

FRED H. SMITH • JAMES C. M. AHERN

THE ORIGINS OF
**MODERN
HUMANS**

Biology Reconsidered



WILEY Blackwell

The Origins of Modern Humans

The Origins of Modern Humans

Biology Reconsidered

Edited by

Fred H. Smith and James C. M. Ahern

WILEY

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First Edition © 1984 Alan R. Liss
Published by John Wiley & Sons, Inc., Hoboken, New Jersey
Published simultaneously in Canada

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Library of Congress Cataloging-in-Publication Data

The origins of modern humans : biology reconsidered. – 2. [edition] / editors, Fred H. Smith, James C. M. Ahern.

pages cm

Summary: “In 1984, Fred Smith and Frank Spencer introduced *The Origins of Modern Humans: A World Survey of the Fossil Evidence*, a volume which introduced two of the major theories of human evolution that would be debated for the next twenty years. The book went on to win Best Book in the Life Sciences 1984. Now Smith, with Jim Ahern, has compiled the second edition of this field classic, incorporating the latest information in paleontological, genetic and developmental biology to pick up where the first edition left off and push the debate forward for the next twenty years” – Provided by publisher.

Includes bibliographical references and index.

ISBN 978-0-470-89409-5 (hardback) – ISBN 978-1-118-65987-8 (eMobi) –

ISBN 978-1-118-65990-8 (ePub) – ISBN 978-1-118-65993-9 (ePdf) –

ISBN 978-1-118-65999-1 (Obook)

1. Human evolution. I. Smith, Fred H. II. Ahern, James C. M.

GN281.O75 2013

599.93'8–dc23

2013007032

Printed

10 9 8 7 6 5 4 3 2 1

In Memory of Frank Spencer (1941–1999)

A Kent Limey in the Court of Queens—and Windsor and Ann Arbor
(with apologies to Mark Twain)

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Introduction: Thoughts on Modern Human Origins: From 1984 to 2012

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Origins of Modern Humans (1984)

A Perspective from a Student (JCMA)

In the late 1980s, I went off to college interested in a handful of possible futures but certain of none. A moment of clarity came in a “theory and method in physical anthropology” class when the topic of the week, and of one of my papers, turned toward modern human origins. This had become the hot topic of paleoanthropology by the late 1980s and had largely eclipsed the field’s obsession with hominin origins. As I delved into its literature for the first time, I encountered a single book that not only was a wealth of information for the paper that I needed to write but also the work that had been instrumental in changing the focus of paleoanthropology. This book, Smith and Spencer’s *The Origins of Modern Humans: A World Survey of the Fossil Evidence* (1984), was a weighty tome that I felt as I carried it around with me for the rest of the semester and well after I had turned in my first paper on modern human origins. Other books on modern human origins had come out by the late 1980s and all had their own strengths. However, what set *Origins* apart, aside from being the first, was its detailed fossil descriptions and decidedly new theoretical explanations combined with comprehensive geographical coverage. Many of the book’s chapters went on to become core readings for any student of physical anthropology, and the book as a whole became essential for all paleoanthropologists. *Origins* transformed me and many others from undeclared college students into anthropology majors determined to become paleoanthropologists.

A Perspective from an Editor (FHS)

My late friend and colleague, Frank Spencer, and I conceived the idea for a volume on the fossil record relevant to the origin(s) of modern humans in the early 1980s. Because paleoanthropology during the 1970s and early 1980s had focused primarily on earlier stages of human evolutionary history, we felt that a volume presenting various perspectives on later human evolution would be a timely and valuable contribution. Furthermore, Frank and I believed those perspectives should be presented within the context of detailed regional analyses of the fossil evidence, so we conceived a series of papers that would take regional, as well as theoretically varied, approaches. We also felt it was important to demonstrate the continuation of some of the same evolutionary trends involved in modern human origins after the appearance of modern people. Thus the *Origins of Modern Humans: A World Survey of the Fossil Evidence* (Smith and Spencer, 1984) covered both late Pleistocene and aspects of early Holocene human skeletal evolution.

In *Origins of Modern Humans*, chapters covered four broadly defined geographical regions: Africa, Western Asia (including the western areas of the then Soviet Union), East Asia, and Europe. Europe was split into Western and Central Europe because of the wealth of the European fossil record and to ensure the Central European evidence was not eclipsed by the tendency to focus on Western Europe, as had been the case through the middle decades of the twentieth century (see, e.g., Boule and Vallois, 1957). This European split also provided for more diversity of perspective as the Western European chapter was written from a decidedly “replacement” explanation for the appearance of modern people in Europe (Stringer et al., 1984), while the Central European chapter took a view of significant continuity between Neandertals and early modern Europeans (Smith, 1984). In addition, Wolpoff, Wu, and Thorne provided the first comprehensive explanation of multiregional evolution (Wolpoff et al., 1984), and Bräuer (1984) presented the most complete initial discussion of his “Afro-European Sapiens Hypothesis.” Wolpoff and colleagues’ discussion centered on the fossil material from East Asia and Australasia, areas that strongly influenced Weidenreich’s trellis model of later human evolution, in many ways the intellectual precursor to multiregional evolution. Although not Bräuer’s first publication with the Afro-European Sapiens theme, it was his earliest comprehensive statement on the African fossil record’s demonstration of the origin of modern humans on that continent. Rightmire (1984) also stressed the importance of Africa, particularly the likely early appearance of modern humans there. While the Western European chapter supported a replacement of Neandertals by incoming moderns in Europe, Stringer and colleagues, like Bräuer, also suggested the possibility of some introgression. However, Stringer and colleagues were more equivocal regarding an African origin for modern humans. They state that “the place of origin of the first hominids with a total morphological pattern matching that of recent humans is not identifiable from the present fossil record” (Stringer et al., 1984: 121). The basis of this statement was not a lack of relevant fossils but the problem of dating the late Pleistocene human fossil record, particularly outside Europe. Dating uncertainties recur in the 1984 papers dealing with initial modern human origins in all regions.

Both the Central Europe and Western Asia (Trinkaus, 1984) chapters supported models that involved considerable continuity from Neandertals to early modern people in these respective regions and more generally from archaic to modern humans throughout the Old World. Both chapters also evoke cultural/environmental adaptation as major factors influencing the timing and pattern of modern human emergence. In 1984, these ideas could be encompassed under a fundamentally multiregional model as opposed to a single-origin, more replacement-focused model. Thus the 1984 volume played a fundamental role in defining the dichotomy of perspective that dominated the debate on modern human origins throughout the remainder of the twentieth century: multiregional evolution versus a single regional origin model in which the spread of modern humans from the source region resulted in replacement of the archaic peoples indigenous to other regions. Focus on this dichotomy continues into the twenty-first century and has been clearly reflected in subsequent edited volumes dealing broadly with modern human origins (Mellars and Stringer, 1989; Trinkaus, 1989; Hublin and Tillier, 1991; Bräuer and Smith, 1992; Aitken et al., 1993; Nitecki and Nitecki, 1994; Clark and Willermet, 1997), as well as those more focused on Neandertals and their role in later human evolution (Conard, 2006; Harvati and Harrison, 2006; Condemi and Weniger, 2011).

New Data and Directions on the Heels of 1984

In the mid-1980s, it seemed important to specify what was needed to falsify one or the other of these dichotomous models. So in 1985, Smith established three criteria that should be met in order to demonstrate replacement of all archaic humans throughout the Old World by

modern humans that emerged in a single region. First, modern humans would have to be found in a single region demonstrably earlier than in other regions. Second, modern humans must be shown to overlap with archaic peoples in some places. And third, there should be some demonstration of a cause for the expansion of modern humans from their natal area to other regions. In the early 1980s, it could still be convincingly argued that modern humans appeared in various areas of the Old World at basically the same time, approximately between 35,000 and 45,000 years ago. Although there were certainly claims for an earlier presence of moderns in both West Asia and Africa, there was no compelling evidence that moderns were significantly earlier in any one specific region, nor was there a strong indication of the movement of modern morphology from any supposed region of origin into other areas. Similarly, if moderns migrated into other regions they should have temporally overlapped with indigenous populations and left, at least in some regions, evidence of that overlap. At that time, no such unequivocal evidence of such overlap was available, nor was there a clear demonstration of the geographic spread of modern people from a single region. Based on these factors, multiregional evolution could not be falsified and actually, in the opinions of many, provided the most parsimonious explanation for modern human origins throughout the Old World.

Just after the mid-1980s, evidence emerged that related directly to these criteria. H. Valladas and colleagues published three papers on the application of thermoluminescence (TL) dating to the Western Eurasian late Pleistocene fossil human record. This work was significant for two reasons. First, it demonstrated, for the first time, use of a reliable technique capable of providing chronometric age estimates during the critical period for modern human origins, between circa 200,000 and 40,000 years ago, albeit not directly on the fossils. Second, results from TL estimates provided convincing support for the early appearance (92 ± 5 kya—or thousand years ago) of modern humans at Qafzeh in the Near East (Valladas et al., 1988) and more recent ages for Neandertals in both Europe (Le Moustier @ 40.3 ± 2.6 kya; Valladas et al., 1986) and in the Near East (Kebara @ 61.6 ± 3.6 kya; Valladas et al., 1987). Soon TL was joined by electron spin resonance, which could provide chronometric dates, often directly on human fossils that broadly supported the pattern emerging from TL dating (Grün and Stringer, 1991). Other chronometric dating techniques also began to have a greater impact on understanding this time period, including accelerator mass spectrometry (AMS) radiocarbon and other aspects of uranium-series dating (see Aitken et al., 1993).

Another line of evidence started to gain attention at roughly the same time. In 1982, a study of over a hundred nuclear genes by Nei and Roychoudhury suggested that modern Eurasia populations split from Africans at 110 ± 34 kya, supporting earlier interpretations (see Howells, 1976). While the large error raised questions about the accuracy of some of these earlier genetic estimates, additional evidence emerged with the initial studies by Cann and colleagues (1987) on worldwide modern human mitochondrial (mt) DNA distribution. This study indicated that all modern human mtDNA originated in Africa and that the first modern Eurasian population diverged from Africans between 90 kya and 180 kya. Although this interpretation of the mtDNA data had its critics, the fact that it was supported by other genetic studies proved very compelling, as did further research on the mt genome that answered many of the initial criticisms (see reviews in Relethford, 2001, and Cartmill and Smith, 2009). Joining this new dating and genetic evidence with morphological evidence presented in the *Origins of Modern Humans* (particularly the works by Bräuer and Rightmire) and other sources, Stringer and Andrews (1988) formulated the Recent African Origin model, which explained modern humans as the result of a speciation event in Africa and as the instrument of archaic human replacement in Eurasia. This model, or very similar variants of it, became almost immediately the most widely embraced explanation for the origin (not origins) of modern people.

By the late 1980s, the classical version of the multiregional model seemed unlikely to be the most parsimonious explanation for modern human origins. This perception was supported by both the morphological and genetic evidence available, but it was primarily influenced by the emerging pattern of chronology indicating earlier appearance of modern humans outside than within Eurasia (except for the Levant). This suggested there likely was a specific region of origin for modern human biology. However, there were reasons to reject the complete replacement of Neandertals and other archaic people by a new species of modern humans. For example, the late Neandertal remains from Vindija suggested that later Neandertals showed a morphological pattern demonstrating integrated change in the direction of the modern human morphological pattern (Smith, 1984). Furthermore, early moderns in Central Europe possessed anatomical features that were best explained as the result of Neandertal contribution to their ancestry. Prior to the dating “revolution” of the later 1980s, these observations could be interpreted as indicating that Neandertals were evolving in the direction of modern Europeans within the multiregional perspective of regionally based, interconnected lineages. But even in 1984 the current volume’s senior editor wrote: “in my estimation the increasing evidence for the early appearance of modern *H. sapiens* elsewhere strengthens the possibility that unidirectional gene flow into Europe . . . played a significant role in the emergence of modern Europeans. However, even if gene flow’s role were significant, the nature of morphological continuity demonstrates that the Neandertal gene pool was a major contributor to that of early modern Europeans” (Smith, 1984: 196).

After 1984, reconsideration of the Central European Neandertal and early modern morphological evidence suggested that the amount of Neandertal contribution generally had been overestimated, including Smith’s 1984 assessment. For instance, it became more evident that continuity was primarily reflected in morphological details, not in overall anatomical form. The combination of this with the dating evidence led to the formulation of the assimilation model for modern human origins by the end of the 1980s (Smith et al., 1989), although aspects of it were emerging earlier (see Smith, 1985; Trinkaus and Smith, 1985). This model differed from the multiregional evolution of the late 1980s and early 1990s in that it supported the likelihood of a specific region of origin for modern human biology as a complex and suggested Southern Africa as likely, but not definitely, that region. Like multiregional evolution, however, assimilation rejected the occurrence of a speciation event associated with that origin and argued that Eurasian regional populations of archaic humans were not totally replaced.

One problem relating to an African origin for modern humans in the 1980s was the uncertainty of the dating of sites like Omo-Kibish KHS and Border Cave (Smith et al., 1989), both of which were claimed to show modern humans in Southern Africa prior to 100 kya. The morphologically modern Omo-Kibish I specimen (from Ethiopia) was dated to ~130 ka on the basis of uranium-thorium dating of mollusk shell (Butzer, 1969), but this was considered problematic because of inherent uncertainties in applying the technique to shell. The morphologically modern Border Cave crania and mandibles were of uncertain context, except for the Border Cave 3 infant and Border Cave 5 mandible. Taking a cautious approach to both of these sites in 1989 was certainly reasonable, but things have changed. New research has led to the bracketing of the Omo-Kibish I skeleton between 172 kya and 196 kya (McDougall et al., 2005, 2008), demonstrating that modern human anatomy was established in Africa at an early date. Subsequently this has been enforced by the discoveries of early modern specimens at the site of Herto, also in Ethiopia, securely bracketed between 154 kya and 160 kya (White et al., 2003). Added to the evidence for an early transition between archaic and modern humans in Africa (see Pearson, this volume; Bräuer, 2008; Cartmill and Smith, 2009), the fossil evidence from Omo-Kibish and Herto establishes that modern human morphology does indeed initially appear in Africa, perhaps specifically in

East Africa. Thus, the criterion of establishing an area of origin for modern humans, as previously discussed, has been met (at least in light of our current knowledge).

Better dating and new discoveries also have improved our picture of the appearance of modern people in much of Eurasia. The robust but fundamentally modern sample from the sites of Qafzeh and Skhul in Israel likely dates between 81 kya and 119 kya (see Cartmill and Smith, 2009). Unfortunately there have been no new early modern specimens from this pivotal region since the 1984 review. The same is not true for further east in Asia and in Australasia, where important finds have been made in China since 1984 (see Rosenberg and Wu, and Durband and Westaway, this volume). Also in Europe, especially Central Europe, there has been significant change in the evidence for early modern people (Ahern and colleagues, this volume). Overall, the pattern of modern human appearance in Eurasia is commensurate with the spread of modern human morphology as a unit from Africa to the Near East and then to other portions of the Old World, likely reaching Europe rather late but perhaps not as late as previously thought. Recent new dates and analyses on specimens from Italy and England possibly push the earliest skeletal evidence for modern humans in Europe to as early as 45,000 years ago (Benazzi et al., 2011; Higham et al., 2011). This pattern is yet another indication that modern human biology emerged and spread fundamentally as a unit (but see Rosenberg and Wu, this volume).

The evidence available today relative to the two other criteria established in 1985 is more equivocal. Temporal overlap of Neandertals and early modern people in the Near East and Europe is highly likely, but in the rest of Asia it is virtually impossible to establish. In the Near East, many scholars argue that there was not extensive overlap but rather a shifting boundary between modern people migrating up from Africa and Neandertals pushed south by European glaciations (see Franciscus and Holliday, this volume). In Europe, evidence for actual temporal overlap is convincing, but for both regions morphological evidence for actual biological introgression is intensely debated, as the various papers in this volume attest.

The third criterion deals with why moderns would have moved out of Africa, especially into an area where well-adapted hominins, the Neandertals, would have to be contended with. The most likely culprits that could provide such a motivation would be population pressure, climate/environmental change, or some combination of both. Past population size is painfully difficult to measure, particularly from a paleontological or archaeological perspective. Based on site density, Hassan (1981) calculated that people associated with Upper Paleolithic/Late Stone Age technology were some three times more common on the landscape than those associated with Middle Paleolithic/Middle Stone Age, some of whom were anatomically modern as well. Additionally, genetic studies indicate that effective population size in Africa was larger than in Eurasia throughout the Pleistocene (Relethford, 2001) and that effective population size was significantly smaller in Neandertals than moderns (Briggs et al., 2009). Still it seems unlikely that these differences were great enough to support an argument of simple population pressure as the cause for modern human expansion out of Africa. From another perspective, these data indicating smaller population sizes for Neandertals, recently supported by additional analysis of Mousterian and early Upper Paleolithic sites in Southwestern France (Mellars and French, 2011) suggest that Neandertals were relatively rare on the landscape. This was likely a significant factor in their seemingly rapid “disappearance” in the face of increasing density of incoming modern human populations (Smith, 2011).

Climatic reconstructions during the Middle and Late Pleistocene have long depended on the use of Marine Oxygen Isotope Stages (or MIS) (see reviews in Cartmill and Smith, 2009, and Klein, 2009) and more recently lake cores from the Rift Valley (Scholz et al., 2007; Cohen et al., 2007). Anatomically modern humans first emerged in East Africa between 196 and 154 kya (MIS 6) and reached the Near East to Israel minimally by 81 kya and perhaps

as early as 119 kya, within MIS 5. MIS 6 was an elongated cold period extending from 186 kya to 127 kya during which temperatures were significantly colder than today. However, new research based on lake sediment cores from Lake Malawi and Lake Tanganyika in the East African Rift Valley (Scholz et al., 2007) suggests the truly marked times of extreme aridity were between 135 kya and 75 kya and that climate was quite variable during this span. More arid conditions in Eastern Africa could have put pressure on populations to roam farther in search of resources, including movement through Northeastern Africa toward the Near East. However, the MIS provide a different picture on a broader scale. By MIS 5e, beginning around 130 kya, the world was getting warmer and wetter during the last major interglacial. The Near East perhaps became even more attractive for African migrants, and even North Africa areas that are today desert yield evidence of wetter, lush conditions during parts of MIS 5 (Castañeda et al., 2009). Thus the combination of potentially dryer conditions in Eastern Africa and possible more attractive conditions in North Africa and the circum-Mediterranean region might explain the modern human migration to the North that ultimately led to further spread into Eurasia as a whole.

It is certainly possible, indeed attractive, to explain the initial anatomically modern human movements out of Africa as the result of interplay between the pressures of arid conditions and population sizes in Africa. However, these might not have been of the magnitude to push people toward an out-of-Africa migration pattern. The fact is we just are not certain why the pattern of migration began and continued. The arguments for overlap of archaic and early modern people in the Near East and Europe, and the potential impact of climate and population pressure, are certainly intriguing. A recent discussion of the impact of refugia also adds insights to the role of climate in the process of modern human origins and the disappearance of Neandertal populations (Stewart and Stringer, 2012). Overall though, the second and third criteria established in 1985 are less clearly supported by the available evidence today as the first criterion is. There is still more work to be done in these areas.

History

Frank Spencer's contribution to the original *Origins of Modern Humans* was an assessment of the history of the study of modern human origins (Spencer, 1984). In his chapter Frank detailed the impact of Piltdown and pre-sapiens perspectives, as well as the changing view of Neandertals from the late nineteenth century, through Boule's influential work—particularly focusing on the analysis of the La Chapelle-aux-Saints skeleton. He also discussed the impact of Hrdlička's "Neanderthal Phase of Man," and the contributions of Schwalbe, Keith, Weidenreich, and Vallois. Frank's assessment of this history became easily the most cited paper on the pre-1980s history of later human evolution. This stems from the fact that few previous articles managed to take such a broad view yet still provided the detail necessary to be useful to other researchers. The issues Frank elucidated in 1984 were expanded in his seminal two-volume work, *History of Physical Anthropology: An Encyclopedia* (Spencer, 1997). In that volume, numerous entries deal with modern human origins, and later works have helped to connect Frank's perspectives with events and discoveries since 1984 (Smith, 2002; Delisle, 2007; Cartmill and Smith, 2009). Because of these recent updates to the history of later human evolution, we felt an independent chapter devoted to history was not as critical as it was in 1984.

Of course, another factor was that there was no Frank Spencer to contribute such a chapter. Frank's untimely passing in 1999 robbed us of a uniquely informed historical perspective on our discipline and left a void yet to be fully filled. As an alternative to an independent history chapter, the contributors to this current volume were asked to include historical perspectives where appropriate, and most of them have provided informative

historical insights in their contributions. Still, for those of us who counted him as a trusted colleague and friend, Frank's words are sorely missed. For all that Frank did and was, we are proud to dedicate this volume to his memory.

Origins of Modern Humans (2012)

In deciding on coverage of Africa, Asia, and Australia for the current volume, we (Smith and Ahern) concluded that the regional approach of the 1984 book was still appropriate, except that we decided to separate East Asia and Australasia. This was based on the fact that more evidence has accumulated in East Asia, as well as the recognition that these regions were different enough from each other to warrant separate considerations. We decided further that there was no need to repeat basic description for all of the fossil material discussed in 1984. Rather, we asked the authors of regional chapters to focus on new fossil discoveries, using older material when relevant. We also asked contributors to place their region in a broader context of modern human origins, including commenting on history, genetics, patterns in other regions, and any other factors they felt were appropriate. Furthermore, we maintained the variation of perspective in these regional chapters that characterized the 1984 volume. In the current volume, Osbjorn Pearson discusses the African fossil material and presents the strong paleontological indicators of an early presence of modern people on that continent, as well as considerations of potential climatic reasons for the spread of modern populations out of Africa and some useful insights on the issue of speciation in later human evolution. Robert Franciscus and Trenton Holliday focus on the complexities of the fossil record in Western and Central Asia and European Russia. They conclude that, despite the potential for temporal overlap, Neandertals and early modern humans remained separate in Western Asia. The mainland East Asian record is considered by Karen Rosenberg and Xinzhi Wu. They note that because East Asia occupies one of the extreme peripheries of human habitation during the Pleistocene, it is an ideal place to test models about human origins. Current consideration of what is a richer, better dated fossil and archaeological record, as well as new genetic data, is consistent with Weidenreich's original impressions emphasizing continuity and varying levels of gene flow with western parts of the Old World. Arthur Durband and Michael Westaway provide an overview of modern human origins in Australasia. Their perspective differs radically from that offered for Australasia in 1984, which touted Australasia as a region strongly demonstrating regional continuity (Wolpoff et al., 1984). Durband and Westaway argue there is no evidence for any morphological continuity between archaic Australasians (e.g. Ngandong) and modern people in island Southeast Asia or greater Australia.

In Europe, we also maintained the geographic split between Central and Western Europe, although we recognize there will be some overlap of coverage around the Rhine River. Jean-Jacques Hublin tackled the issue of cultural and biological identity of makers of the early Upper Paleolithic in Europe, with a focus on Western Europe (including Germany). He asserts that there is little compelling evidence for either biological or cultural continuity between Neandertals and early modern human populations. Central Europe is discussed by Ivor Janković, Jean-Luc Voisin, and us. Although we maintain that there was some continuity between late Neandertals and early modern people in this part of Europe, the nature and extent of that continuity is recognized to be different from that proposed by Smith in 1984. There are also significant changes to the fossil record in Central Europe since 1984, particularly with regard to early modern specimens.

In addition to the regional papers, we wanted to include other biological parameters that have become much more significant to the understanding of modern human origins than

was the case in 1984. Recent years have witnessed a great deal of work on Neandertal ontogeny and developmental biology, most of which has identified significant differences between Neandertals, the only archaic hominin for which such data can be reliably generated, and modern people. Frank L'Engle Williams reviews the craniodental evidence in Neandertals and moderns. He concludes that while some differences are demonstrable, Neandertals appear to achieve craniofacial maturation at stages of dental maturation comparable to those characterizing modern humans. Williams asserts this result suggests fundamental patterns of human life history arose in an ancestor of archaic and modern *Homo*. Another factor that has engendered considerable interest concerns differences in Neandertal and modern energy requirements. Andrew Froehle, Todd Yokley, and Steven Churchill determine that the pattern of reduction in body size and in naso-facial morphology that distinguishes modern humans from archaic populations is almost certainly associated with a reduction in adult maintenance energy requirements, with potentially major consequences for reproductive success. Such differences, from their perspective, would have provided early modern humans who migrated into Europe with a distinct advantage in over the existing, larger-bodied Neandertals.

Without doubt, the most influential biological parameter largely absent from the 1984 volume is genetics. In the current volume, John Relethford considers the pattern of genetic variation and cranial variation in modern humans with an eye to understanding our origins. He concludes that both datasets support a primarily African origin of modern people but with small (but not insignificant) contributions from archaic peoples outside of Africa. John Hawks and Zach Throckmorton focus on the interpretation of the Neandertal and Denisovan genomes and the evidence of their contribution to modern Eurasians. They demonstrate that a single, large-scale bottleneck, as would result from a classic speciation event, is not compatible with existing genetic data and that a longer, more complex process of population interactions must have taken place between and among archaic and modern people. In addition to their contributions, essentially all of the regional papers have also discussed the impact of current genetic knowledge from both ancient and living populations to the perspectives now held on modern human origins.

Finally, papers by Rachel Caspari and Milford Wolpoff and by Erik Trinkaus provide a comparative assessment of biocultural changes occurring during the Late Pleistocene. Trinkaus finds that the only shifts associated primarily with early modern humans are reductions in the use of the anatomy for manipulation and in apparent stress levels. Most of the other changes seem to be related, directly or indirectly, to modern human population expansion with the early and then mid Upper Paleolithic, and existing information argues for only subtle differences in adaptive effectiveness among populations. Caspari and Wolpoff describe modernity as reflected in accelerated change and see this as an evolutionary pattern that differs from archaic patterns in both tempo and mode. They assert that the modern pattern, which begins with an increase in longevity and other evolutionary changes, is one of increasingly rapid genetic, biological, and social changes within a widespread, interconnected human species.

While we feel that all of the papers in this volume provide important viewpoints and consideration of the record of later human evolution, we certainly harbor no misconception that all pertinent biological perspectives are covered. We would like to have included more chapters written by more of our colleagues, but space limitations and our desire to have comprehensive regional papers precluded the possibility of including more than we have. We also recognize that some discussion of cultural factors, especially the changing ideas concerning the initial Upper Paleolithic (Châtelperronian and Uluzzian especially) and new discoveries relating to aesthetic expression in both Europe and Africa, would have been

valuable. Several authors do comment on these issues, but extensive coverage of the archaeological evidence would have certainly made the volume unwieldy.

Genetics and Genomics

There is no doubt that the most influential non-paleontological perspectives of later human evolution have been provided by the study of ancient DNA. From the first announcement of the isolation of a segment on Neandertal mtDNA in 1997, the potential of ancient DNA to shed light on modern human origins has been widely accepted. Beginning with this initial article (Krings et al., 1997), the consistent interpretation has been that Neandertal mtDNA haplotypes are not represented in modern humans (Caramelli et al., 2006, 2011). Still, Serre and colleagues (2004) pointed out that available mtDNA data could not rule out a small amount of Neandertal contribution to modern human gene pools. Similar suggestions were made by others based on various lines of genetic evidence (e.g., Relethford, 2001; Templeton, 2005; Eswaren et al., 2005).

In 2006, initial sequencing of Neandertal nuclear DNA was reported. While one study found no indication of a Neandertal contribution to early modern humans based on a sequence of 62,500 base pairs (Noonan et al., 2006), the other found something different. This second study, based on about a million base pairs, suggested that modern humans and Neandertals shared too many derived single-nucleotide polymorphisms (SNPs) to explain them as totally separate lineages that split several hundred thousand years earlier and remained completely separate (Green et al., 2006). Green and colleagues posited that low levels of gene exchange between Neandertals and modern humans following the split between these groups were probably responsible for their results. However, these results were widely criticized as the product either of statistical problems or contamination (Wall and Kim, 2007). Other Neandertal nuclear DNA studies soon provided interesting results, including demonstrations that Neandertals and modern people shared the same form of the important FOXP2 “language gene” (Krause et al., 2007) and that some Neandertals would have likely had lighter hair and skin pigmentation (Lalueza-Fox et al., 2007). It is also possible that modern humans might have gotten genetic material critical for development of a “modern” human level of neurological complexity from Neandertals (Evans et al., 2006). Although these examples are generally not explained as indicating any Neandertal contribution to modern human gene pools (Culotta, 2007; Lari et al., 2010), they might demonstrate just that (Cartmill and Smith, 2009). It is not surprising that Neandertal haplotypes may differ slightly from modern haplotypic variation, particularly given that modern human genetic patterns have changed appreciably since the Pleistocene. In fact we should not expect Neandertal and modern haplotypes to always be totally identical as long as the differences are not functionally relevant. Even given the slightly different haplotypes in Neandertals than those found in modern humans, the fact is that the earliest evidence of a character discovered in the fossil record is generally accepted, at least provisionally, as the origin of that character. That should be valid also for genetic features. If that premise is accepted, then the origin of these two important modern human traits may well lie in the Neandertal gene pool, as some aspects of the modern human immune system apparently do (Abi-Rached et al., 2011).

The most influential ancient human genetic work to date has certainly been the publication of the draft Neandertal genome (Green et al., 2010). This impressive accomplishment was based on segments derived largely from three small long bone fragments from Vindija and, not surprisingly, showed that Neandertals and modern humans were 99.8% identical genetically. More shocking for many scholars was that this study fundamentally confirmed the 2006 study by Green and his colleagues regarding the relationship between Neandertals

and modern humans, but with a bit of a twist. Green and colleagues' data show that Neandertals are more similar to modern Eurasians than to modern Africans and that Neandertals apparently contributed between 1% and 4% of the genetic material of modern Eurasians. This means Neandertals were not reproductively isolated from modern people in Eurasia, although they certainly were not the major source of the latter's gene pool. Still if a 1% to 4% Neandertal contribution survives in living human populations, it may well be that the original contribution to early modern populations was significantly larger. This is because we know there has been extensive change in modern human gene pools during and after the Pleistocene (see Cochran and Harpending, 2009), so much of the original Neandertal (and perhaps other archaic) contributions have been lost. While we believe the Neandertal and Denisova (Reich et al., 2010) genomic data are most commensurate with the assimilation model, a case perhaps could be made for a more classical version of multiregional evolution if the original contribution was indeed significantly larger.

A rather different explanation has been offered for this greater similarity of Neandertals to Eurasian moderns. Eriksson and Manica (2012) used simulation to demonstrate that the patterns documented by Green and colleagues might not be due to admixture between Neandertals and expanded moderns but might actually reflect common ancestry of these two lineages in Africa prior to the supposed speciation that resulted in the emergence of Neandertals in Eurasia. They argue that African populations prior to this split were "structured," meaning that they only exchanged genes with neighboring populations and thus maintained a considerable amount of genetic and morphological distinctiveness, at least in differing regions of Africa. Eriksson and Manica then assume that contact between Northern African and Eurasian populations was broken between 350 and 300 thousand years ago, leading to the evolution of Neandertals in Eurasia. However, the Northern African populations were likely to share SNPs with the populations that eventually evolved into Neandertals in Eurasia and also were more likely to represent the populations that moved into Eurasia as early modern people. Eriksson and Manica's simulations show that statistically this scenario is just as likely to result in the degree of shared SNPs that Green and colleagues interpret as being the result of hybridization between Neandertals and early modern populations.

It is important to remember that this is a statistically based scenario. It does not demonstrate that the original interpretation of introgression between Neandertal and early modern Eurasians is incorrect. It simply offers another possible explanation. In fact, analysis of linkage disequilibrium data in recent Europeans supports the recent interbreeding hypothesis rather than the genetic structuring model of Eriksson and Manica (Sankararaman et al., 2012). This study also indicates that introgression could have occurred anytime between 37 ka and 86 ka but most likely between 47 ka and 65 ka. The more recent dates might suggest that introgression could have occurred as early peoples first entered Europe, rather than in the Near East as previously thought (Green et al., 2010). If the new dating of the Kent's Cavern maxilla and the Grotta del Cavallo teeth establish modern humans in Europe by 41–45 ka that possibility is enhanced.

The Eriksson and Manica model does raise an important point. The two African genomes used by Green and colleagues were a San from Southern Africa and a Yoruba from West Africa. No African from North or East Africa was compared in this study. Even before the Eriksson and Manica study, it was clear that other African genomes were needed to be compared in order to substantiate the Green et al. conclusions (Smith, 2011). This situation is similar in principle to the genetic interpretation of mitochondrial DNA haplotypes in Neandertals, early modern Europeans, and more recent populations. Neandertal mtDNA haplotypes do not fall in the range of modern human haplotypes, and early modern Europeans do fall in that range. This was widely hailed as proof that Neandertals were a different species than modern humans and did not contribute to their ancestry (Klein, 2009).

However, although there was no evidence for a Neandertal contribution, the limited number of early modern specimens ($N = 7$) made it statistically impossible to rule out a Neandertal contribution of up to 25% (Serre et al., 2004), far higher than the Neandertal genome data suggests. In fact to rule out a Neandertal contribution of $\leq 5\%$, a sample of sequences greater than the number of all known early modern European skeletons would be needed! Critiques of earlier genetic studies arguing for total replacement of Neandertals by the senior editor (Smith et al., 2005; Weiss and Smith, 2007; Cartmill and Smith, 2009) focused on the limitations of relatively small sample size in the ancient mtDNA studies and stressed the interpretation of Serre and colleagues (2004) that small sample sizes did not allow exclusion of a relatively small Neandertal contribution to modern humans. Given this, it would be an inexcusable inconsistency to claim that the issue of Neandertal contribution to modern Eurasians has been solved by the 2010 analysis of the Neandertal genome. In fact, even if the SNPs that reflect Neandertal-modern Eurasian similarities are not found when several North or East African genomic samples, it will still not disprove conclusively the Eriksson-Manica scenario. There will still linger the specter of small sample size.

Finally, there are now arguments that genetically modern humans left Africa after anatomically modern humans, so that the earliest evidence of modern human skeletons does not represent the earliest evidence of genetic modernity. For example, Macaulay and colleagues (2005) assert that genetically modern people left Africa around 60,000 years ago and very quickly spread throughout the coastal regions of Asia, all the way to Southeast Asia. Only after this do they spread north into the Near East and ultimately into Europe. This must be, of course, several tens of thousands of years after the first Skhül-Qafzeh people were in the Near East. Other studies see this process as a bit more complicated but still occurring after the first anatomically modern people have left Africa (see Gibbons, 2011). Some morphological studies have also identified morphological evidence of this latest “out-of-Africa” migration phenomenon (Grine et al., 2007; Crevecoeur et al., 2009). While we do not find the morphological evidence compelling, we certainly believe that the modern human gene pool in Eurasia has been altered substantially since the first morphologically modern people arrived. Despite the indication that these changes were substantial (Cochran and Harpending, 2009), we have yet to see a claim that such late genetic changes must reflect another speciation event in later human evolution.

From our perspective, the ancient DNA from Vindija and Denisova is best interpreted within the framework of assimilation, as are the morphological data. There is great excitement over the ancient DNA from these samples, and rightly so. The sequencing of these genomes is an incredible scientific accomplishment and provides data of inestimable value. However, the genetic data also have limitations and are open to differing interpretations. This often stems, especially in the study of ancient DNA, from a problem that also haunts paleontology—sample size. Thus it is unlikely that genetics alone will resolve current controversies concerning modern human origins, no matter how much more reliable genetic studies are perceived to be. The importance of morphology cannot be subsumed by the excitement of genetic breakthroughs. Rather the genetic and morphological evidence must both continue to play equally important roles in our search to explain the biological beginnings of people like us.

Acknowledgements

We hope that the papers included in this volume will contribute to the current understanding of modern human biological origin(s) and the roles of archaic humans in that process. We thank our contributors, our reviewers, and all of our colleagues who have shared their ideas, insights, and criticisms with us. We are happy to acknowledge the wisdom they imparted to us,

but our failures to implement that wisdom in this volume are ours alone. We also particularly thank Dr. Karen Chambers, our editor at Wiley Blackwell, for her tremendous help to, and patience with, us during the realization of this volume. We thank Anna Ehler at Wiley Blackwell for her assistance and advice and Whitney Karriger and Micca Metz, graduate students at Illinois State University, for their editorial assistance. We are grateful to our universities, Illinois State and Wyoming, for their support. To our families: Maria Ostendorf Smith, Burton Smith and Linda Chisholm, Matt and Maria Newman, Meredith McLaughlin, and Abijah, Rowan, and Sage Ahern we owe a greater debt than we can express. We thank them for their support during our efforts to produce this book and for so many, many other things!

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Chapter 1

Africa: The Cradle of Modern People

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This chapter is intended as a survey of the African fossil record relevant to the origin of modern humans. This record has been summarized in detail fairly often over the four decades (e.g., Howell, 1978, 1994; Klein, 1989, 1999, 2009; Cartmill and Smith, 2009; Smith et al., 1989; Wolpoff, 1996; Bräuer, 1984a, 1984b, 1989, 1991, 1992, 2001a, 2001b, 2007, 2008; Bräuer and Rimbach, 1990; Stringer, 2002, 2011; Rightmire, 1976, 1978a, 1978b, 1984a, 1991, 1992, 1994, 1998, 2001a, 2008, 2009), so the present chapter will seek to cover some of the more recent and smaller finds in more detail while providing a basic overview of the better-known finds. Also considered are some of the attendant issues that surround human evolution during the Middle to Late Pleistocene. These issues include speciation, the impact of genetic data, and the role of climate in the human evolution in Africa.

Within 5 years of the publication of Smith and Spencer's *The Origins of Modern Humans: A World Survey of the Fossil Evidence* in 1984, knowledge of the timing and pattern of key events in the origin and spread of modern humans had increased substantially. The most plausible interpretation of new data from mitochondrial DNA (mtDNA) was that a common ancestor (a mother in this case) of all modern human mtDNA sequences had lived in Africa between 200,000 and 100,000 years ago (Cann et al., 1987; Stoneking and Cann, 1989; Delson, 1988). These initial findings were confirmed and refined by subsequent studies (Vigilant et al., 1991; Stoneking et al., 1992). At the time, these findings were subjected to criticism by multiregionalists (e.g., Wolpoff, 1989; Smith et al., 1989; Frayer et al., 1993) and some geneticists (Templeton, 1991, 1993, 1996, 1997). Nevertheless, the findings from mtDNA were supported by some early, worldwide analyses of polymorphisms in human proteins and blood groups (Jones and Rouhani, 1986; Wainscoat et al., 1986, 1989; Nei and Roychoudhury, 1982, 1993), which also showed a likely African origin of modern humans and a divergence time on the order of 100,000 years between populations, although other contemporary analyses suggested a different pattern (e.g., Excoffier et al., 1987).

The Origins of Modern Humans: Biology Reconsidered, Second Edition.

Edited by Fred H. Smith and James C. M. Ahern.

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It proved to be more difficult to find and characterize patterns of DNA sequence variation in human Y chromosomes because the vast majority of the sequence was identical between individuals, but once researchers began to identify polymorphic sites, Y chromosomes showed a very similar pattern to mtDNA (Lucotte, 1992; Hammer, 1995; Hammer and Horai, 1995; Pääbo, 1995; Jobling and Tyler-Smith, 1995; Hammer and Zegura, 1997; Hammer et al., 1997; Seielstad et al., 1999). Early estimates were that the variation present in human Y chromosomes inferred the coalescent age for the most recent common ancestor to be around 50–100 ka, most likely in Africa (Hammer, 1995). The most recent analysis of a larger dataset indicates the common ancestor lived 141.5 ± 15.6 ka in Africa (Cruciani et al., 2011). An African origin of Y chromosomes has continued to be supported in later analyses (Underhill et al., 2001; Semino et al., 2000, 2002; Kayser et al., 2001, 2004; Ke et al., 2001; Tyler-Smith, 2002; Tishkoff et al., 2007; Karafet et al., 2008). Additional analyses of Y chromosomes have demonstrated that after a Late Pleistocene dispersal from Africa, some men returned to the continent from Eurasia (Hammer et al., 1998; Cruciani et al., 2002). This back migration may be linked with the spread of modern humans across Northern Africa (Olivieri et al., 2006).

At the same time that genetic studies were amassing new insights, advances in dating using electron spin resonance (ESR), uranium-series (U-series) dating, thermoluminescence (TL), optically stimulated luminescence (OSL), amino acid racemization on ostrich eggshell (Miller et al., 1999), and, to a lesser extent, obsidian hydration (e.g., Clark et al., 1984) began to raise the curtain on events lying beyond the limit of radiocarbon and to provide an absolute chronology for Middle Paleolithic (MP) from Eurasia and Middle Stone Age (MSA) sites from Africa. Early and influential applications of these novel methods demonstrated that the Israeli sites of Skhül and Qafzeh, which both contained multiple interred skeletons of nearly modern humans (McCown and Keith, 1939; Howell, 1958; Vallois and Vandermeersch, 1972; Vandermeersch, 1981; Trinkaus, 1984), were older, dating to 80–120 ka (Valladas et al., 1988; Schwarcz et al., 1988; Mercier et al., 1993, 1995), than the Neandertals from the Levant, most of which dated to around 60 ka (Valladas et al., 1987; Schwarcz et al., 1989; Mercier et al., 1995; Grün and Stringer, 2000). These dates confirmed Bar-Yosef and Vandermeersch's (1981) deduction of the age of the hominins from Qafzeh and overturned arguments that Neandertals had evolved into modern humans in the Levant by 50 ka (e.g., Trinkaus, 1984).

By the late 1980s, new genetic data, new dates, and new discoveries of fossils had combined to reinforce the synthesis presented earlier that modern humans had evolved early in Africa and subsequently spread to the rest of the world (Rightmire, 1984a; Bräuer, 1984a, 1984b; Stringer and Andrews, 1988; Cavalli-Sforza et al., 1988). This conclusion was based on the age of Omo I (Day, 1969) and championed later by Rightmire (1979, 1981) and Beaumont, de Villiers, and Vogel (Beaumont et al., 1978; Beaumont, 1980; de Villiers, 1973, 1976) for the Border Cave fossils, and Singer and Wymer (1982) for the hominins from Klasies River Mouth.

In Africa, application of some of the new dating techniques made it clear that the archaeological contexts for the hominins from Border Cave and Klasies River Mouth (Klasies River) dated to 70–120 ka (Grün et al., 1990a, 1990b; Grün and Stringer, 1991; Grün and Beaumont, 2001; Grün et al., 2003, 2005), although controversy remained over the issue of whether all of these hominins were contemporaneous with the archaeological sediments that had been dated. Nevertheless, these absolute ages confirmed inferences from the geology and stratigraphy of the sites that the MSA in both had to be older than the limit of radiocarbon (Vogel and Beaumont, 1972; Butzer, 1978, 1984; Butzer et al., 1978; Beaumont et al., 1978) and corroborated earlier K-Ar and