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Edited by Clark Spencer Larsen

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**A Companion to Biological Anthropology**

Edited by

Clark Spencer Larsen
CHAPTER 20
Species, Populations,
and Assimilation in
Later Human Evolution

Fred H. Smith

The late part of the middle and late Pleistocene witnessed the continued spread of the genus Homo throughout most of Africa, Europe, Asia, Australasia, and finally into the Americas. An earlier form of Homo, probably Homo erectus, first migrated out of Africa in excess of 1.5 mya and established a human presence in southern Eurasia. During the final 600,000 years (600ky) of the Pleistocene, regional human populations became increasingly differentiated from each other. Over this span, there is at least one additional major episode of migration 'out of Africa.' This post-cranial out of Africa migration period reflects the spread of modern human anatomical form from an African homeland. Both the genetic and the morphological data point to migrations beginning probably from East Africa sometime between about 150,000 and 100,000 years ago. These movements extended throughout other parts of Africa, and ultimately throughout the remainder of the earth (Bräuer 2008; Trinkaus 2005; Pearson 2008; Cartmill and Smith 2009). However, whether this phenomenon represented the spread of a new species of human, which essentially replaced aboriginal groups throughout Eurasia, or a novel population of a polyploid single species is still a matter of intense debate. In either case, a complex pattern of interaction between migrant and indigenous populations must have characterized this part of the human evolutionary record, much as it has in more recent human history.

By 400,000 years ago (400kya), humans in Europe, Africa, and Asia were beginning to exhibit regional morphological differences. Certainly these humans were still quite similar across the continents in having expanded brains and braincases compared to those of Homo erectus (Figure 20.1). They also retained a number of primitive (ancestral) features: prognathic faces and prominent supraorbital tori, receding mandibular symphyses with no 'chin,' large anterior teeth, and muscular postcranial skeletons. But there are also differences in body shape and in the details of craniofacial anatomy from region to region. About 100,000 years ago regional differentiation was
clearly established. This included the appearance of the distinctive Neandertals in Europe and central Asia, of early modern people in Africa and the Levant; possibly the survival of late *Homo erectus* in Australasia; the existence of some form of archaic *Homo* in eastern Asia; and perhaps the existence of predecessors to the pint-sized people living on the Indonesian island of Flores. For many paleoanthropologists, these hominin samples could represent as many as five separate species coexisting as separate entities in the later Pleistocene.

**The Basis for Splitting, the Nature of Species, and Some Theoretical Issues**

In a 1986 essay, Tattersall deciphered the classification of all post-*Homo erectus* hominins as members of *Homo sapiens*, and particularly the designation of the pre-modern forms of *Homo* as members of "archaic" *H. sapiens* (Tattersall 1986). The concept of an archaic *H. sapiens* stage or grade was declared to be out of touch with modern evolutionary biology and a case of ‘special pleading’ applied to human evolution. Tattersall based these criticisms on patterns observed in other organisms, particularly in cercopithecine primates, which suggested that the morphological variation observed in the post-*H. erectus* sample must represent multiple species. This argument for increased species diversity in later human biological history is intimately tied to the 'punctuated equilibrium' perspective on macroevolution. Essentially, this perspective emphasized that speciation was always a branching process (cladogenesis), and thus reflected the axiom that evolution was a 'bush, not a ladder.' The use of a 'grade' concept reflected in the concept of archaic *H. sapiens* was labeled as outmoded 'ladder thinking' (Eldredge and Tattersall 1982). Although punctuated equilibrium is rarely mentioned any more, its principles still underlie the quest for "busheens" in the later human fossil record.

Cladogenesis is essentially allopatric speciation, a form of speciation that normally occurs when peripheral populations of a species become physically isolated from the main body of that species. This isolation is most commonly from some natural barrier to gene flow. In these relatively small marginal populations, environmental stresses are likely to be greater and genetic changes are more likely to become established during isolation. Thus the biology of these populations may develop significant differences by comparison with those displayed by the main body of the species. However, in Mary’s "biological species" concept (BSC), another step must occur to make true speciation (Mayr 1963). It does not matter how distinctive, from a morphological point of view, two populations may become in relation to each other; they remain the same species until a reproductive barrier is established. Sometimes such a barrier occurs despite the presence of relatively little morphological divergence (as happened in the case of Old World monkeys of the genus *Cercopithecus*). In other cases, significant degrees of morphological differences exist without the establishment of reproductive isolation. An excellent example is that of feral and domesticated suids in the mountains and valleys of East Tennessee, which differ markedly in anatomy but are intersterile (Smith 1994).

In the fossil record, reproductive isolation is difficult, if not impossible, to identify. Thus most paleontologists do not recognize species on the basis of the BSC. Paleontological species are based on assessments of morphology which include both the patterns of similarities among groups and the gaps between groups. Many different approaches to such assessments have been developed, and some of them have attempted to relate morphology to implications of reproductive separation among groups of fossils (Foley 1991; Holliday 2003; Cartmill and Smith 2009). Notable among these are Patterson’s (1992) "specific mate recognition" concept and Simpson’s (1961) "evolutionary species" concept. The former asserts that species should be recognized only on the basis of features related to mate recognition and actual reproduction, and the latter implies that species maintained their morphological identity through reproductive exclusivity. The reality is that these species concepts are essentially variants of morphospecies. They can be defined as various approaches to the assessment of morphological patterning. Currently the emphasis is on finding patterns of shared derived (synapomorphic) features in order to define alpha taxonomic groupings, and the search for such features has dominated modern paleoanthropology for many years. However, a quarter of a century ago, Gingerich (1984) pointed out that the judicious use of other types of features should not be excluded uncritically from taxonomic decisions.

How much splitting of lineages, and thus formation of separate species, is to be expected in the evolution of a specific mammal depends particularly on three factors: geographic range, adaptive pattern, and body size. Mammals with large ranges, which cover multiple ecological zones, are more likely to speciate, as are those living at the tropics compared to those living at higher latitudes (Foley 1991). Foley also suggests that speciation rates increase in taxonomic groups with ranges which extend to islands, where the possibility of isolation is increased. While these characteristics apply to hominins in general, they particularly explain the species diversity of pre-Pleistocene hominins; and the latter observation may be particularly pertinent to the case of the tiny late Pleistocene Flores hominins. However, Foley also notes that lineages with broad dietary and overall adaptive strategies show reduced speciation rates. He argues that, compared to earlier hominins, *H. erectus* and latter members of *Homo* probably exploited a much wider range of dietary resources, including significant amounts of meat. On the basis of a northern canid analogy, another study demonstrates the probable high habitat tolerance of middle and late Pleistocene hominins, considering it a significant factor in limiting the opportunities for hominin speciation (Arcadi 2006).
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and middle and late Pleistocene members of \textit{Homo} emerge as consummate generalists. Compared to specialized species, generalized species tend to exploit wider geographic and ecological ranges, show greater intraspecific variation, and exhibit less of a tendency to split (Vrba 1984; Arcari 2006).

The cultural capabilities of middle and late Pleistocene \textit{Homo} bear special mention in this context. Viewed in the modern world, culture is seen more as a specializing agent, promoting separation between groups on the basis of differences in behavior and other cultural accomplishments (Klein 1999; Premo and Hildebrand 2009). But, as White emphasized sixty years ago, culture is also a means of adaptation (White 1949), defining a very unique and all-encompassing resource exploitation strategy for humans. Culture as an adaptive mechanism further defines humans as the consummate generalist species; it is reasonable to expect that the impact of this generalist adaptive strategy would have severely limited the ability of the middle and late Pleistocene hominin lineage to specialize.

Body size also must be considered in comparative assessments of mammalian speciation. Species diversity in mammals is generally tied to overall body mass, as larger forms exhibit less taxonomic diversity. Conroy (2002) compared speciosity in Pleistocene \textit{Homo} with that of all the available mammals that fall within \textit{Homo}'s body size range of 20–65 kg. He found that mammals of early \textit{Homo} body size generally do not exhibit large numbers of species. In fact, he argued that recognition of more than two synchronic species in early \textit{Homo} would put the human lineage at odds with the pattern for similar-sized mammals.

A final critical issue concerns how long it takes for reproductive isolation, complete or partial (according to Eldredge's rule: sterility of one sex), to be established in medium-size mammals. Using estimates from the fossil record and data or documented extant species hybridization, Holliday (2006) determined that the most rapid attainment of partial reproductive isolation was between the genera \textit{Bos} and \textit{Bison}, in 1 million years, and the most rapid attainment of complete isolation was between horses and zebras (genus \textit{Equus}), in approximately 2 million years. Employing molecular clock data, partial isolation is established most quickly between lions and tigers (genus \textit{Panthera}), in 1.55 million years, and complete isolation is most rapidly established between red-fronted and Thompson's gazelles (genus \textit{Gazella}), in 1.4 million years. These time spans are all longer than the entire late middle and upper Pleistocene.

The combined results of these studies do not necessarily demonstrate that multiple species of \textit{Homo} could not have existed during the middle and late Pleistocene, but they do suggest that the insistence on relatively high species diversity in this span of hominin biological history may not necessarily reflect biological reality. But another way, the recent proliferation of Pleistocene \textit{Homo} species appears questionable, not unequivocally supported on theoretical grounds. At the very least, the burden should be on those who defend multiple species to demonstrate the biological validity of each species.

**HEIDELBERGERS AND THE ORIGIN OF REGIONAL HUMAN DIVERSITY**

In Africa, post-\textit{erectine} humans are represented by remains from a geographically diverse series of sites widely spread in Africa, Europe, and possibly Asia. Currently many paleoanthropologists place these remains in \textit{Homo heidelbergensis}, but of course not all agree (see below). To avoid the taxonomic quagmire, these hominins will be referred to as 'Heidelbergers.'

The dating of the African Heidelberg sites is difficult. The oldest is probably Bodo, at around 600,000 years ago (Clark et al. 1994). Recent faunal assessments suggest a comparable age for Saldanha, but possibly that age might even approach 1 million years (Klein et al. 2006). Most other specimens generally are estimated at 300,000–600,000 years ago, but these dates are generally based on fauna and thus are approximate. Probably the most informative site is Kabwe, or Broken Hill, in Zambia, which has yielded a complete cranium (Kabwe 1), a second maxilla, and a series of postcranial remains. Despite the relatively strong chemical homogeneity of these remains, the association among the cranial and postcranial ones is not certain (see Cartmill and Smith 2009). The Kabwe 1 cranium (Figure 20.1) is the best known specimen among the African Heidelbergers. Like others in this group, it shows the combination of primitive and advanced cranial features described previously, except that here there is no mandible. The face exhibits total facial prognathism similar to that of erectines: the lateral face (zygomatic region) is placed forward, along with the midface. Other features are more advanced. The cranial capacity measures 1325 cm$^3$, which is relatively large for this time period. Compared to many erectines, African Heidelbergers exhibit a 30 percent increase in brain size, which is likely to reflect a significant shift in human brain-to-body size patterning during this time span (Ruff et al. 1997), and changes in the nose and palate, which are shared with other later members of \textit{Homo} (Richtmire 2008). The postcranial elements have distinctly primitive features (Pearson 2000; but the most significant characteristic of the most complete specimen, a tibia, is that its length suggests body proportions reflecting a relatively warm environment. This indicates that a relatively 'tropical' body form continues to characterize the Pleistocene African Heidelbergers.

In Europe, the Heidelbergers range from Greece (Petralona) to Germany (Steinhheim, Reilingen, and Mayer), to England (Swanscombe and Boxgrove), and to Spain (Sima de los Huesos). Dating estimates range from about 400,000 to as recently as 200,000 years ago (Cartmill and Smith 2009), but many of the specimens are not directly dated. Similarities between European and African representatives have been observed for some time (Richtmire 1998, 2008). The general similarity is based on their shared advanced features by comparison with erectines (increased cranial capacity and expanded neurocrania; see Figure 20.1), as well as on shared primitive retentions (prominent supraorbital tori, total facial prognathism, absence of chin). However, the two regional samples differ in some details. For example, European forms often exhibit incipient suprainiac fossae and occipital bunning, features generally associated with Neandertals (Santa Luca 1978). In addition, the infraorbital area in specimens like the Petralona cranium and skull 5 from Sima de los Huesos closely approach the Neandertal pattern. Also, aspects of the postcrania from Boxgrove (England) and from Sima de los Huesos suggest that body forms were more adapted to cold than the African body forms (Trinkaus et al. 1999; Arsuaga et al. 1999). On the basis of the presumably shared derived features, there is a consensus that the European Heidelbergers represent a clear ancestral line to the Neandertals (Wolpoff 1999; Richtmire 1990, 1998; Arsuaga at al. 1997; Dean et al. 1998).

Certain Asian specimens are best considered Heidelbergers as well (Cartmill and Smith 2009). These include Zhuliang and the Tabun pre-level C remains (Israel),
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is an intriguing idea, but the fossil record to date can neither support nor refute it. Interestingly, the recently discovered Kocabuy specimen (Kappelman et al. 2008) might provide a 500,000-year-old indication of a connection between Africa and Europe, but more fossil evidence is needed to address this issue adequately.

Finally, there is the question of taxonomy. Do Heidelbergers form a cohesive species, separate from other members of Homo? Can the African and European Heidelbergers be accommodated in one species? Some have argued that the African forms should be placed in a separate species from the European Heidelbergers: that the latter (H. heidelbergensis) would be ancestral to Neanderthals, and the former (H. rhodesiensis) would be ancestral ultimately to modern humans in Africa (Bermúdez de Castro et al. 1997). However, the morphometric similarities among the African and European Heidelbergers argue against this dual species model (Rightmire 2008). While the emerging consensus is that H. heidelbergensis is the valid taxon for these humans, it has not been defined on the basis of specific, uniquely derived features. Rightmire (1990, 1998, 2008) has marshaled the characteristic features for H. heidelbergensis, but, as he accurately notes, these features are a mosaic of traits shared either with more primitive or with more derived forms of Homo. There are no unique and defining features that unite the Heidelbergers (Smith and Cartmill 2009). While the concept of H. heidelbergensis plays an important role in the quest for 'business' in the later human evolutionary record, the fact is that the species' existence as a distinctly defined unit is contentious. Certainly the Heidelberg sample is broadly intermediate between cretines and later humans, but that, in itself, is weak justification for a formal taxonomic distinction.

**Neanderthals and Their 'Contemporaries'**

Neandertals, a distinct form of Homo neanderthalensis in the later Pleistocene, are by far the best known and most intensely studied fossil human sample. First recognized at the original Neandertal site in Germany in 1856, Neanderthals are found in all but the northern-most reaches in Europe and in western and Central Asia. In addition to their entire skeletal anatomy, an impressive amount is also known about their behavior, adaptive pattern, and genome. There is a consensus that in Europe Neandertals gradually emerged from European Heidelbergers, but there is disagreement as to whether they emerged by accretion of Neandertal features over time, in isolation (Dean et al. 1998), or simply as the European lineage in the interconnected web of regional lineages that form the basis of the multiregional evolution perspective (Wolpoff 1999). Both viewpoints agree that the boundary between Heidelberg and Neandertal in Europe is rather arbitrary. In fact, some would include European Heidelbergers in the presumptive Neandertal species Homo neanderthalensis.

A case can be made that the hominins from the 210,000-year-old site of Ehringsdorf in Germany represent the earliest sample which can be unequivocally considered Neandertals in the strict sense, and a series of sites dating from between 200,000 and 100,000 years ago exclusively yield Neandertals. These sites include Bisčće-St Vranst (France), Kratina (Croatia), and Saccopastore (Italy). The 'classic Neandertal' sites — including La Chapelle-aux-Saints and La Ferrassie (France), Guattari (Italy), and the Neander Valley — span a period from approximately 75,000
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Finally, there is the question of taxonomy. Do Heidelbergers form a cohesive species, separate from other members of *Homo*? Can the African and European Heidelbergers be accommodated in one species? Some have argued that the African forms should be placed in a separate species from the European Heidelbergers; that the latter (*H. heidelbergensis*) would be ancestral to Neandertals, and the former (*H. rhodesiensis*) would be ancestral ultimately to modern humans in Africa (Bermúdez de Castro et al. 1997). However, the morphometric similarities among the African and European Heidelbergers argue against this dual species model (Rightmire 2008). While the emerging consensus is that *H. heidelbergensis* is the valid taxon for these humans, it has not been defined on the basis of specific, uniquely derived features. Rightmire (1990, 1998, 2008) has marshaled the characteristic features for *H. heidelbergensis*; but, as he accurately notes, these features are a mosaic of traits shared either with more primitive or with more derived forms of *Homo*. There are no unique and defining features that unite the Heidelbergers (Smith and Cartmill 2009). While the concept of *H. heidelbergensis* plays an important role in the quest for ‘bushmen’ in the later human evolutionary record, the fact is that the species’ existence as a distinctly defined unit is contentious. Certainly the Heidelberg sample is broadly intermediate between erectines and later humans, but that, in itself, is weak justification for a formal taxonomic distinction.

**Neandertals and Their ‘Contemporaries’**

Neandertals, a distinct form of *Homo neanderthalensis* in the later Pleistocene, are by far the best known and most intensely studied fossil human sample. First recognized at the original Neandertal site in Germany in 1856, Neandertals are found in all but the northern-most reaches in Europe and in western and Central Asia. In addition to their entire skeletal anatomy, an impressive amount is also known about their behavior, adaptive pattern, and genome. There is a consensus that in Europe Neandertals gradually emerged from European Heidelbergers, but there is disagreement as to whether they emerged by accretion of Neandertal features over time, in isolation (Dean et al. 1998), or simply as the European lineage in the interconnected web of regional lineages that form the basis of the multiregional evolution perspective (Wolpoff 1999). Both viewpoints agree that the boundary between Heidelberg and Neandertal in Europe is rather arbitrary. In fact some would include European Heidelbergers in the presumptive Neandertal species *Homo neanderthalensis*.

A case can be made that the hominins from the 210,000-year-old site of Ehringsdorf in Germany represent the earliest sample which can be unequivocally considered Neandertals in the strict sense, and a series of sites dating from between 200,000 and 100,000 years ago exclusively yield Neandertals. These sites include Biache-St Vrast (France), Krapina (Croatia), and Saccopastore (Italy). The ‘classic Neandertal’ sites – including La Chapelle-aux-Saints and La Ferrassie (France), Guattari (Italy), and the Neander Valley – span a period from approximately 75,000
to 40,000 years ago. The latest Neandertal fossil sites include Zafarraya (Spain: 33,200 years ago), St Cesaire (France: 36,000 years ago), Hyena Cave at Arce-sur-Cure (France: 33,800 years ago), and Vindija (Croatia: 32,000 years ago) (Habilin et al. 1995, 1996; Higham et al. 2006; Lévêque and Vandermeersch 1981), but archaeological sites without remains suggest that Neandertals may have survived on the Iberian Peninsula for some 8,000 more years (Zilhão 2006; Finkel 2004).

Like in the case of Heidelbergers, much of the distinctive morphology of Neandertals is based on the retention of primitive features: their large, prognathic faces – accompanied by chimplike mandibles, pronounced supraorbital tori, low cranial vaults, and large anterior teeth derive from Neandertal ancestry (Figure 20.3). In other ways, Neandertals are clearly derived compared to earlier forms. Neandertals exhibit expanded brains, with the average Wiürm European Neandertal cranial capacity at 1423 cm³. Consequently the cranial vault is also expanded relative to the cranial base, the width of the braincase being now markedly larger than that of the cranial base (Figure 20.3). Some other features appear to be distinctive, or apomorphic, for Neandertals, although earlier stages in the development of many of these features can be seen in European Heidelbergers. For example, due to the expanded width of the brain case, Neandertals have a characteristic oval shape when viewed from the rear. Other distinctive features include the form of the temporal bone, the inferior projection of the occipitomastoid region of the cranial base, the presence of supraorbital fossae on the occipital, the formation of occipital bunning on the rear of the cranium, and a series of mandibular details. However, perhaps the most distinctive proposed apomorphy of Neandertals is their facial prognathism. Neandertals exhibit prognathism along the midline of the face, but the lateral face (the lateral part of the zygomatic bone) is relatively less forwardly projecting. One view holds that the facial midline area is moved forward relative to the lateral face, which would constitute an apomorphic condition (Rak 1986). Another view is that the lateral face retreats in relation to the midline of the face, which would reflect an intermediate stage between the total facial prognathism of earlier humans and the relative lack of prognathism (or orthognathism) of modern humans (Trinkaus 2006; Smith and Passarino 1989).

Neandertals also have distinctive features in their postcranial skeleton. Many of these are primitive retentions. For example, the thick cortical bone of Neandertal long bones reflects a pattern of heavy loading of the limbs, particularly the lower limb, relating to locomotor and other activities. This, along with other indications of powerful musculature, characterizes the Neandertals. Probably the most significant features concern their overall body form. Neandertals had a barrel-shaped thorax and relatively short distal limb segments in both arm and leg (Holliday 1997a, 1997b; Ruff et al. 2002). These features are generally considered to indicate a body form adapted to cold, evolved so as to enhance heat conservatism. In fact, the Neandertal body form has been called ‘hyper-arctic’ because it appears to be even more cold-adapted than that of living people such as the Inuit and Lapps. It has even been suggested that climate adaptation and the resulting thorax shape might explain certain unusual features in the Neandertal pelvis, including the long, thin superior pubic rami at the front of the pelvic girdle (Rosenberg 1988; Cartmill and Smith 2009).

Neandertals in western Asia are known from a range extending from the Levant of Israel into Iraq and the Caucasus region of Russia. Near-Eastern Neandertals exhibit the distinctive features noted for European Neandertals, except that they have relatively higher cranial vaults, lack occipital bunning, and do not show as extreme a pattern of distal element shortening in the arm. Purported Neandertal remains from Central Asia also show differences from the European representatives. Teshik Tash in Uzbekistan has yielded a burial of an 8 or 9-year-old, with Mousterian tools and a Pleistocene fauna. Despite its young age at death, the Teshik Tash skull already manifests a Neandertal-like cranial vault with a suprainiac fossa, the characteristic Neandertal morphology of the mastoid and occipitomastoid eminence, an oval shape from the rear, and a continuous supraorbital torus. The facial skeleton also appears to be Neandertal-like. Analysis of mitochondrial DNA from the Teshik Tash left Femur, as well as from subadult limb bones from Okladnikov Cave, also in central Asia, reveal the presence of uniquely Neandertal sequences (Krause et al. 2007). The record strongly suggests that Teshik Tash exhibits Neandertal biological affinities (contra Glantz et al. 2009) and indicates that Neandertal influences reached further east than has traditionally been accepted.

Even further east, the sparse human fossil record yields archaic folk who are apparently not so closely related to Neandertals. These fossils include the Dali cranium (see above), the partial skeleton from Jinniushan (about 200,000 years), the fragmentary Maba cranium (about 135,000 years), and a series of other less complete specimens, all from China (Wu and Poirier 1995). These remains are relatively primitive, but they are certainly not Neandertals. While they share features with late Chinese erectines, it is unclear if they primarily evolve from erectines in China (Wolpoff 1999) or derive from a Heidelberg expansion into East Asia. The Jinniushan skull is more gracile than Dali's, with a higher, rounder cranial vault, thinner vault bones, and a much thinner supraorbital torus. The cranial capacity is 1390 cm³, comparable to that of other late archaic peoples. The face is also gracile, but generally similar to Dali's in that it appears to be relatively flat (total facial prognathism), with a broad nose and interorbital area. A detailed analysis of body form for the Jinniushan skull shows that the specimen had a wide trunk, large body mass and short limbs (Rosenberg et al. 2006). On the basis of its location relatively far north in China, Jinniushan represents a cold-adapted population, with an overall body form much like that of the similarly adapted European Neandertals, but with a different cranial anatomy.
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ARCHAIC HUMAN ADAPTATION AT HIGHER LATITUDES

Regardless of whether the anatomy results from genetics or from other factors (Serrat et al. 2008), European Neandertals and higher-latitude Asians are adapted for life in the cold. The same seems also true for archaic humans farther east. But, all other things being equal, body form alone has limited impact on adaptation to cold (Allsop and Wheeler 2003). However, all other things were probably not equal. On the basis of analogy with modern circumpolar populations, it is likely that Neandertals had significantly higher basal metabolism rates (BMR) than more equatorial populations, due in part to the effects of temperature and day lengths on thyroid function (Leounard 2002; Leounard et al. 2002). The combination of a stocky, beefy body build with the generation of more internal heat would seem to be key to the survival of high-latitude Neandertals under periglacial conditions, and possibly to that of north-latitude archaic humans in general. Some form of body covering and other cultural factors provided additional buffering.

A large body and an elevated BMR are energetically expensive features to maintain. One model calculates that an adult Neandertal would have required 3,500–5,000 kilocalories a day to survive in cold conditions (Churchill 2006). There is evidence from stable-isotope studies and from archaeology that Neandertals obtained those calories primarily from meat— from a diet rich in fat and high in calories (Richards et al. 2000; Kuhn and Steiner 2006).

The total energy budget of an organism is expended on normal maintenance or survival activities (moving and various physiological functions), growth and development, and reproduction (Leonard 2002; Sorensen and Leonard 2001). Given the pattern of adaptation, maintenance or survival demands would have literally required almost all of the energy which the Neandertal diet could provide, leaving precious little energy for reproduction. In this context, it is likely that Neandertals had lower long-term fertility rates than modern humans. Also, archaeologically based calculations of overall population size indicate that middle Paleolithic people were slightly more than 1 million and that population density was 0.03 persons per square kilometer (Hasan 1981). While such estimates are far from secure, they are about three times smaller than the equivalent estimates for early modern people. These studies strongly suggest that Neandertals and other archaic folk were very rare on the landscape, particularly in the north.

AFRICA AND THE ORIGIN OF MODERN HUMANS

While European Heidelbergs gave rise to Neandertals, the descendants of African Heidelbergs did not continue to exhibit large, prognathic faces. They were characterized instead by reduced faces, which appear to approach orthognathism, and by such modern-like features as canine fossae. However, braincases are still primitive, showing relatively low cranial vaults and pronounced supraorbital tori. Cranial capacity averages 1367 cm³, which is virtually identical to the overall European Neandertal mean (Cartmill and Smith 2009). These African Heidelberg descendants are found at a smattering of sites extending throughout Africa. The sites themselves date from approximately 270,000 years ago to some time between 190,000 and 130,000 years ago (Bräuer 2008; Cartmill and Smith 2009). Unfortunately there are no surviving adult mandibles, only one postcranial element, and virtually no teeth. Still, the cranial mosaic clearly indicates a lineage evolving toward the modern human morphological pattern. Taxonomically, this sample has been assigned to the species Homo heidelbergensis (see Stringer 1994), but it is more informally known as the African Transitional Group (ATG).

Whereas the ATG is widely spread in Africa, the earliest evidence of modern humans is more restricted. Three sites in East Africa yield evidence of very early modern anatomy. Herto (Ethiopia) yields two adult crania, a child’s cranium, and other fragments that date between 154,000 and 160,000 years ago (Clark et al. 2003). The most complete adult (Herto 1) exhibits a high and relatively rounded cranial vault, a modern face, and a rear vault contour that shows a maximum breadth high on the parietals, just like in recent humans (Figure 20.4). The face is modern and orthognathic, but still has a well developed supraorbital torus. The 6.7-year-old Herto 5 cranium also exhibits a modern form (White et al. 2003). Over forty years ago, the Omo Kibish site KE6 yielded a partial skeleton referred to as Omo 1 (Day 1969). The skull of this specimen is fragmentary but clearly shows a modern cranial form, a chin, and a modern face. However, like Herto 1, the Omo Kibish skull maintains a supraorbital torus. The even more fragmentary postcranial skeleton has been recently described in detail as fully modern and relatively tall (Pearson et al. 2008). The latter suggests a likely tropical body form, but there is simply not enough data to be certain of this. The Omo 1 skeleton was excavated just above the

Figure 20.4 Early modern human crania from Herto (Herto 1), Ethiopia (top left); Omo Kibish 1 (top right); Shuil (Shuil 3), Israel (bottom left); Coo Magono (Coo Magono 1) from France (bottom right). © Matt Cartmill
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Radiation of Modern Humans

From East Africa, modern humans spread throughout Africa and ultimately into Eurasia. The first evidence of modern human morphology outside of Africa is from the sites of Skhul and Qafzeh in the Levant of southwest Asia. These sites yield a very informative sample of skeletal remains of both adults and subadults, which are associated with Mousterian tools very similar to those associated with European and Asian Neandertals. A good summary estimate for the dates of the Skhul/Qafzeh sample is 80,000 to 100,000 years ago, although some Skhul specimens might be younger (Goren 2006). The total morphology of the specimens, both young and adult, is essentially modern. The crania have a vault shape very similar to that described for early modern Africans, even in the maintenance of a supraorbital torus in most adults (Figure 20.4; Vandermeersch 1981). There are also several relatively complete mandibles, which show the development of chin and other modern human features (Rak et al. 2002). The postcranial anatomy is modern and the body form is linear, with relatively long distal limb segments. This body shape comes closest to that of recent African populations, who are adapted to a more tropical climate, and contrasts markedly with that of the Neandertals (Holliday 2000). However, one individual (Skhul 5) is somewhat more like Neandertals in body form; and this along with other features could mean that the biological boundary between Neandertals and early moderns in western Asia may be more porous that the promoters of multiple species claim it to be. Another study uses morphometric analysis of crania to indicate the likelihood of a small degree of interbreeding between early moderns and Neandertals in the Near East (Thackeray et al. 2005).

Early Modern Europeans and the Pattern of Modern Human Origins

Current evidence points to an age of about 35,000 years for modern humans in Europe, although some archaeological evidence may suggest an initial date of 40,000 years ago (Bar-Yosef 2006; Mellars 2006; Churchill and Smith 2000; Trinkaus 2005). In either case, Europe is probably a late frontier for early modern people. The earliest fossil remains are from Oase (Romania) and Mladec (Czech Republic), dating to 35,000 and 32,000 years ago respectively (Trinkaus 2005); followed by a series of other remains, including the Cro-Magnon (France) specimens, that falls between 26,000 and 32,000 years ago (Churchill and Smith 2000; Trinkaus 2005, Cartmill and Smith 2009). Early modern Europeans (EME) are fundamentally modern in skull form and are, overall, more similar to early modern West Asians and Africans than to the indigenous Neandertals (Figure 20.4). EME also lack supraorbital tori, which are present in earlier moderns from Asia and Africa. Additionally, the EME body form also differs from that of Neandertals in being more linear and having longer distal limb segments – which suggests an origin for EME in warmer environments (Holliday 1997a, 2000). The extent of cortical bone in the long bones is reduced, but there is no striking reduction of musculature. These morphological differences have long been interpreted by many researchers as reflecting a migration into Europe of modern people who ultimately replaced the Neandertals. The European replacement is viewed as the archetypical case supporting a cladogenetic speciation explanation for modern
Nakazairetuff, dated to 196,000 +/− 2,000 years in member 1 of the Kibish Formation (Brown and Fuller 2008). While the skeleton may come close to this age, the fact is that it could be somewhat younger. Finally, the Sinaa cranium (Sudan) exhibits a modern overall form (Stringer and Andrews 1988) and appears to span between 133,000 and 160,000 years ago (see discussion in Cartmill and Smith 2009).

The first comprehensive case for an early transition to modern humans in Africa on the basis of the fossil record was made by Bräuer (1984). Stringer and Andrews (1988) supplemented the fossil argument with genetic data, particularly the mitochondrial DNA study by Cann and colleagues (1987), to establish the ‘recent African origin’ model of modern human origins. This perspective generally views the origin of modern people as the result of a cladogetic speciation that resulted in the species Homo sapiens. Recent statements of this perspective can be found in several sources (Stringer 1994; Bräuer 2006, 2008; Mellars 2006; Pearson 2008; Hublin and Bailey 2006; Tattersall and Schwartz 2008), although Bräuer does not place Neandertals in a separate species. Following Cann and colleagues’ influential study, many researchers have used genetic data to argue for separate species status for modern humans from Neandertals, and presumably other archaic humans as well. These data have been derived from studies of modern human genetic variation and extrapopulations from these, as well as from results of ancient DNA analysis conducted on Neandertals and early modern humans (Weaver and Rosenman 2008, Sere et al. 2004, Green et al. 2006, Noonan et al. 2006).

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The earliest well-dated modern specimen from mainland East Asia is the approximately 34,000-year-old Tianyuan 1 skeleton near Zhoukoudian, which preserves a partial mandible and some thirty postcranial elements (Shang et al. 2007). The mandible exhibits modern features, and the postcrania are also modern. On the basis of partially reconstructed elements, Tianyuan 1 also appears to have high cranial indices, which indicates a relatively tropical ancestry. H. Shang and colleagues (2007) conclude that substantial gene flow from early modern populations to the south and west probably explains the origin of modern populations in this region; but they also note that the Tianyuan 1 specimen also preserves a few features which reflect some local archaic contributions to the early modern population of China. Other modern specimens may be older, for instance the Luzjiang cranium in southern China; but the association of the specimen with dates higher than 68,000 years ago is not reliable (Wu and Poirier 1995). Thus it is not certain that moderns reached eastern mainland Asia earlier than 34,000 years ago – but it is possible.

In Australia, controversial dates on the Willandra Lakes (Lake Mungo) 3 skeleton indicate that people could have reached Greater Australia (Sahulland) about 62,000 years ago (Thorne et al. 1999), but others argue that a more reasonable time frame is 35,000–40,000 years (Bowler et al. 2003). The earliest Australians are all modern people morphologically, and the Willandra Lakes 3 skeleton suggests a relatively linear body build. Early Australians exhibit considerable variability. The oldest known modern specimen from Sundaland is a Niah Cave (Borneo) juvenile recently dated to at least 35,000 years ago (Barker et al. 2007). Niah is also modern, and there is no evidence of any potential post-cerite specimines here, except possibly the Ngandong people.

EARLY MODERN EUROPEANS AND THE PATTERN OF MODERN HUMAN ORIGINS

Current evidence points to an age of about 35,000 years for modern humans in Europe, although some archaeological evidence may suggest an initial date of 40,000 years ago (Bar-Yosef 2006; Mellars 2006; Churchill and Smith 2000; Trinkaus 2005). In either case, Europe is probably a late frontier for early modern people. The earliest fossil remains are from Oase (Romania) and Mladéč (Czech Republic), dating to 35,000 and 32,000 years ago respectively (Trinkaus 2005); followed by a series of other remains, including the Cro-Magnon (France) specimens, that falls between 26,000 and 32,000 years ago (Churchill and Smith 2000, Trinkaus 2005, Cartmill and Smith 2009). Early modern Europeans (EME) are fundamentally modern in skull form and are, overall, more similar to early modern West Asians and Africans than to the indigenous Neandertals (Figure 20.4). EME also lack supraorbital tori, which are present in earlier moderns from Asia and Africa. Additionally, the EME body form also differs from that of Neandertals in being more linear and having longer distal limb segments – which suggests an origin for EME in warmer environs (Holliday 1997a, 2000). The extent of cortical bone in the long bones is reduced, but there is no striking reduction of musculature. These morphological differences have long been interpreted by many researchers as reflecting a migration into Europe of modern people who ultimately replaced the Neandertals. The European replacement is viewed as the archetypical case supporting a cladogetic speciation explanation for modern
humans (H. sapiens) and the placement of Neandertals in a different species (H. neanderthalensis) (Gould 1987, 1988).

Supporters of the ‘recent African origins’ model (RAO) generally hold that early modern humans replaced archaic folk throughout the Old World. In this view, the replacement by the Homo sapiens lineage-species is essentially complete, with no neg-
ligible contributions of archaic people to regional modern populations. In addition to
morphological discontinuity, the proponents of RAO also point to genetic evidence as
demonstrating a recent African origin for the modern human gene pool. This
generic evidence involves extrapolations from patterns of diversity among living
human genetic diversity, as well as apparently distinctive differences between
Neandertal DNA and recent human DNA (see reviews in Relethford 2001, Weaver
and Rowanman 2008). The strength of this evidence makes RAO a very robust and
widely accepted explanation for the beginning of people like us worldwide.

The best-known competing perspective is the ‘multiregional evolution’ model
(MRE; Wolpoff 1999). MRE argues that there is no specific geographic region where
the total modern human morphological complex developed. Rather, it argues that
specific features develop in different regions and then spread through gene flow. These
features coalesce at different times in different regions, depending mainly on the pattern
of gene flow, on the local selective environment, and on genetic drift. This is a
complex process and, theoretically, a sound model. The major issue concerns whether
MRE fits the available evidence from the fossil and molecular biological records.

In general MRE argues that in various regions of Eurasia local continuity could be
as important as gene flow, or even more so (with or without migrating populations).
The extent of continuity would, of course, be variable; but it seems that MRE sees more
continuity in Australasia and East Asia than in Europe (Wolpoff 1999).

However, even in Europe MRE studies have suggested that a Neandertal
contribution of as much as 50 percent cannot be excluded (Wolpoff et al. 2004).

Opponents of MRE have argued that the traits used to support continuity actually
represent shared primitive retentions, characteristics of limited or questionable
of regional indicators – or some combination of the above (Pearson 2004; Hublin
and Bailey 2006; Brauer et al. 2006).

MRE supporters have argued that the genetic data are open to other interpretations
than replacement and the recognition of multiple species. For example, the evolution-
ary neutrality of the mitochondrial genome has been questioned (Hawks 2006), which
would call into doubt the projected timing of the modern human appearance in Africa
and of the migrations out of that continent. Differences in relative population size dur-
ing the Pleistocene may also be responsible for genetic patterns that mimic replace-
ment (Relethford 2001). A final example involves the analysis of ten human genetic
systems (mtDNA, six nuclear DNA sequences, a Y chromosome and two X-linked
sequences), which showed that these data were not commensurate with the thesis of a
single, recent migration out of Africa, but rather suggested three major events of ‘out
of Africa’ migrations (Figure 20.2). The two earlier migrations established lines of
alleles in various areas of Eurasia – lines that were not derived from the recent migra-
tion defined by RAO (Templeton 2005). These ancient alleles are also found in recent
Eurasian populations, which means that not all alleles originated from the most recent
migrations out of Africa, recognized by RAO as the modern human lineage-species.

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† Projection of nasion anterior to the bi-max plane. This is the plane that extends between the two frontonasal temporalis (see Appendix).

‡ Frayer (1992) considers one Neandertal from Krapina (K 11.5) to lack a fossa. However, FS believes that this specimen does not preserve the area necessary to make a judgment on presence or absence of the fossa. Frayer (1992) identifies supranasal fossae in both Qafzeh 6 and Skhul 9, FS identifies a fossa only in the latter specimen.

### The Assimilation Alternative

In 1989, an alternative model for modern human origins was proposed – the ‘assimila-
tion’ model (AM; Smith et al. 1989). The AM agrees with RAO that the preponder-
ance of available evidence, both morphological and genetic, indicates an initial origin
of modern human morphology in Africa around 160,000 years ago. However, the AM
sees evidence for introgression between expanding modern populations and the archaic
aborigines they encountered in various regions of Eurasia. The AM differs from MRE
by positing that the archaic contribution to modern populations was always relatively small,
and thus continuity would only be found in limited details of anatomy.

As an example, Table 20.1 presents data for four features, three of which show a
closer connection between EME and Neandertals than between EME and their pre-
sumptive ancestors from the Near East. These data can be potentially explained in
three ways. First, these features – as well as others, like occipital bunting (also highly
frequent in Neandertals and EME, but not in Skhul/Qafzeh) and the cold-adapted
limb proportions of the 24,500-year-old Lagar Velho child from Portugal (Trinkaus
and Zilhão 2002) – may represent Neandertal contributions to EME populations.
Second, these same features may not be homologous in Neandertals and EMEs and
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Supporters of the 'recent African origins' model (RAO) generally hold that early modern humans replaced archaic folk throughout the Old World. In this view, the replacement by the Homo sapiens lineage-species is essentially complete, with no negligible contributions of archaic people to regional modern populations. In addition to morphological discontinuity, the proponents of RAO also point to genetic evidence as demonstrating a recent African origin for the modern human gene pool. This genetic evidence involves extrapolations from patterns of diversity among living human genetic diversity, as well as apparently distinctive differences between Neandertal DNA and recent human DNA (see reviews in Relichthof 2001, Weaver and Rowan 2006). The strength of this evidence makes RAO a very robust and widely accepted explanation for the beginning of people like us worldwide.

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MRE supporters have argued that the genetic data are open to other interpretations than replacement and the recognition of multiple species. For example, the evolutionary neutrality of the mitochondrial genome has been questioned (Hawks 2006), which would call into doubt the projected timing of the modern human appearance in Africa and of the migrations out of that continent. Differences in relative population size during the Pleistocene may also be responsible for genetic patterns that mimic replacement (Relichthof 2001). A final example involves the analysis of ten human genetic systems (mtDNA, six nuclear DNA sequences, a Y chromosome and two X-linked sequences), which showed that these data were not commensurate with the thesis of a single, recent migration out of Africa, but rather suggested three major events of 'out of Africa' migrations (Figure 20.2). The two earlier migrations established lines of alleles in various areas of Eurasia – lines that were not derived from the recent migration defined by RAO (Templeton 2005). These ancient alleles are also found in recent Eurasian populations, which means that not all alleles originated from the most recent migrations out of Africa, recognized by RAO as the modern human lineage-species.

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Specifically, they argue that features claimed to demonstrate such continuity are homoplasies. Supporters of continuity try to counter such arguments. A detailed assessment of these arguments is beyond the scope of the present review, but one may wish to ask if other data might shed light on this question. Although most of the genetic evidence probably indicates an African origin for the vast majority of modern human genes, that is not true for all genes. The evidence in question is reviewed by Templeton (2000), who demonstrates that some nuclear genes are likely to have an Asian origin (Figure 20.2). Also, Evans and colleagues (2006) identify a specific group of closely related variants of the microcephalin (MCPH1) gene: the haplotype D group, which arose from a common ancestor about 37,000 years ago. According to this research, the mutation arose from a lineage that diverged from the modern human one significantly earlier; entered the modern human gene pools through admixture with the representatives of this lineage; and rose quickly to a frequency of about 70 percent, through positive selection. The positive selection stems from the fact that, although the exact function of MCPH1 is unclear, it is critical to normal brain development and function. Evans and colleagues note that finding a gene that reflects relatively low levels of admixture is generally difficult because weakly selected or neutral alleles from such a source would tend to be lost by drift or other factors. MCPH1 is an exception, because of the strong positive selection acting on it. They conclude that their work on microcephalin supports the possibility of low levels of admixture between modern and archaic humans around 37,000 years ago.

The ‘mostly out of Africa’ genetic model reflected by the above examples (see Relethford 2001) fits nicely with the AM and with the assertion that what probably happened to Neandertals and other archaic fossils was demographic and genetic swamping by numerically superior populations of modern humans over a few millennia (Smith et al. 2005; Cartmill and Smith 2009). Such a model is commensurate with the previously stated argument that archaic people, especially Neandertals, were relatively rare on the landscape compared with early moderns (Hassan 1981; Premo and Hublin 2009); it is also commensurate with indications of ecological niche (and of resulting geographic) expansion by early moderns (Banks et al. 2008). Thus relatively little archaic Eurasian biological contribution would be expected in early moderns; and, as the data in Table 20.1 also reflect, this contribution would generally decrease over time, with the increased impacts of swamping. The only exception could be certain genetic features with strong positive selection; but it may be that no such features exist in the skeletal morphology.

Perhaps evidence of archaic contributions could be found in the ancient DNA of early modern people. In Europe, the available mtDNA sequences in European upper Paleolithic skeletons (of 32,000 to 24,000 years ago) reveal no Neandertal contribution (Caramelli et al. 2003; Serre et al. 2004); but it is noted by Serre and colleagues that the available data can only exclude a Neandertal contribution of more than 25 percent. Twenty-five percent is far above what the AM would predict. A single mtDNA sequence from an early modern Australian, Willandra Lakes (Mungo) 3, represents a haplotype not found in modern Australians or in other recent humans (Adcock et al. 2001). If this lineage could go extinct in less than 30,000 years, so too could any mitochondrial lineages potentially contributed by Neandertals or other archaic Eurasians to the earliest modern populations.

A final issue concerns the amount of time, or generations, necessary for speciation in medium-sized mammals (Holiday 2006). Even if one adopts the maximum suggestion of 700,000-800,000 years for the divergence of Neandertal and modern human lineages, there is still not sufficient time, presumably, for the establishment of reproductive isolation between these lineages, even if the morphology appears to be very different (Cartmill and Smith 2009). This is especially true in view of the larger body size (Conroy 2002) and the very broad, generalist adaptation of the genus Homo.

‘Races,’ Not Species

Based on these factors, the argument that post-equine humans represent a single lineage (species) is much more robust than many supporters of RA0 imply. Neandertals (and other archaic populations) are regional human groups with distinctive sets of anatonical and genetic features, but they are not unequivocally different species. Rather, they conform to the textbook definition of subspecies (or races) as given by Mayr (1963). Many anthropologists have argued for some time that living humans do not conform to the biological concept of race (for an overview, see Lerner 2008), and genetic studies show that living humans have truncated genetic diversity compared to other wide-ranging mammalian species. In fact it has been shown that, if one combines Neandertal and living human mitochondrial DNA, the variation is similar to that seen in the living subspecies (races) of chimpanzees (Morin et al. 1994). The fact is that all living humans are evolved from what was the late Pleistocene African ‘race’ of humans which became Homo sapiens sapiens. To see true ‘racial’ variation in humans, one has to go to the fossil record. It is the Neandertals, the Ngandong people, the archaic East Asians, and possibly others that reflect the original regional adaptations of humans. Thus a good case can be made that these groups should be taxonomically designated as subspecies, and not as species. These earlier subspecies are extinct, but not in the classic sense of the concept. Rather they have been assimilated into a larger human subspecies – us. This ‘extinction’ through assimilation (cf. Levin 2002) has been, and continues to be, a common theme in recent history of mankind. The evidence suggests that it probably explains the evolutionary history of middle and late Pleistocene humans as well.

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Bioarchaeology: Health, Lifestyle, and Society in Recent Human Evolution

Clark Spencer Larsen and Phillip L. Walker

The study of human remains from archaeological contexts has a long history. Indeed, it is the study of remains of past humans that begins the history of biological anthropology. Much of this record—event into recent times—was dominated by a focus on cranial typology and classification (for discussion, see Cook 2006 and Little and Susman’s chapter in the present volume). In the twentieth century, as biological anthropologists began to explore in further detail variations within and between populations, temporal trends in cranial morphology, the influence of extrinsic factors on skeletal growth and development, and modern statistical analysis, it became clear that the typological—racial paradigm, so entrenched in anthropological method and theory, was inappropriate for interpreting biological variation. Rather, variation—in present and past populations—is best understood as the result of dynamic processes involving the interaction between biology and culture. This bio-cultural approach came into play in the late 1960s and 1970s, especially with the influence of George Armelagos, Jane Buikstra and their students on the study of archaeological human remains from diverse settings in Africa and North America (Armelagos 1969; Carbon and Van Geenen 1977, 1979; Buikstra 1977, 1988). Their work set the course of modern bioarchaeology and established its central role in understanding recent human adaptation and evolution.

The current usage of the term ‘bioarchaeology’ was first introduced by Jane Buikstra (1977) in reference to multidisciplinary research on human remains in the lower Illinois River Valley, especially in relation to mortuary behavior and social organization, health, demography, population history, and activity. Her approach to the study of archaeological human remains was grounded in the scientific method and it