Human Revolution” paradigm that has predominated over the past 25 years, the Neandertals cannot be considered to represent an evolutionary dead-end. He therefore argues that biogeography, demography and paleoethnography will permit us to reach different explanations to account for their differentiation and eventual demise.

Finally, in Chap. 26, M. Wolpoff and R. Caspari raise the question concerning the concept of modernity, or “humanness”. In a discussion of an essay by Robert Proctor (2003), who suggested that a series of intellectual transitions gave rise to current understanding of the concept of “humanness”, Wolpoff and Caspari explore transitions in our understanding of Neanderthal humanity.

At the conclusion of the arduous editorial process which was required for the publication of this volume, and also on behalf of my co-Editor, I would like to thank each of the authors for their presentations which shared with us their ideas concerning the state of research in our different fields.

We regret the absence of articles by some participants in the Bonn conference, above all several paleoanthropologists who presented a different viewpoint than that found in this volume, namely that the Neandertals did not contribute to the peopling of the Upper Paleolithic. It is understandable that those who had already written extensively on this theme did not feel that they had anything new to offer in print. I am deeply grateful also to all the reviewers who have helped to improve the papers. I would like to extend my gratitude to E. Delson for deciphering and editing the recording of the lecture by F. Clark Howell and for his invaluable assistance and advice during the different stages of preparation of this volume. I would also like to extend my heartfelt thanks to the Alexander von Humboldt Foundation, Bonn, for its generous support which made the Bonn conference possible.

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