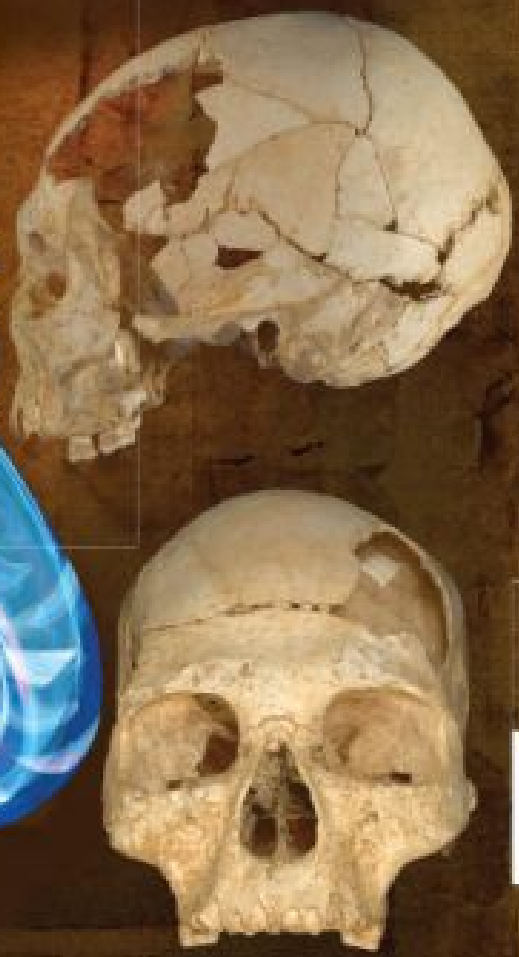
FRED H. SMITH • JAMES C. M. AHERN

THE ORIGINS OF MODERN HUMANS

Biology Reconsidered



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Edited by

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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
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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 Skhūl 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, lusher 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