

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

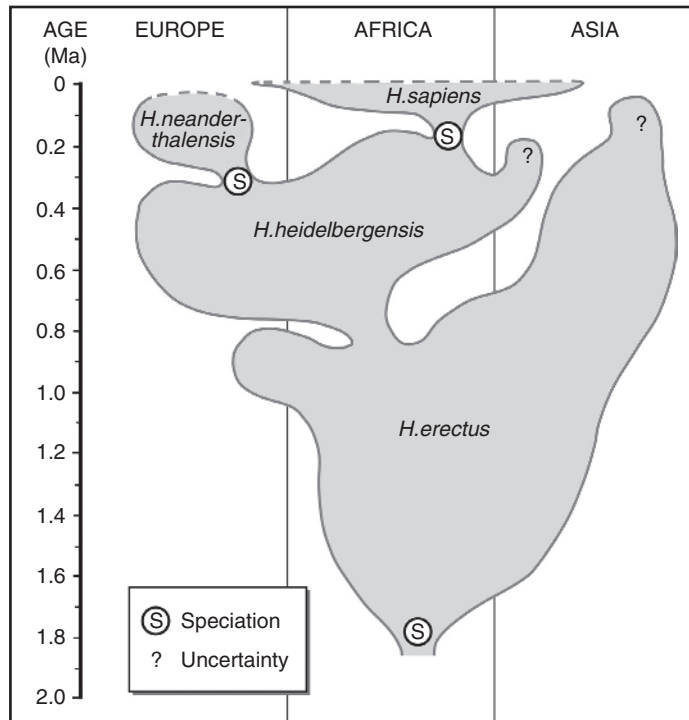


Figure 1.1. Rightmire's phylogeny (after Rightmire, 1998).

uranium-series dates of Middle Stone Age sites such as Evernden and Curtis's (1965) 240 ka K-Ar date for the MSA site Malawa Gorge, the geological, radiocarbon, and uranium-series dates for the Omo-Kibish sequence (Butzer, 1969; Butzer et al., 1969; Butzer and Thurber, 1969), and Wendorf et al.'s (1975) date of 180 ka for the MSA site of Gademotta in Ethiopia. The rapid accumulation of absolute dates confirmed the antiquity of the MSA and placed it on center stage as the cultural milieu for the origin of modern humans (Clark, 1988, 1989, 1992; Klein, 1989, 1999, 2009; McBrearty and Brooks, 2000).

Turning to the African fossil record itself, by the mid-1980s, researchers had established a broad outline of later hominin evolution in Africa that remains the consensus today (Rightmire, 1984a, 2008; Bräuer, 1984b, 2008) (Figures 1.1 and 1.2). Figure 1.1 shows Rightmire's (1998) phylogeny. Figure 1.2 shows a recent version of Bräuer's (2008) division of the Pleistocene African fossil record into a series of morphological grades leading to anatomically modern *Homo sapiens* between 200 and 150 ka.

This consensus model of later hominin evolution in Africa generally emphasizes a continuous, anagenetic process of evolution and builds upon earlier syntheses (e.g., Howell, 1978). The model starts with the establishment of *Homo erectus* throughout the habitable portions of the continent (i.e., areas not covered by deserts or the tropical forests of the Congo Basin) between 1.5 and 1.0 Ma. Due to the finds from Dmanisi and more precise, absolute dates for early hominin sites in Israel, southern China, and Indonesia, anthropologists now know that some populations of *Homo erectus*

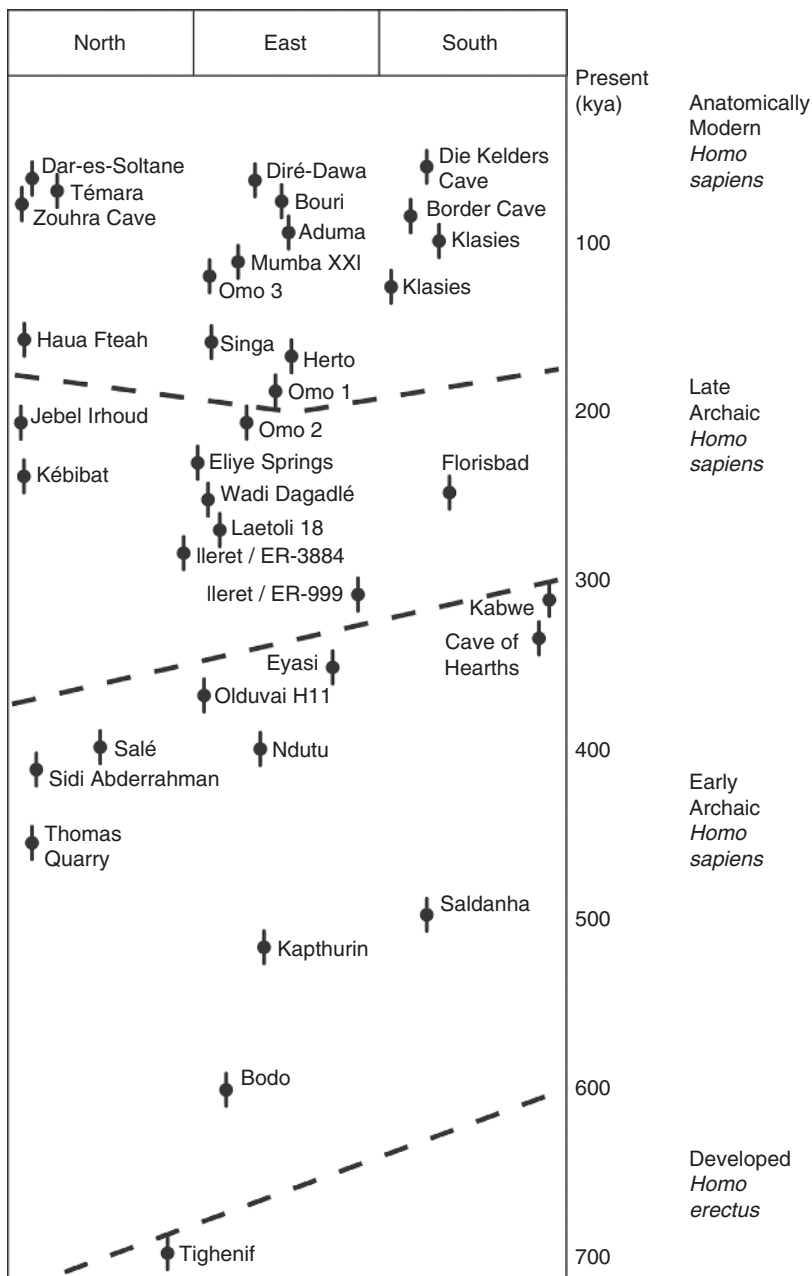


Figure 1.2. Bräuer's grades of *Homo sapiens*, from Bräuer (2008), courtesy of Günter Bräuer.

(or, perhaps, an even more primitive species such as *Homo habilis*) spread from Africa into Eurasia by 1.8–1.9 Ma, almost doubling the widely held view for the duration of human occupation outside of Africa that had seemed likely in the mid-1980s (Klein, 1989). The populations of *Homo erectus* that reached China and the island of Java changed only subtly in cranial morphology over the next million to million and a half years, allowing

many experts to group the Asian specimens together with early African fossils as members of a single species (Santa Luca, 1980; Rightmire, 1981, 1990, 1991; Walker, 1993; Gilbert et al., 2003; Gilbert, 2008a). By 1.0 Ma in Africa, the hominin cranium from the Danakil Depression in Eritrea shows evidence of evolution toward a more modern architecture with more vertical parietals (Abbate et al., 1998). The nearly contemporary cranium from the Daka Member of the Middle Awash fits more broadly within the hypodigm of *H. erectus* and possesses a mosaic of features that had formerly been argued to be more typical of Asian or African members of the species (Asfaw et al., 2002; Gilbert et al., 2003). As such, it cautions against placing too much emphasis on the importance of those regional differences, and tends to reinforce notions of the fundamental morphological homogeneity of the species (Asfaw et al., 2008; Gilbert et al., 2003, 2008; Gilbert, 2008a).

The next widely recognized stage in the emergence of modern humans involves the appearance of a larger-brained hominin between 800 and 600 ka that different authors call early archaic *Homo sapiens*, *Homo heidelbergensis*, *Homo rhodesiensis*, or perhaps *Homo antecessor* (Figure 1.2). By 230–300 ka a new form had evolved with a vertically shorter face, smaller browridges, and diminished angulation of the upper and lower tables of the occipital. This form is often called late archaic *Homo sapiens* or *Homo helmei*, although as Bräuer (2008) explains in detail, authors disagree about which specimens belong in the group and which do not. The last phase involves the first appearance of anatomically modern *Homo sapiens*, which makes its first appearance between 200 and 150 ka in the Ethiopian sites of Omo-Kibish and Herto (McDougall et al., 2005, 2008; Brown and Fuller, 2008; White et al., 2003; Clark et al., 2003). These dates are substantially earlier than the earliest date envisioned in the late 1980s, when the 130 ka uranium-series date for Omo I and II was repeatedly contested by multiregionalists (Wolpoff, 1989; Frayer et al., 1993) and proponents of the assimilation model (Smith et al., 1989; Smith, 1993), as documented in detail by Fleagle et al. (2008). Wolpoff (1989: 65) essentially dismissed the dates, writing:

The Omo radiometric dates have been continuously disputed ever since their first publication because radiocarbon determinations based on shells are notoriously inaccurate, and recent Uranium/Thorium dates are problematic. Various faunal and stratigraphic “dates” have been suggested as replacements for these radiometric estimates (Day, 1972; Stringer, 1989) and according to these the age of the three fossils could range between 40,000 and 130,000 years. However, which of the various date estimates may be correct cannot be established, and the fact is that there is no particular reason to accept any of them as valid!

In contrast, contemporary proponents of various versions of a Recent African Origin Model for the origin of modern humans generally accepted that Omo-Kibish I and II had to be approximately 100,000 years old, and possibly older.

Rather than repeat the basic descriptions of the large number of fossil specimens that make up the fossil record for the emergence of modern humans in Africa (Figure 1.3), this review concentrates on new fossil finds and other developments that have occurred since the summaries of the African evidence by Rightmire (1984a), Bräuer (1984b), and Hublin (1985, 1992). Howell (1994, 1999), Bräuer (2008), and Rightmire (2008) have written recent updates to their earlier syntheses, and recent paleoanthropological textbooks, especially Klein (2009) and Cartmill and Smith (2009), present overviews of the material, and most of the fossil specimens are also described and pictured in Schwartz and Tattersall (2003).



Figure 1.3. Map of Africa showing the key hominin sites from Bräuer (2008), courtesy of Günter Bräuer.

Homo erectus

Little controversy surrounds the idea that early African *Homo erectus* (or *Homo ergaster*, if the early African examples of the taxon constitute a separate species) forms the starting point for the evolutionary lineage that ultimately led to *Homo sapiens*. Rightmire's (1990) synthesis of the available fossil evidence and the publication of the monograph on the Nariokotome skeleton, as well as the discovery of the Dmanisi hominins (Vekua et al., 2002; Antón, 2003; Lordkipanidze et al., 2005, 2006, 2007; Rightmire et al., 2006b, 2008; Skinner et al., 2006; de Lumley et al., 2006; Wallace et al., 2008; Pontzer et al., 2009), stand as important milestones in our understanding of this species. A number of other important discoveries of fossils of African *H. erectus* were made in the 1990s and 2000s, including a left half of a mandible, parietal, frontal, occipital, and four isolated teeth from Konso in southern Ethiopia (Suwa et al., 2007), all of which are associated with an early occurrence of the Acheulean dated to 1.6 Ma (Asfaw et al., 1992). Exploration of the Daka Member at Bourri in the Middle Awash led to the discovery of a calvaria, cranial fragments from two other individuals, a left tibia lacking its distal end, three partial femora, a talus, and a partial mandible (Asfaw et al., 1992, 2008; Gilbert et al., 2008; Gilbert, 2008b). Research at Lainyamok in the Kenyan Rift Valley produced four hominin fossils, a left femoral diaphysis and three teeth

(right P⁴-M²). All were collected from Middle Pleistocene sediments that date to 0.70–0.53 Ma on the basis of a K-Ar date for an overlying tuff and the presence of a more modern fauna than that of Members 1–7 at Olorgesailie (Shipman et al., 1983; Potts et al., 1988). The femoral fragments from Daka and Olorgesailie resemble fossils attributed to *H. erectus* from East Turkana (Day and Leakey, 1973; Day, 1976) and Bed IV at Olduvai Gorge (Day, 1971). The femora of *Homo erectus* generally have thick cortical bone and a greater medio-lateral than antero-posterior diameter at midshaft that distinguish *H. erectus* femora from the great majority of living humans (Kennedy, 1983, 1984, 1985, 1992).

KNM-ER 42700

Other and recent developments in the study of *Homo erectus* in Africa include the discovery in East Turkana of KNM-ER 42700 (Spoor et al., 2007), a fully adult but remarkably small calvaria with a cranial capacity of only 691 cc. The specimen dates to 1.55 Ma. Another specimen (KNM-ER 42703) announced in the same publication is a right maxilla attributed to *H. habilis*, which dates to 1.44 Ma and suggests the two taxa of early *Homo* overlapped in the Turkana Basin for ~0.5 Ma (Spoor et al., 2007). KNM-ER 42700 may simply be an extreme manifestation of the allometric pattern described by Antón et al. (2007) in which larger crania of *H. erectus* tend to have larger browridges, more sagittal keeling, and development of other cranial superstructures. However, based on the patterns present in a geometric morphometric analysis of available *H. erectus* crania (Baab, 2008a), KNM-ER 42700 may belong to a different taxon (Baab, 2008b).

KNM-OL 45500

Research in an upland sector of Olorgesailie led to the discovery of a second very small *H. erectus* cranium, KNM-OL 45500 (Potts et al., 2004), which dates to 0.97–0.90 Ma. Only the frontal part of the cranium is preserved, but enough survives so that Potts et al. (2004) could estimate the cranial capacity at around 650–780 cc. Although small, this endocranial capacity is similar to OH 12 and Dmanisi D2282 and D2280. Its late date coupled with its small size, however, suggest that populations of *H. erectus* either featured a striking amount of individual variation or were more sexually dimorphic than Walker (1993) had concluded in his assessment of the Nariokotome skeleton and other available data.

Gona Pelvis

Simpson et al. (2008) described a female *H. erectus* pelvis from the Busidima Formation in Gona, Ethiopia. The pelvis dates between 1.7 and 0.7 Ma. Contrary to expectations (Ruff and Walker, 1993), the Gona pelvis is very broad like later Middle Pleistocene pelves from Atapuerca (Arsuaga et al., 1999; Bonmatí et al., 2010) but has a small acetabulum, implying a short stature of 120–146 cm (Simpson et al., 2008). Also contrary to expectations, it features large dimensions of its birth canal. Ruff (2010) argued that the body mass (~33 kg) predicted from the acetabulum is substantially lower than that derived from any other femoral head or acetabulum attributed to *H. erectus* and thus the Gona pelvis might derive from an australopith. Simpson (personal communication) rejects this interpretation; the only craniodental fossils known from the Busidima Formation are of *H. erectus*.

In the 1990s, the brain size in *H. erectus* suggested a life history almost precisely midway between chimpanzees and australopiths and modern humans (B. H. Smith, 1993, 1994).

Examination of enamel microstructure of the teeth of *H. erectus* specimens showed a faster pattern growth and development in *H. erectus* than expected based on brain size (Dean et al., 2001; Dean and Smith, 2009), with maturation in *H. erectus* closer to one-third of the way from a chimpanzee-like pace to a human-like one rather than halfway. A similar acceleration in the tempo of maturation appears to be evident in postcranial growth (Graves et al., 2010). Some of the new studies and finds of *H. erectus*, especially the Gona pelvis and the revised estimates of the rate of maturation of KNM-WT 15000, suggest that *H. erectus* may not have been either as static over evolutionary time or as human-like as the available evidence led Walker (1993) to conclude.

The Transition to *Homo heidelbergensis* or “Archaic *Homo sapiens*”

By 600 ka, the Bodo cranium shows a clear change in morphology in the form of a larger cranial capacity of around 1,250 cc (Conroy et al., 2000). A series of other, morphologically similar hominins such as Kabwe (Broken Hill) and Saldanha share a similarly large brain. Coincident with the larger cranial capacity are higher and more vertical parietal bones, a higher temporal squama, and a coronally broader frontal bone (Conroy et al., 1978, 2000; Adefris, 1992; Rightmire, 1996, 2008; Bräuer, 2008). Unfortunately, very few fossil hominins are known from sub-Saharan Africa for the period between the Buia and Daka crania at 1.0 Ma and Bodo at 0.6 Ma.

The gap in the African hominin fossil record for between 1.0 and 0.6 Ma is further complicated in that more complete fossil evidence is now known from Europe in the form of *Homo antecessor* (Bermúdez de Castro et al., 1997, 1999, 2003; Carretero et al., 1999; Lorenzo et al., 1999; Rosas and Bermúdez de Castro, 1999; Manzi, 2004; Martínón-Torres et al., 2007; García-González et al., 2009; Gómez-Olivencia et al., 2010). The existence of *H. antecessor* poses new questions about the pace and mode of evolution away from the morphology of *H. erectus*. If *H. antecessor* is a viable ancestor of later European and African hominins, an important step in hominin evolution must have occurred between 1.0 and 0.8 Ma, but much remains to be learned about this evolutionary transition (Rightmire, 1998; Stringer, 2003).

The primary criticism that has been leveled at *H. heidelbergensis* as a distinct, new species is that no unified set of features exists that can be used to diagnose it throughout its existence. Many specimens placed in the taxon by some researchers lack or have equivocal traces of one or more of the features that characterize Bodo, Kabwe, and Petralona (Wolpoff, 1993, 1996). However, a recent geometric morphometric study of available crania by Harvati et al. (2010) demonstrates that, in fact, early Middle Pleistocene European and African hominins share substantial similarities in the morphology of their face, temporal bone, and posterior cranial vault. The morphology of these areas diverged after MIS 7 (Marine Isotope Stage 7), supporting the view (Hublin and Tillier, 1992) of a gradual accretion of Neandertal features in Europe and modern traits in Africa.

Two other specimens that likely belong among early archaic African hominins, the partial mandible from Kanam, Kenya (Tobias, 1960), and the partial cranium from Salé in North Africa (Hublin, 1985, 1992), display pathologies that hinder an unambiguous assessment of their affinities to other specimens in the group and are not considered in more detail here.

Bodo

The partial cranium from Bodo was discovered in 1976 (Conroy et al., 1978; Kalb et al., 1980). Later work at the site by the Middle Awash project clarified some details of the stratigraphy and collected a thick-walled parietal of a second hominin (BOD VP 1/1) (Asfaw,

1983) and a fragment of a distal humerus (BOD VP 1/2) (Carretero et al., 2009). Importantly, the Middle Awash project was also able to obtain a K-Ar date of 600 ka for these hominin remains (Clark et al., 1994).

The Bodo cranium is massive, with a vertically thick and highly projecting browridge, large orbits, a wide interorbital distance and pyriform aperture, and a very broad and tall midface. Conroy et al. (1978) presented a detailed initial description of the cranium, and Adefris (1992) wrote the first comprehensive description of it. Rightmire (1996) followed with an evaluative description, arguing that the cranium differed from *H. erectus* and likely provided evidence that speciation had taken place within *Homo* during the Middle Pleistocene of Africa. Kappelman (1996) predicted a body mass for Bodo of approximately 117 kg from its orbital area.

In the process of cleaning the cranium, White (1985, 1986) noted the presence of a series of fine cutmarks on the frontal and around the orbit, apparently made by stone tools around the time of death rather than a metal implement after discovery of the fossilized remains. Conroy et al. (2000) used volumetric reconstruction of the cranium from CT scans to estimate the cranial capacity as of around 1250 cc, with a probable range of 1200–1325 cc, depending upon how the base and posterior of the cranium are reconstructed. Copies of CT scans of the specimen are available to researchers through the Digital Archive of Fossil Hominoids of the Department of Anthropology at the University of Vienna (Seidler et al., 1999).

A partial left parietal (BOD-VP-1/1) from a second individual was collected by T. White in 1981 320 m SSW of the cranium's find-spot during a visit to the site (Asfaw, 1983). The fragment has thick diploë, a pronounced angular torus, and a prominent extension of the supramastoid crest (Asfaw, 1983). These features are commonly encountered in *H. erectus* and, among Middle Pleistocene hominins, could be considered primitive.

The humerus from Bodo (BOD VP 1/2) consists of a distal left shaft that lacks its articular surface (Carretero et al., 2009). Like the distal humeri from other Middle Pleistocene hominins, it has a wide olecranon fossa and comparatively narrow medial and lateral pillars flanking the fossa (Carretero et al., 2009). Carretero and colleagues used regressions based on recent human samples and the Sima de los Huesos sample to estimate the bi-epicondylar breadth of BOD VP 1/2, obtaining a probable value of 62–63 mm, which falls near the middle of the Sima de los Huesos sample, suggesting it belonged to an average-sized individual rather than a small one as originally reported (Clark et al., 1994).

Saldanha

Other possible examples of *H. heidelbergensis* include the calotte from Saldanha (also known as Elandsfontein or Hopefield) (Drennan, 1953; Drennan and Singer, 1955; Singer, 1954; Singer and Wymer, 1968). Saldanha has long been likened to Kabwe, which it resembles closely. While there has been a considerable amount of archaeological work on Acheulean sites around Saldanha Bay since the 1980s (e.g., Klein et al., 2007), there have been few new investigations focused on the hominin calotte or mandibular fragment.

Kabwe

The well-known and exquisitely preserved fossils from Kabwe (Broken Hill) in Zambia comprise a cranium, maxilla of a second individual, two proximal femora, two femoral diaphyseal fragments, a distal femur bearing its condyles, a humerus, complete tibia, sacrum, and fragmentary innominate. The cranium was described as the type specimen of *Homo rhodesiensis* (Pycraft et al., 1928), and probably a geographic or individual variant of the same hominin species or lineage represented by Bodo (Rightmire, 1984a, 1996, 1998, 2008; Bräuer, 1984b, 2008), whether one calls that lineage *H. heidelbergensis*, *H. rhodesiensis*, or something else.

Obtaining a precise age for the Kabwe cranium and other remains has proven difficult, with dates based on fauna and archaeological associations placing the specimen around 120–300 ka (e.g., Klein, 1999). Recent ESR dates on a chip of enamel from one of Kabwe's teeth indicate a date between 300 and 200 ka, with more likelihood of an age closer to the younger limit of the range (Stringer, 2011). Thus despite the archaic morphology of the cranium, it now appears to have been penecontemporaneous with morphologically more advanced specimens like Florisbad and KNM-ER 3884.

Since the 1980s, there have been a number of new morphological analyses of these fossils. Stringer (1986) noted that the innominate fragment had greatly thickened cortical bone on the acetabulo-cristal buttress, an archaic trait that makes it resemble OH 28. Calcagno and Gibson (1992) revisited the remarkable tooth decay evident in the cranium, as did Bartsiokas and Day (1993), who speculated that lead poisoning could have contributed to the decay. In comparisons to the Berg Aukas femur, both proximal femora from Kabwe are much more similar to modern humans (Grine et al., 1995; Pearson, 1997), which agrees with Kennedy's (1984) observations that the Kabwe femora had fundamentally modern morphology. Kappelman (1996) predicted a body mass for the Kabwe cranium of approximately 118 kg based on its orbital area. CT scans of Kabwe highlighted the vast extent of its paranasal sinuses and facilitated comparisons of other endocranial details (Seidler et al., 1997).

Yokley and Churchill (2006) included the E.898 humerus from Kabwe in a morphometric analysis of distal humeri, concluding Neandertals could be distinguished from recent humans but the Kabwe specimen could not. Trinkaus (2010) presented an analysis of the Kabwe tibia, concluding it came from a tall individual but one of uncertain body mass, with a range of 63.7–81.1 kg, depending on the ecogeographic adaptations that one assumed. It also has a retroverted tibial plateau and a blunt anterior crest, traits it shares with other archaic tibiae.

Ndutu

The small cranium from near Lake Ndutu in Tanzania (Mturi, 1976; Clarke, 1976, 1990; Rightmire, 1983) has generally been included in the same group or grade as Bodo, Kabwe, and Saldanha. Ndutu is imprecisely dated by tuff correlation with the upper part of the Masek Bed at Olduvai (Rightmire, 1983); most authorities favor an age of around 400 ka, give or take 100 ka. The cranium is small in overall size and fragmentary; Holloway and Rightmire estimated its brain size to be between 1,070 and 1,120 cc (Rightmire, 1983). The cranium is broadest across the supramastoid crests, but the parietals rise almost vertically above them (Rightmire, 1983). The upper and lower tables of the occipital are less angled than in *H. erectus* and more comparable to Kabwe and later specimens (Rightmire, 1983). The preserved portions of the supraorbital tori project strongly from the squama of the frontal but are vertically thin. Although fragmentary, the face must have been vertically short (Clarke, 1990).

Manega (1993) worked to clarify the age of the Ndutu Beds at Olduvai, obtaining four single crystal laser fluorescence $^{40}\text{Ar}/^{36}\text{Ar}$ dates for samples from tuffs in the upper Ndutu Beds spanning 0.21 ± 0.02 Ma to 0.45 ± 0.04 Ma, with a bulk weighted mean of 0.23 ± 0.01 Ma.

CT scans of Ndutu are available from the University of Vienna's database of fossil hominins.

Baringo Kapthurin

McBrearty and colleagues' excavations in the Kapthurin formation at Lake Baringo, Kenya, have provided some of the best-documented and most influential work on the late Acheulean

and earliest MSA cultural context for Middle Pleistocene *Homo* in Africa. Work in the 1960s by Margaret Leakey (Leakey et al., 1969) led to the discovery of a mandible (KNM-BK 8518) attributed to *H. erectus* (although in Africa, there seem to be few, if any, differences in the mandibles of *H. erectus* and Middle Pleistocene *Homo*), a right ulna lacking its distal end, a slender right first metatarsal, and two proximal manual phalanges (Solan and Day, 1992; McBrearty et al., 1999). McBrearty's more recent research has provided more precise dates for the hominin fragments as well as the earliest known chimpanzee fossils, three teeth that date to between 284 ± 12 ka and 545 ± 3 ka (and likely much closer to the older age based on stratigraphic position) (McBrearty and Jablonski, 2005). Solan and Day (1992) described the right ulna (KNM-BK 66) from the Kapthurin Formation, from levels dating to 510–512 ka (Deino and McBrearty, 2002). The specimen is long, slender, has only weakly imprinted muscle origins and insertions, and has a relatively low coronoid process, a primitive feature in later *Homo* that also occurs in Neandertals and some specimens of early “modern” humans from the MSA (Churchill et al., 1996; Pearson and Grine, 1996). The archaeological record from the Kapthurin Formation has produced a series of surprises, including sites with evidence of precociously early production of blades as early as 500 ka (Johnson and McBrearty, 2010) and evidence of a technological transition to the MSA as early as 285 ka (Tryon and McBrearty, 2002).

Berg Aukas

New hominin fossils discovered or described since the mid-1980s that may belong to *Homo heidelbergensis* (or other Middle Pleistocene *Homo*) include a proximal femur from Berg Aukas in Namibia and a tibia and teeth from Hoedjiespunt in the Western Cape of South Africa. Berg Aukas is a massive proximal half of a right femur that has a very large head that measures 56.4 mm vertically, a low neck-shaft angle, and very thick cortical bone (Grine et al., 1995). The femur was recovered from deep underground in a mine in 1965, and its stratigraphic associations were not studied in detail at the time (Grine et al., 1995). Its antiquity remains uncertain. Its morphology most closely recalls Neandertals from Europe. Its original length is estimated at 518 mm, which would correspond to a tall stature, and the large head predicts a mass of ~93 kg (Grine et al., 1995). A later analysis by Trinkaus et al. (1999) argued the femur came from a tropically adapted human based on subtrochanteric shape and diaphyseal robusticity.

Hoedjiespunt

Remains that may derive from Middle Pleistocene hominins came from a small assemblage of bones that were found eroding from an ancient hyena den in eolian sand dunes lining Saldanha Bay in the Western Cape Province, South Africa (Berger and Parkington, 1995, 1997). Teeth from the site include two maxillary molars (a left M^2 and right M^3) and a left central and left lateral mandibular incisor (Berger and Parkington, 1995; Stynder et al., 2001). All of the teeth belonged to a subadult and are larger than homologous teeth of living Africans but similar in size to those of African and European Middle Pleistocene hominins. The tibia from the site consists of most of a right shaft, preserved from just below the tibial tuberosity to the distal metaphysis. Like other archaic tibiae, it has a blunt and straight anterior crest (Churchill et al., 2000). Its original length was estimated at more than 360 mm; body mass predicted from the bone is in excess of 60 kg (Churchill et al., 2000). Micromammals from the site, which were likely consumed and deposited by barn owls, show a habitat similar to today but perhaps more arid (Matthews et al., 2005).

The excavators of Hoedjiespunt place it between 200 and 350 ka; it seems to have been associated with a period of low sea level, possibly MIS 8 (Churchill et al., 2000). However,

Butzer (2004) has argued that the hominin fragments and other fossils may actually derive from the neighboring Late Pleistocene site of Sea Harvest and were redeposited by the action of road grading in the 1970s and 1980s. An effort to directly date these hominins is needed.

Late Archaic/Transitional Specimens

Hominins similar to Bodo persisted in Africa until around 300ka, and possibly until 200ka (Stringer, 2011). The tempo and mode of transformation to Bräuer's next grade, late archaic *Homo sapiens*, which had occurred by between 300 and 230ka, remains unclear. The "late archaic" group is populated by an abundance of finds including Florisbad, Eliye Springs, KNM-ER 3884, KNM-ER 999, Ngaloba (Laetoli Hominid 18), Jebel Irhoud 1-4, Wadi Dagladlé, Kébibat (Rabat), and Omo II (Bräuer, 1984b, 2008; Rightmire, 1984a, 2008). They present a substantial amount of variation in browridge size and morphology, ranging from fairly large, protruding browridges (e.g., Florisbad, Ngaloba, and KNM-ER 3884) to more reduced forms (e.g., the preserved portions of Omo II and Jebel Irhoud 2). They also show a wide range of variability in occipital morphology from substantial reduction in angulation between the upper and lower tables and weak development of the occipital torus (e.g., Ngaloba) to a strongly angled form that is reminiscent of *Homo erectus* (e.g., Omo II). In some cases, these specimens show temporal overlap with the earliest modern humans, further complicating evolutionary scenarios that invoke a smooth, anagenic transition from one form to another.

Another intriguing detail was reported by Stringer (1993), who found that these "late archaic" or "intermediate" fossils from Africa are, in terms of their cranial metrics, strikingly similar to the Chinese specimens of Maba and Dali (and likely also Jinniushan, although Stringer did not have measurements for this specimen). Stringer (1993) noted that the phenetic similarity between his samples of African and East Asian late archaic humans was so close that it resembled the distance between geographically widely separated groups of humans in Howells's data set (Howells, 1973, 1989, 1995, 1996).

Florisbad

Florisbad consists of a partial cranium consisting of the face, the right M³, and much of the anterior portions of the cranial vault. It was discovered in 1932 in a fossiliferous spring eye in the Orange Free State, South Africa. The cranium was initially described by Dreyer (1935) as the type specimen of a new species, *Homo helmei*. Subsequent descriptions of Florisbad noted that it shared more features with modern humans than did Kabwe. These traits include a shorter face, canine fossa, and incipient division of each half of the supraorbital torus into supraorbital and superciliary segments (Drennan, 1935; Galloway, 1937; Keith, 1938). More recent descriptions largely agree, recognizing the cranium as intermediate in morphology between modern humans and archaic crania like Kabwe (Rightmire, 1978a, 1984a; Clarke, 1985). The cranium bears a canine toothmark on its frontal and may have been killed or scavenged by a large carnivore (Tappen, 1987). Curnoe and Brink (2010) have described other changes in the cranium, including lesions on the orbital roof and areas of thinning of the otherwise thick cranial vault, that indicate the individual had suffered from a pathology of indeterminate cause. Kappelman (1996) predicted a body mass of approximately 96kg for Florisbad based on its orbital area.

Early attempts to date sediments associated with the Florisbad cranium produced dates of 41–37 ka (Day, 1986); Protsch (1974, 1975) reported a direct ¹⁴C date of the cranium of 38–39 ka. These ¹⁴C dates should be read as infinite instead, as Vogel surmised (Day, 1986). More recently, Grün et al. (1996) obtained an ESR date from the hominin's tooth enamel of 259 ± 35 ka.

Additional studies of the locality include recent work on the site's vertebrate paleontology and archaeology (Brink and Henderson, 2001), as well as a brief report on Erfkroon, a contemporary fossil vertebrate locality in the Orange Free State (Churchill et al., 2000).

Eliye Springs (KNM-ES 11693)

The cranium from Eliye Springs was discovered by Dr. and Mrs. Darnhofer, who spotted its dark, round occipital protruding from the sediment while they were walking along a beach on the western shore of Lake Turkana (Bräuer and Leakey, 1986a). The cranium likely eroded by wave action from a nearby deposit bearing later Pleistocene fauna, but, unfortunately, its original provenience is unknown. It was originally described by Bräuer and Leakey (1986a, 1986b), who emphasized its affinities with other specimens of African late archaic *H. sapiens*. The cranium is heavily mineralized, stained very dark brown, and very well preserved except for the anterior portions of the supraorbital torus and face, which have been abraded. The cranial vault is long, low, and quite broad, with a rounded occipital, a greatest breadth of the cranium situated across the supramastoid crests, pronounced bossing on the parietals, a more vertical forehead than Kabwe or Bodo but not as vertical as in modern humans, and a broad but vertically short face.

Examination of the gross morphology of the cranial vault coupled with CT scans demonstrated that much of the cranial vault of KNM-ES 11693 is pathologically thickened to as much as 20.1 mm in the posterior portions of the parietal, 14 mm at lambda, and 16 mm at the temporal lines (Bräuer et al., 2003). The external surface of the vault also shows marked porosity, leading to the conclusion that the individual probably suffered from anemia from childhood onward (Bräuer et al., 2003).

Although the inside of the cranium of Eliye Springs remains filled with consolidated sediment, CT scans have permitted a study of the details of the virtual anatomy of the specimen's endocranial surfaces (Bräuer et al., 2004). The digital reconstruction showed that the endocranial capacity is approximately 1,210 cc (with a range between 1,170 and 1,245 cc). The anterior cranial fossa is relatively small, and the middle cranial fossa is at the shorter end of the few recent humans used for comparison. Otherwise, almost all of thirty-five endocranial features studied by Bräuer et al. (2004) fell within, or close to, the modern range of variation. The cranial base, however, is even more strongly flexed than in modern humans.

KNM-ER 3884

The partial cranium of KNM-ER 3884 was collected from the former Guomde Formation, which now has been divided between the underlying Chari and overlying Galana Boi formation (Feibel et al., 1989) in Ileret, East Turkana. It consists of the posterior parts of the cranium (occipital and fragments of the parietals), the frontal bone, and the palate and maxillary dentition (Bräuer et al., 1992a). It resembles other late archaic specimens like LH 18, Jebel Irhoud 1 and 2, Florisbad, and Omo II in various features, including a large cranial capacity, estimated at ~1,400 cc from the occipital's dimensions, which align the cranium with these late archaic specimens and show that it possessed some but not all of the apomorphies of later anatomically modern humans (Bräuer et al., 1992a; Bräuer, 2001b, 2008). Bräuer et al. (1997) reported a direct date on the fossil of 272 ka (range: 159 ka to infinity) to 279 ka (range: 162 ka to infinity) by $^{234}\text{U}/^{230}\text{Th}$ gamma ray spectrometry.

KNM-ER 999

A second specimen recovered from the formerly recognized Guomde Formation at Ileret in East Turkana, KNM-ER 999 consists of most of a left femur (Day and Leakey, 1973).

Trinkaus (1993) provided further analysis of the specimen, noting that it had a high neck-shaft angle like some of the Qafzeh and Skhul hominins, a distinct pilaster, and a point of minimum breadth located high on the shaft. All of these features resemble traits present in early modern and later hominins rather than *H. erectus* or archaic hominins like Neandertals, leading Trinkaus to argue that KNM-ER 999 showed affinities to modern humans. Bräuer et al. (1997) reported an absolute, direct date of the fossil of 301 ka (range: 205 ka to infinity) by $^{234}\text{U}/^{230}\text{Th}$ gamma ray spectrometry.

Ngaloba (Laetoli 18)

The Ngaloba cranium (also designated Laetoli Hominid 18 [LH 18]) comprises a calvaria and partial face (palate and maxillae). Collected in 1976 by Mary Leakey and her co-workers, LH 18 derives from the Ngaloba Beds at Laetoli, which also contain MSA tools (Day et al., 1980). Its anatomy, including a vertically short face, high vault, greatest cranial breadth located fairly high on the parietals, strong parietal bossing, small and medio-laterally narrow mastoid processes, and rounded occipital lacking a strong torus, clearly link the cranium with modern humans; only the receding forehead and large browridges indicate archaic affinities (Day et al., 1980; Magori and Day, 1983a, 1983b). The architecture of the cranial vault corresponds to the cranial “globularity” described by Lieberman et al. (2002) as a key morphological change that, along with facial retraction (Lieberman, 1998, 2008), produced modern cranial morphology.

The initial estimate of the age of LH 18 was approximately 120 ± 30 ka based on correlation with the trachytic marker tuff in the lower unit of the Ndutu Beds at Olduvai (Day, 1986). In an effort to clarify the age of the Ngaloba Beds and LH 18, Manega collected a series of ostrich eggshell fragments from the Upper Ngaloba Beds that contained the hominin. Amino acid racemization analysis (D/L ratio) of these suggested a minimum age of 205 ± 17 ka or 290 ± 25 ka for LH 18, after applying appropriate controls and adjustments for paleotemperatures (Manega, 1993). Subsequent summaries of hominin evolution (e.g., Bräuer, 2008) have tended to emphasize the younger revised age (~200 ka), but the cranium could well be older. Either way, Manega’s (1993) results provide another indication that hominins with nearly modern morphology lived in East Africa between 300 and 200 ka.

CT scans of Ngaloba are available from the Digital Archive of Fossil Hominoids of the Department of Anthropology at the University of Vienna.

Eyasi Remains

Continued work around Lake Eyasi in Tanzania (Mehlman, 1987; Domínguez-Rodrigo et al., 2007) has added to the fragmentary Eyasi cranium, occipital of a second individual, and vault fragments and teeth from a third (L. Leakey, 1936, 1946; Bräuer, 1984b). The new specimens include fragments of two mandibles and an occipital (Bräuer and Mabulla, 1996) and a frontal bone (Domínguez-Rodrigo et al., 2008). Trinkaus (2004) observed that the occipital of Eyasi 1 bears a suprainiac fossa, a feature usually associated with European hominins. Domínguez-Rodrigo et al. (2008) reported ESR (104 ± 13 to 207 ± 26 ka) and $^{230}\text{Th}/^{234}\text{U}$ (92.4 ± 4.1 to 138.3 ± 0.7 ka) ages for a wildebeest tooth found 5 m away from the new frontal.

Omo II

Since its initial description by Day (1969), the archaic affinities of the Omo II cranium have consistently been emphasized (Day and Stringer, 1982, 1991; Rightmire, 1984a; Bräuer, 1984b; Schwartz and Tattersall, 2003). Nevertheless, Day (1969) reported an estimate of the cranial capacity as $1,435 \pm 20$ cc. Most of the preserved basicranial details of Omo II recall

the anatomy of *Homo erectus*, and Stringer (1974) found that it clustered with Ngandong in multivariate space. However, the specimen has the same geological antiquity as Omo I (see below).

Jebel Irhoud Remains

Discoveries from Jebel Irhoud in Morocco consist of two adult crania and a juvenile humerus and mandible (Ennouchi, 1962, 1968; Holloway, 1981; Hublin and Tillier, 1981; Hublin et al., 1987; Hublin, 1992; Grün and Stringer, 1991; Grimaud-Hervé, 2005). Debate has swirled around possible Neandertal affinities of the crania; they certainly have long, low, and broad vaults, but the resemblance ends there. They have none of the apomorphic features that characterize Neandertals (Santa Luca, 1978; Hublin, 1992). Controversy also surrounds the degree of development of the chin on the juvenile mandible (Jebel Irhoud 3): Hublin et al. (1987) argued it has all of the components of a modern chin but weakly expressed on a vertical symphysis; other commenters have stated it does not bear a modern chin (e.g., Schwartz and Tattersall, 2000, 2003, 2010). T. Smith et al. (2007) reported an ESR and uranium-series date of 160 ± 16 ka for the site and also demonstrated that Jebel Irhoud 3 had a slow, fully modern pattern of dental development.

Earliest Modern Humans

Omo I

The partial skull and skeleton of Omo I was initially described as anatomically modern by Day (1969). Subsequent analysis supported Day's assessment (Day and Stringer, 1982, 1991; Day et al., 1991) and emphasized the differences with Omo II, which also derived from Member I of the Kibish Formation. The initial age estimate was of 130 ka based on a $^{230}\text{Th}/^{234}\text{U}$ date on a bed of Nile oyster shells in Member I and two ^{14}C dates on the same bed of greater than 39 ka (i.e., potentially infinite) (Butzer et al., 1969). At the time, Butzer et al. (1969) expressed caution about the $^{230}\text{Th}/^{234}\text{U}$ date, because it was known that uranium was water-soluble and could move in or out of deposits depending upon precipitation and the level of the water table; the effects of these uncertainties on mollusk shells had not been established. Although uncertainty over the antiquity of the specimen became a mainstay of multiregionalists' criticism of Omo I (see Fleagle et al., 2008), virtually all accepted that its cranial morphology was modern, or nearly so (although see Bartsiokas [2002] on Omo I's relatively thin layer of diploë in its cranial vault). Omo II, however, differed from modern humans in almost every preserved nuchal and basicranial detail, instead resembling *Homo erectus* (Day, 1969). This prompted Day to surmise that Omo II might be of greater geological antiquity, and many researchers have adopted a similar perspective. Renewed research in the Kibish Formation has pinpointed the find-spots of both Omo I and II. Both of these crania clearly derive from Member I, are underlain by the Nakaa'kire Tuff (dated to 196 ± 2 ka by $^{40}\text{Ar}/^{39}\text{Ar}$) low in Member I of the Kibish Formation and constrained in age by the Aliyo Tuff (dated to 104 ± 1 ka by $^{40}\text{Ar}/^{39}\text{Ar}$) near the middle of Member III, and approximately 24 meters above the level of KHS, the site where Omo I was discovered (McDougall et al., 2005, 2008; Brown and Fuller, 2008). Deposition of sediments in the lower Omo Valley appears to be closely linked to the amount of precipitation that falls on Ethiopia and thus also appears to correlate with sapropel deposition in marine sediments in the eastern Mediterranean. It seems likely that Member I of the Kibish Formation correlates with sapropel S7 (~195), Member II with sapropel S5 (~172 ka), Member III with sapropel S4 (~124 ka), and Member IV with sapropel S1 (~8 ka) (McDougall et al., 2005, 2008; Brown

and Fuller, 2008). Each sapropel accumulated fairly rapidly (at least in geological terms), over a span of approximately 10 ka, which corresponds to the spread of radiocarbon ages (13.1–3.6 ka) for Member IV atop the Kibish Formation (Brown and Fuller, 2008; McDougall et al., 2008). Given these facts, the best age estimate for Omo I, II, and the other hominins from Member I is 195 ± 5 ka.

There is no taphonomic or stratigraphic evidence to support assertions that Omo I is intrusive into Member I or that Omo II had been transported or eroded from older sediments and redeposited in Member I (Fleagle et al., 2008; Brown and Fuller, 2008; McDougall et al., 2008).

The renewed work in the Kibish Formation identified the find-spot of Omo I and led to the recovery of additional hominin remains at the site including two fragments of the left os coxae, the right talus, a fragment of the distal right femoral diaphysis that refits with the femoral condyles collected in 1967, and two right manual phalanges (Pearson et al., 2008a). Measurements of the acetabulum and humeral head predict a vertical diameter of the femoral head of 47.28 ± 1.24 mm, which implies a body mass of 70.73 ± 5.14 kg; height estimates range from 162.4 ± 5.1 cm to 172.3 ± 6.5 cm based on the length of the right metatarsal to 178.2 ± 4.25 cm to 182.3 ± 4.43 cm for the partial left humerus (Pearson et al., 2008a). The new fragments of os coxae provide a perplexing set of indications of sex including a large acetabulum (male), a greater sciatic notch shape that is intermediate between males and females, and the presence of a pre-auricular sulcus (female). It is possible that the pattern of sexual dimorphism at this point in human evolution differed from that of living humans, as Bonmatí et al. (2010) have documented for the Sima de los Huesos pelvis. Voisin (2008) concluded that Omo I's left clavicular morphology aligns it with living and Upper Paleolithic humans rather than Neandertals or earlier forms of *Homo*.

Work at other sites in the Kibish Formation produced additional finds, including a diaphysis and distal epiphysis of a left tibia (Kib 158-1a, from site AHS in Member I) and a piece of the diaphysis of a left fibula (Kib 158-1b) from the same site (and possibly from the same individual) and two cranial vault fragments (a posterior portion of an adult's right parietal [Kib 170-1] and a fragment of a juvenile's occipital [Kib 170-4]) from CHS, a site near the junction of Member III and IV, with an uncertain date (~8.6–104 ka) (Pearson et al., 2008b; Brown and Fuller, 2008).

If Omo I dates to 195 ± 5 ka, it would be older than most likely genetic dates for the origin of modern humans such as Fagundes et al.'s (2007) estimate of a speciation date of 141,455 BP (95% posterior probability density interval of 103,535–185,642 BP). Fagundes et al. (2007) derived this estimate from the best-fitting model of the origin and spread of modern humans to East Asia and the New World, a complete replacement of archaic Eurasians by African immigrants followed by exponential growth of the immigrants later in time. If the simulation approach and approximate Bayesian computation that Fagundes et al. (2007) used to explore the likely outcomes of complex demographic histories provide a reasonable approximation of reality, an age of ~141 ka for the origin of modern humans as a genetically distinct species has at least two interesting implications for the fossil record. There is reason to expect the ~141 ka date is reasonable: the values it derives from nuclear DNA polymorphisms in fifty loci resemble dates from mtDNA and Y chromosomes for the exodus from Africa and the settlement of the New World. Two implications for the fossil record are, first, that individuals whose morphology can be identified as “anatomically modern” appeared *before* the species originated, antedating it by ~50,000 years. Second, the date reinforces the impression from mtDNA (and human Y chromosomes with a coalescent age of 141.5 ± 15.6 ka [Cruciani et al., 2011]) that one or more events during MIS 6 (195–128 ka), a period of very low sea level and a massive glacial advance (the Riss Glaciation) in Europe, led to the origin of the genes that make up ~90–100% of the genotype of every living member of *Homo sapiens* (Green et al., 2010; Reich et al., 2010).

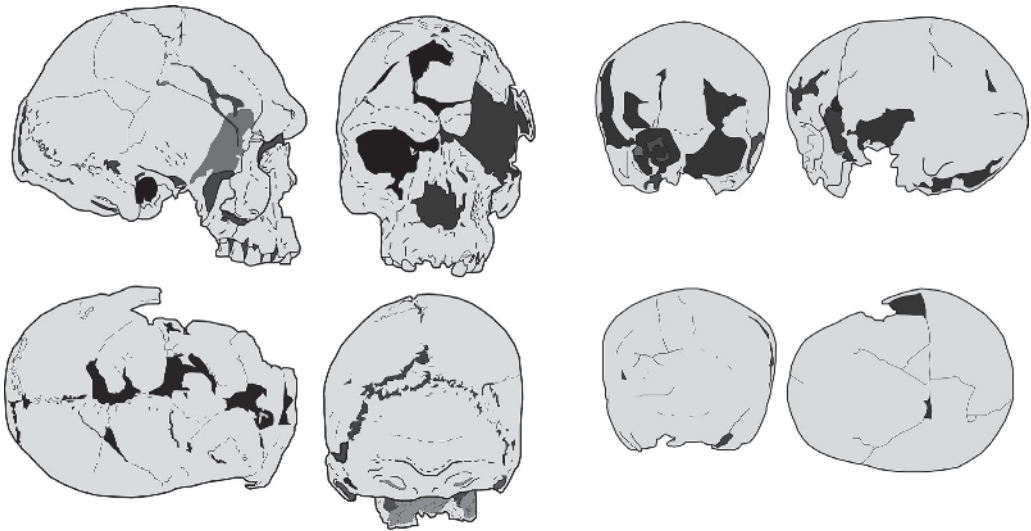


Figure 1.4. The best-preserved crania from Herto, scaled to the same size (after photographs by David Brill in White et al., 2003). Left: four views of BOU-VP-16/1, a strikingly large male cranium. Right: four views of BOU-VP-16/5, a cranium of a 6- to 7-year-old child.

Herto

White et al. (2003) described one juvenile and two adult crania from Herto in the Middle Awash, Ethiopia (Figure 1.4). Craniodental fragments of seven other individuals were reported in 2003, and the sample has now grown to fragments from a minimum of twelve individuals (White, 2009). All three of the most complete crania are arguably anatomically modern, or nearly so, but very robust. The best preserved cranium, BOU-VP-16/1 is easily distinguished from living humans, in part by its size alone given its glabella-opisthocranium length of 219.5 ± 2 mm and its nasion-prosthion length of 79 ± 3 (White et al., 2003). To put these values in perspective, the longest of the 2,524 crania in Howells's online data has a glabella-opisthocranium length of 206 mm, and only 30 individuals have a nasion-prosthion length of 79 mm or greater. The proportions and morphological traits of the Herto crania, however, match the expectations for a modern human (e.g., Day and Stringer, 1982, 1991; Stringer, 2003), leading White et al. (2003) to propose the subspecific designation of *Homo sapiens idaltu* for the Herto specimens. The crania have a high cranial vault, a widest point of the cranium located high on the parietals (which give them an *en maison* shape in posterior view), a more obtuse angle between the upper and lower tables of the occipital than in *H. erectus*, higher frontal angle, a modern cranial capacity (1,450 cc for BOU-VP-15/1 and 1,250 cc for BOU-VP-15/5), a distinct canine fossa, a supraorbital torus divided by a sulcus into a thick supraorbital segment and a thinner superciliary segment, medio-laterally narrow mastoid processes, and a face that appears to be retracted beneath the frontal bone (White et al., 2003). The child's cranium differs from the adult in being substantially smaller (especially with respect to maximum length) and has minimal development of its supra-orbital torus, and a much less projecting mastoid process and a smaller face, as one might expect in a juvenile. It also has very well-developed parietal bosses and a much more rounded contour of the external surface of the occipital. These details combine to endow BOU-VP-15/5 with an unequivocally modern morphology.

The crania were found in association with a stone tool industry that has handaxes as well as MSA components, and all three crania bear peri-mortem cutmarks likely made by a stone

tool (Clark et al., 2003). The sediments that yielded the crania have been precisely assigned to the interval between 160 and 154 ka by $^{40}\text{Ar}/^{39}\text{Ar}$ dating of over- and underlying tuffs (Clark et al., 2003).

Singa

The cranium from Singa was collected from the bank of the Blue Nile in Sudan about 320 km south of Khartoum. It was initially described as an ancestral Bushman by Woodward (1938) on the basis of its pronounced parietal bosses and strongly developed browridges. A later analysis by Stringer et al. (1985) noted that the exaggerated parietal bosses may stem from pathology. Its browridge is reduced in size versus Kabwe, Bodo, and even Florisbad but still prominent compared to most living Africans. Singa features a high cranial vault, fairly vertical forehead, and a rounded occipital. Stringer (1979) applied a multivariate analysis of Penrose distances to Singa and a set of other recent and fossil crania and found that no other Pleistocene cranium provided was especially close to it. Jebel Irhoud 1 lay closest to Singa in Penrose space, leading Stringer (1979) to conclude that the specimen's affinities lay with African late archaic specimens like Jebel Irhoud.

Removal of the matrix filling the cranium and preparation of an endocast allowed the specimen's cranial capacity to be ascertained to be 1,340 cc (Stringer et al., 1985). McDermott et al. (1996) obtained a U/Th date for the cranium of $> 133 \pm 2$ ka on calcrete matrix inside the cranium, placing it near the end of MIS 6. Although the overall morphology of the Singa cranium differs from what one would expect in a modern human, the U/Th dates suggest it is substantially more recent than the earliest examples of anatomically modern (or nearly modern) Herto crania and Omo I.

Aduma

Haile-Selassie et al. (2004) described four partial crania from Aduma (ADU-VP-1/1, ADU-VP-1/2, ADU-VP-1/3, and ADU-VP-1/6) and a right parietal from Bouri (BOU-VP-5/1) in the Middle Awash research area in Ethiopia. The best preserved cranium, ADU-VP-1/3, bears a suprainiac fossa on its occipital but otherwise is modern in form, resembling those of Omo I, LH 18, Skhül V, and Qafzeh 9 (Haile-Selassie et al., 2004). The overall affinities of ADU-VP-1/3 clearly lie with early modern humans. The same appears to be the case for the long BOU-VP-5/1 parietal and, as far as can be gauged, the much more fragmentary remains of the other Aduma crania. The Aduma crania and Bouri parietal derive from sediments with sites bearing MSA tools and dating between 80 and 100 ka (Yellen et al., 2005). The tools recovered from Aduma represent a distinctive regional tradition defined by a range of point, scraper, and core types as well as tools of small, almost microlithic size (Yellen et al., 2005).

Klasies River (Klasies River Mouth)

Originally excavated by J. Wymer and R. Singer (Singer and Wymer, 1982) and later by H. Deacon (1989, 1992; Deacon and Geleijnse, 1988; Deacon and Shuurman, 1992), the site of Klasies River has figured prominently in the debate over the origin of modern humans for two reasons. First, it yielded a series of human remains, which are rarely recovered from MSA contexts in southern Africa, that had modern morphological affinities and that, by the early 1980s, had a suggested antiquity of around 100 ka (Butzer, 1978; Volman, 1978; Singer and Wymer, 1982). Later work to obtain ESR dates for the site has confirmed this antiquity,

placing all of the hominins from the MSA within the time span of 60–120 ka, with most centering around 100 ka (Grün et al., 1990b; Deacon and Shuurman, 1992). Second, the degree to which the hominin fossils were anatomically modern or not became the subject of debate throughout the 1990s. Arguments against the anatomical modernity of the specimens generally occurred in the context of multiregionalists' attempts to argue that fossils of modern humans had not appeared earlier in Africa than elsewhere (e.g., Wolpoff, 1989; F. Smith, 1992, 1993, 1994; Smith et al., 1989; Frayer et al., 1993). Although the hypothesis that modern humans did not make an early appearance in Africa has been disproven (White et al., 2003; McDougall et al., 2005), how to interpret the anatomy of the hominins from Klasies River remains an interesting issue.

The initial sample of hominin remains from the MSA levels at Klasies River (Singer and Wymer, 1982) has been augmented by recent finds and now comprises five partial mandibles, a frontal bone, a left zygomatic, two maxillary fragments from the LBS Member (Bräuer et al., 1992b), at least ten isolated teeth (Rightmire and Deacon, 2001), a small part of a left os coxae, temporal (Grine et al., 1998), the proximal end of a right radius (Pearson and Grine, 1997), a proximal left ulna (Rightmire and Deacon, 1991), a partial atlas (Grine et al., 1998), a lumbar vertebra, a left metatarsal I, a very long left metatarsal II, and a more moderately sized right metatarsal V (Rightmire et al., 2006a). Singer and Wymer's (1982) description of the hominins from the MSA levels at Klasies River emphasized the modern affinities of the material, although they noted that some of the mandibles had minimal development of a chin and that there was a considerable amount of size variation in the height of the mandibular corpus and molar dimensions. Additional analysis of this material showed that some of the cranial remains appear to have been defleshed by humans wielding stone tools that left cutmarks on the bones (White, 1987). Metrical analysis of the ulna showed it to have a comparatively low coronoid process that aligned it with many archaic humans including Neandertals and the KNM-BK 66 ulna (Churchill et al., 1996).

Controversy regarding the Klasies material sprang from claims that the modern morphological affinities of the material had not been clearly established. F. Smith (1992, 1993, 1994) and Frayer et al. (1993) emphasized that the degree of development of the chin on many of the mandibles was, in fact, weak (or even absent); the late Neandertals from Vindija in Croatia could be considered, they argued, to have a similar degree of chin development. Lam et al. (1996) reassessed the external midsagittal profiles of the mandibles, concluding that each chin that could be evaluated fell within the 95% envelope of variability for modern humans but that it was unlikely that a sample of more recent humans would produce such a high proportion of individuals with weakly developed chins. Lam et al. also noted that the variation in size between corpus dimensions at M_1 of the mandibles KRM 16424 and KRM 13400 would be unlikely ($p < 0.05$) to be encountered in a sample of recent humans. The same applies to the tiny size of the molars of KNM 16424. Royer et al. (2009) performed a more complex resampling study of the molar and mandibular corpus dimensions of the Klasies specimens and confirmed that they showed elevated variability compared to samples of recent humans, but that hominins from Skhul, Dolní Věstonice, and Sima de los Huesos also showed elevated variability, although Neandertals did not. A second argument focused on the Klasies zygomatic bone, which is vertically high, implying a tall face, and has a thick, column-like frontal process that is characteristic of archaic humans (Wolpoff, 1992; Wolpoff and Caspari, 1990, 1996; F. Smith, 1992, 1994). Among modern humans, however, both of these morphological details are variable and the Klasies specimen's morphology does not exclude it from the modern range of variation (Bräuer and Singer, 1996a, 1996b). The debate continues; Cartmill and Smith (2009) have reiterated their view of the archaic affinities of the Klasies zygomatic.

Border Cave

The hominin fossils, especially the cranium (Cooke et al., 1945; de Villiers, 1973; Rightmire, 1979, 1981) and mandibles (de Villiers, 1973, 1976) from Border Cave, played a large role in the debate over the origin of modern humans due to early and successful efforts to establish the antiquity of the MSA deposits at the site (Klein, 1977; Butzer et al., 1978; Beaumont et al., 1978; Beaumont, 1980) and the obviously modern morphological affinities of the cranium and mandibles (de Villiers, 1973, 1976; Rightmire, 1979, 1981, 1984a; Bräuer, 1984b).

Fossils from Border Cave that have been described since the 1980s comprise a fragment of a right humeral diaphysis, proximal right ulna, and right metatarsals IV and V, lacking their heads (Morris, 1992). The humerus was later evaluated by Pfeiffer and Zehr (1996) and Pearson and Grine (1996), and the ulna by Pearson and Grine (1996). The ulna has a relatively low coronoid process like the Klasies River specimen (Churchill et al., 1996). Sillen and Morris (1996) measured bone mineral crystallinity via infrared spectroscopy in fauna from Border Cave as well as the ulna, humerus, and the two mandibles from the MSA. Their results showed that the ulna and humerus matched the MSA-derived fauna in crystallinity, but the mandibles did not and thus might be of recent date rather than ~90 ka. However, a more recent ESR and laser ablation study of an enamel chip from the Border Cave 5 mandible (Grün et al., 2003) placed the specimen at 74 ± 5 ka, which indicates it derives from the MSA, although it is of a more recent age than it had appeared to be in the 1990s.

Other MSA sites in South Africa have yielded a few hominin fossils. These include isolated hominin fragments, primarily teeth, from the sites of Die Kelders (Grine et al., 1991; Grine, 1998, 2000), Blombos (Grine et al., 2000; Grine and Henshilwood, 2002), Equus Cave (Grine and Klein, 1985), Sea Harvest (Grine and Klein, 1993), and Witkrans (McCrossin, 1992). The teeth tend to be large relative to the recent inhabitants of southern Africa, although a few specimens are smaller like the M² from Witkrans (McCrossin, 1992). The record for additional postcranial remains is even sparser. Grine and Klein (1993) described a slender distal manual phalanx from the MSA levels of Sea Harvest. The site of Blind River produced a left femoral diaphysis lacking the proximal end that was originally reported and described in the 1930s (Laidler, 1933; Wells, 1935); Wang et al. (2008) have reanalyzed the specimen and reported OSL and geological dates that indicate that the sediments that contained the femur began to accumulate immediately following the period of high sea level during MIS 5e.

The only other fossil that might derive from the MSA in Southern Africa is Oranjemund, a calvaria from terrace deposits near the mouth of the Orange River in southern Namibia (Senut et al., 2000). It has a relatively low vault, receding frontal bone, and moderately strongly developed browridges. It is, unfortunately, effectively undated at present.

Hominins from the Late MSA or Early LSA

Hofmeyr

The partial skull from Hofmeyr is an important specimen for understanding the later stages of human evolution in southern Africa. The cranium was originally discovered in 1952 in a dry bed of the Vlekpoort River in the Eastern Cape Province of South Africa, but languished in obscurity because its antiquity could not be established. An attempt to obtain a radiocarbon date in the 1960s sacrificed a large part of the left parietal to no avail because no date was published; another smaller piece was submitted for AMS dating at Oxford in the 2000s but lacked enough collagen to obtain a date (Grine et al., 2007). Instead, sediments in the endocranium of Hofmeyr were dated to 36 ± 3.3 ka through a combination

of OSL and uranium-series dating (Grine et al., 2007). This age establishes the cranium as one of the very few specimens from South Africa from the period between the earliest fossils of modern humans in the region at ~100 ka and the Holocene population.

Grine et al. (2007) noted that the cranium displays a number of primitive traits in comparison to more recent African crania including large molar crowns, a prominent glabella and fairly thick, salient, and continuous browridges, and a high and flat zygomatic bone with a thick frontal process. Metrically, however, after Procrustes superimposition of 3D landmarks on the cranium, Hofmeyr falls among a variety of recent populations in a canonical variates analysis, and, intriguingly, falls closest of all to the mean of the Upper Paleolithic European crania included in the analysis (Grine et al., 2007). This fact suggests the cranium represents a relatively undifferentiated specimen of early modern humanity and corroborates the view that most of the morphological differences that distinguish geographically separate populations of modern humans developed only within the last 36 ka (de Villiers and Fatti, 1982; Stringer and Andrews, 1988; Habgood, 1989; Howells, 1989, 1995; Lahr, 1996). Grine et al. (2010) have presented a geometric-morphometrics-based reconstruction of missing portions of Hofmeyr and, using the reconstruction, estimated the endocranial capacity to be $1,580 \pm 2.7$ cc.

Outside of South Africa, a number of other finds document human evolution through the later MSA, including Mumbwa in Zambia, Mumba in Tanzania, Porc-Épic in Ethiopia, Taramsa Hill and Nazlet Khater 2 in Egypt, and Dar-es-Soltane 5.

Mumbwa

The site of Mumbwa in Zambia was excavated by Del Grande (Dart and Del Grande, 1931) and Desmond Clark (Clark, 1942), followed by renewed work by Barham (1995, 1997, 2000). Barham's expedition uncovered traces of the use of red ochre from MSA levels at Mumbwa as well as from the late Acheulean site of Twin Rivers (Barham, 1998). Barham also uncovered a number of new hominin specimens from the MSA (or possibly from the MSA), including three molars or molar fragments, a left femoral diaphysis, and a proximal and distal fragment of a right radius (Pearson et al., 2000), as well as a small fragment of a hominin humerus from Twin Rivers (Pearson, 2000).

Mumba

Mehlman's (1989) excavation of Mumba Cave in Tanzania yielded two upper molars from the MSA layers. The teeth are notably small in comparison to homologous teeth from recent Africans (Bräuer and Mehlman, 1988). McBrearty and Brooks (2000) reported amino acid racemization on ostrich eggshell of 65–45 ka for Level V at Mumba, which contains the Mumba Industry (Mehlman, 1989). New excavations are under way at Mumba (Prendergast et al., 2007); hopefully additional dates for its MSA deposits will be forthcoming.

Porc-Épic (Diré-Dawa)

Early excavations at Porc-épic Cave near Diré Dawa, Ethiopia, produced a partial hominin mandible (Vallois, 1951) that likely belonged to an early modern human. Later excavations (Clark et al., 1984) recovered additional human craniodental fragments that were discovered while cleaning brecciated fauna from the site (Assefa, 2006) in preparation for study (Assefa, personal communication). Additional recent work from the site has analyzed the lithics (Pleurdeau, 2003, 2005) and uncovered a series of pierced gastropod opercula that were likely used as beads (Assefa et al., 2008).

Taramsa Hill

Excavations at Taramsa Hill near Qena in Upper Egypt, discovered a juvenile burial consisting of a skull and skeleton, of an approximately 8- to 10-year-old child who had been buried in a pit in a Middle Paleolithic chert quarry (Vermeersch et al., 1998). An additional stratum of Middle Paleolithic quarrying debris covered the grave and provided an initial guide to its antiquity. OSL dating sediments from Middle Paleolithic chert extraction pits associated with the skeleton yielded ages ranging from 49.8 to 80 ka, with a weighted average of 55.5 ± 3.7 ka (Vermeersch et al., 1998). Preliminary morphological observations based on excavation photographs show the teeth to be large, the cranium highly domed and gracile, and much of the bone of the mandible to have disintegrated. The skeleton remains in Egypt, awaiting conservation, excavation, and further study.

Nazlet Khater

Nazlet Khater is a skull and partial skeleton recovered from an Upper Paleolithic quarry in Upper Egypt (Vermeersch et al., 1984). The burial and the main flint mining at the quarry date to ~40–35 ka based on OSL and AMS ^{14}C dates (Crevecoeur, 2008). Nazlet Khater was initially described by Thoma (1984); subsequent studies have analyzed the mandible (Pinhasi and Semal, 2000), inner ear (Crevecoeur, 2007; Bouchneb and Crevecoeur, 2009); and, most recently, the entire skeleton (Crevecoeur, 2008) and comparative cranial morphology (Crevecoeur et al., 2009). The skeleton is of a young man, around 161 cm in stature, with a body mass of around 53.4 kg based on the size of his femoral head (Crevecoeur, 2008). The skull and postcranial skeleton show a number of primitive and idiosyncratic features but are modern in overall morphology (Crevecoeur, 2008). A recent analysis of three nearly contemporary crania, Nazlet Khater, Peștera cu Oase, and Hofmeyr, shows that they are surprisingly variable, more so than recent humans (Crevecoeur et al., 2009), a finding replicated in other studies (Gunz et al., 2009).

Dar-es-Soltane II

Dar-es-Soltane II, a cave in Morocco, contained the partial cranium and hemimandible of a strikingly robust adult male, Dar-es-Soltane 5, as well as an adolescent's mandible and the calvarium of another juvenile (Débenath, 1975, 1980; Ferembach, 1976). The hominin remains from the site date to the upper Aterian, which in the late 1980s appeared to date between 40 and 20 ka (Hublin, 1992). Recent work has established a much greater antiquity for the Aterian. Richter et al. (2010) have reported TL dates of 83.3 ± 7.8 and 145 ± 9 ka for two levels of Aterian artifacts from Ifri n'Ammar, Morocco, and Bouzouggar et al. (2007) announced OSL dates of 82 ka for Aterian levels containing pierced shell beads from the site of Grotte des Pigeons at Taforalt, Morocco. At Taforalt, the MP (Aterian) lasts into Bed C, dated by ^{14}C , OSL, and TL to at least 20.2–37.4 ka, although Upper Paleolithic tools make their first appearance at the top of the Bed C and the Aterian disappears (Bouzouggar et al., 2007).

Descriptions of Dar-es-Soltane 5 have emphasized its affinities to anatomically modern humans (Ferembach, 1976; Hublin, 1992), but it also has a heavily developed, strongly projecting browridge, a very broad face, interorbital distance, and cranial vault, and very large teeth (Hublin, 1992; Schwartz and Tattersall, 2003). The other Aterian hominin remains described so far, including a mandible and occipital from Temara and another mandible and an isolated canine from Zouhra Cave, are also anatomically modern but robust and megadont (Hublin, 1992).

Given the great antiquity of the Aterian in North Africa, if recent results from mtDNA of a spread across North Africa at 40–45 ka of people whose mtDNA is closely related to the oldest surviving lineages in Europe and the Near East (Olivieri et al., 2006) also reflects

what happened in the rest of the genome, then the Aterian inhabitants of the Maghreb contributed very little to the genetic heritage of the living population of the region. Instead, the evidence from mtDNA suggests that they were largely replaced, much like Neandertals in Western Europe, despite the evidence for their supposedly modern cognition in the form of shell beads (Bouzouggar et al., 2007) and their anatomically modern morphology.

Haua Fteah

Two partial mandibles were recovered from MSA layers in the massive cave of Haua Fteah in Libya and described in the 1950s and 1960s as having Neandertal affinities (McBurney et al., 1953; Trevor and Wells, 1967; Tobias, 1967). Bräuer (1984b) concluded that this was more a product of the interpretive framework of the time in which Middle Paleolithic industries around the Mediterranean were automatically associated with Neandertals; the mandibles lack any Neandertal apomorphies and likely derive from early modern humans. Additional recent work has focused on analyses of old collections, including the fauna from the Middle Paleolithic levels (Klein and Scott, 1986) and the lithics (Chazan, 1995), and new excavations led by Graeme Barker of Cambridge University have been under way since 2007.

Hominins Formerly Thought to Date to the MSA

Fish Hoek 1

Fish Hoek 1, a well-preserved cranium and mandible, has long figured in discussions of the fossil record of southern Africa as a possible representative of the MSA population (e.g., Sampson, 1974). It was excavated between 1927 and 1929 by V. and B. Peers, amateur archaeologists, from the Howiesons Poort levels of Peers Cave (Skildergat) near the town of Fish Hoek on the Cape Peninsula, South Africa. Keith (1931) provided an initial description and illustrations of the cranium, noting that it generally resembled the skulls of modern Khoesan people but was larger in size. Recently, the controversy over the specimen's age was settled by direct AMS ^{14}C dating, which showed the specimen dates to 7,457–7,145 cal BP (Stynder et al., 2009).

Tuinplaas

Tuinplaas (Springbok Flats) is a partial skull and skeleton (Toerien and Hughes, 1955; Hughes, 1990) from Gauteng Province, South Africa. Uranium-series dating by Pike et al. (2004) determined the skeleton's age to fall between 11.0 ± 0.7 and 20 ± 3 ka. These dates remove the skeleton from the MSA, but show that, if the skeleton provides a reasonable window on the population from which it came, the terminal Pleistocene inhabitants of northeastern South Africa were substantially taller and had larger cranial dimensions than the late Holocene San inhabitants of the area. If so, this would support the idea that a substantial amount of morphological change happened in the early Holocene human population in southern Africa.

Emergence of Distinctive Regional Groups in Africa

Curiously, although modern humans appeared very early in Africa, there was a very long delay until the appearance of individuals who can not be distinguished metrically and morphologically from the living inhabitants of each part of Africa. In fact, almost all Africa Late Pleistocene hominins are easily distinguished from living Africans (Anderson, 1968; Brothwell and Shaw, 1971; Gramly and Rightmire, 1973; Twiesselmann, 1991; Muteti et al., 2010;

Angel et al., 1980; de Villiers and Fatti, 1982; Angel and Olsen Kelly, 1986; Habgood, 1989; Howells, 1989; Boaz et al., 1990; Allsworth-Jones et al., 2010), and it is not until the Holocene that this situation changes (Rightmire, 1975, 1978b, 1984b; de Villiers and Fatti, 1982; Bräuer, 1984b; Habgood, 1989).

The Climatic Background

The 1990 view of the impact of climate that prevailed in the 1990s stressed the importance of Marine Oxygen Isotope Stages (or MIS) as a possible key for understanding the origin of modern humans. The first fossils of modern humans occurred in Africa between 200 and 150 ka (MIS 6) and had spread to Israel by at least 100 ka (MIS 5). This spread from Africa possibly occurred during MIS 5e, a warm and wet period of higher sea level than today between 127 and 115 ka. MIS 6, which corresponded to the Riss Glaciation in Europe and low sea levels worldwide, is intriguingly associated with the origin of modern humans. It is possible that a drier Africa would have supported a small and perhaps fragmented human population. Demographic contraction and isolation could have served as the trigger for the origin of modern humans, either by drift or selection (or perhaps both).

Recent work has produced a somewhat different view of what happened, especially during the last 100 ka in equatorial Africa. The new view stems largely from terrestrial records, especially cores from Rift Valley lakes, rather than the marine record. Cores from Lake Malawi show several periods of marked aridity between 135 and 75 ka, especially between 135 and 127 ka and 100 and 85 ka, with a dramatic rise in lake levels with the return of wetter conditions at around 70 ka and modern level by 60 ka (Scholz et al., 2007; Cohen et al., 2007), the approximate date of the exodus from Africa that led to the establishment of modern humans throughout Eurasia and beyond (Macaulay et al., 2005). These geological findings of megadroughts in the Late Pleistocene likely explain why there was such a long delay between the origin of modern morphology in Africa and the spread of modern people outside of the continent.

Speciation

Perhaps no other question has vexed anthropologists as much recently as the issue of how many hominin species lived in the Middle to Upper Pleistocene. Speciation may have occurred during the transition from *Homo erectus* to *Homo heidelbergensis* (or *Homo rhodesiensis* or *Homo antecessor*) (Rightmire, 1996; Stringer 2003). The range of opinion on the issue falls along a familiar spectrum from splitters to lumpers. On the extreme splitter side of the divide, Schwartz and Tattersall (2003) recognize a large number of “morphs,” presumably (or at least possibly) distinct species. Arsuaga’s (2010) recent overview of the place of the Sima de los Huesos material indicates he too is inclined to recognize a number of distinct populations of Middle to Upper Pleistocene fossils that could be designated as distinct species. Rightmire (1996, 1998, 2001a, 2001b, 2001c, 2008) favors the recognition of *H. erectus*, *H. heidelbergensis*, and two descendants of *H. heidelbergensis*, *H. sapiens* and *H. neanderthalensis*. Stringer (2003) follows suit but recognizes that *H. antecessor* or some other, earlier fossil may also have played a role as the ancestor of both modern humans and Neandertals, thereby complicating Rightmire’s phylogeny and possibly making *H. heidelbergensis* an exclusively European taxon and the African forms that resemble it *H. rhodesiensis*.

Lumpers adopt a seemingly simpler view of hominin diversity during the Middle to Upper Pleistocene, but, on closer inspection, their view contains all of the same morphological

complexity but assigns much or all of it to a lower taxonomic rank. A case in point is Bräuer's (1984a, 1984b, 2008) view that hominin species in Middle to Late Pleistocene Africa are all *Homo sapiens* from the Middle Pleistocene, (i.e., a single evolving lineage), divided into different grades (Figure 1.2). This scheme has, however, drawn criticism. F. Clark Howell (1994: 303–304) wrote:

The informal appellation, archaic *Homo sapiens*, which increasingly gained currency over the past quarter-century, has served more to obscure than to clarify aspects of hominid phylogeny. It, of course, implies attribution *both* to a particular species ((*H.*) *sapiens*) on the one hand, and simultaneously a grade within said species on the other hand. The latter is usually contrasted with “archaic modern” and “anatomically modern.” Thus, although the usage seemingly appears straightforward it is, in fact, informal: no basis for this practice exists within the International Code of Zoological Nomenclature. The term has no formal basis, and it has been applied almost wholesale to an extraordinary diversity of fossil hominid remains from Eurasia as well as Africa, which often differ substantively one from the other, and both spatially and temporally, it is frankly best abandoned altogether.

Howell's alternative to the unsatisfactorily vague term of “archaic *Homo sapiens*” was to place fossils in paleodemes (or “p-demes”), ostensibly members of potentially interbreeding populations in very close geographic and temporal proximity (Howell, 1994, 1999). Howell recognized that some paleodemes seemed clearly more similar to one another than to others, but in these late contributions, he was quite circumspect about specifying which ones constituted bona fide species.

The multiregional view, as championed by Milford Wolpoff, of Middle to Late Pleistocene species has always been much simpler than the schemes endorsed by splitters. Wolpoff's view (e.g., Wolpoff et al. 1984; Wolpoff, 1989, 1996; Frayer et al., 1993) is that there has only been one species of *Homo* since the appearance of what most researchers would term *H. erectus*, if not from even earlier. Wolpoff and his co-authors have made clear that they certainly recognize geographic and temporal variants within the species that they consider to be the products of selection and genetic drift. Despite the existence of these variants, Wolpoff and colleagues emphasize that those variants were of less importance than the overall coherence of the species, which was maintained by gene flow throughout the entire span of the Pleistocene. Wolpoff (1996) made logical extension of this argument by designating all of the members of the species as *Homo sapiens*, with the specimens many other researchers assign to *H. erectus* designated as early *Homo sapiens*.

A potentially useful alternative to endless debates over how many species one should recognize comes from de Queiroz's (1998) insight that speciation is a process, often a long one, and that the criteria that paleobiologists use to differentiate species (e.g., statistically significant differences in the means of metrical traits despite substantial overlap, a diagnosable morphological difference, reduced fitness of hybrids, a difference in the mate recognition system, hybrid infertility, no interbreeding that produces viable offspring, no interbreeding, or the appearance of many discrete morphological and genetic differences with no overlap in polymorphisms) all merely represent different criteria that will be eventually met the further two populations move along a pathway to complete separation and divergence. It is likely that de Queiroz's model applies to human evolution during the Middle to Late Pleistocene (Pearson, 2008), and that the divergences that can be observed between populations of hominins reflect the fact that they had moved part of the way along the path of speciation (Figures 1.5 and 1.6). Studies of baboon hybridization in Africa (Jolly, 2002) caution that the million or so years that are the subject of this chapter are almost certainly too little time to produce hybrid inviability (Holliday, 2003), and the recent revelations that approximately 1–4% of the genetic heritage of people outside of sub-Saharan Africa derive

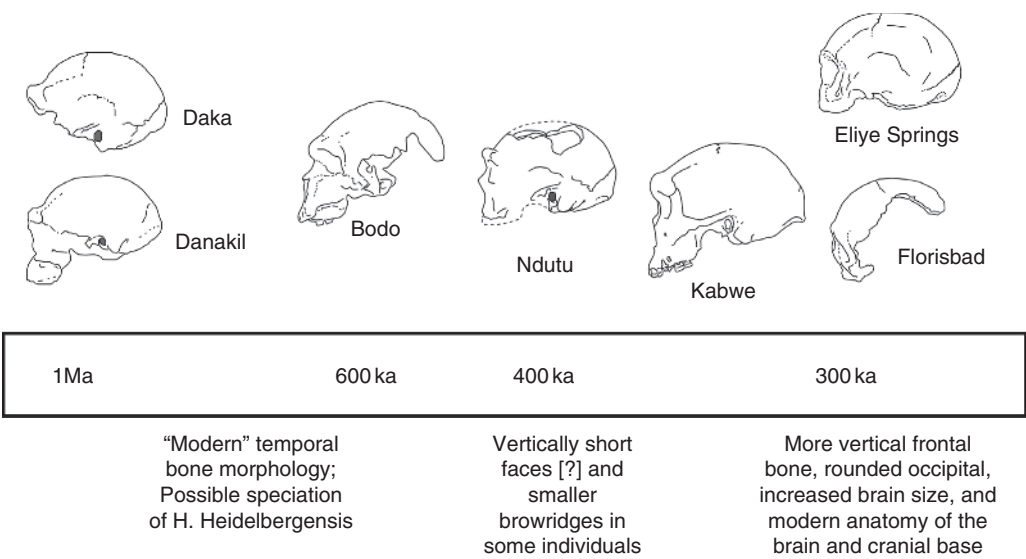


Figure 1.5. Sequence of cranial evolution in Africa, Part A (from Pearson, 2008).

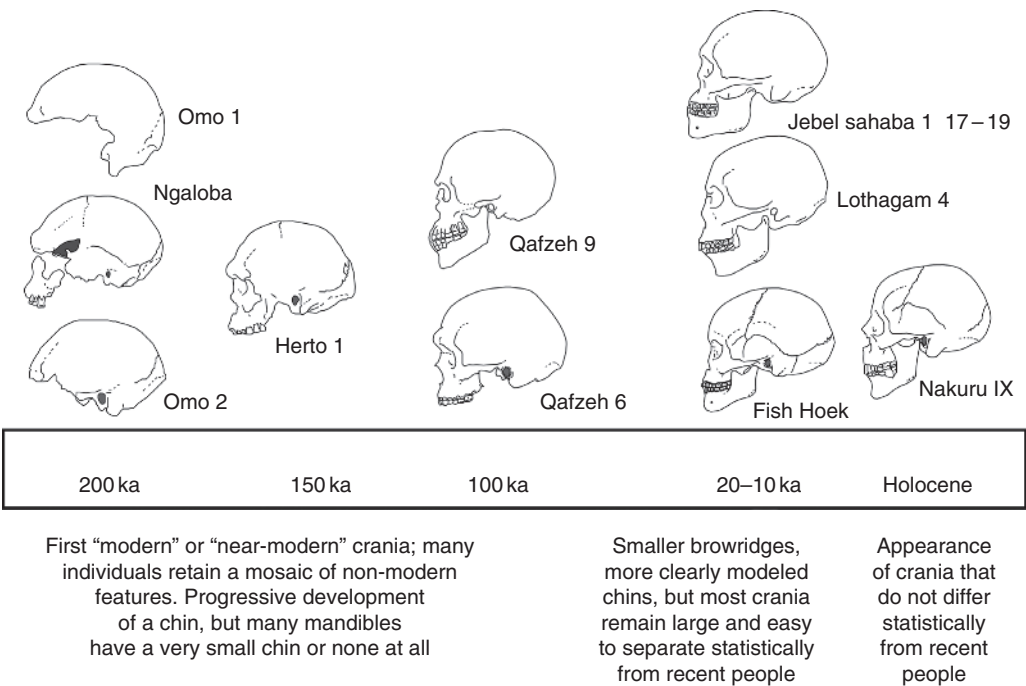


Figure 1.6. Sequence of cranial evolution in Africa, Part B (from Pearson, 2008).

from Neandertals (Green et al., 2010), and hominins like the “Denisovans” from Siberia contributed 4–8% of the genes present in Melanesians (Reich et al., 2010), indicate conclusively that interbreeding occurred at least occasionally between genetically (and almost certainly morphologically) distinct populations in the Pleistocene (Figure 1.7).

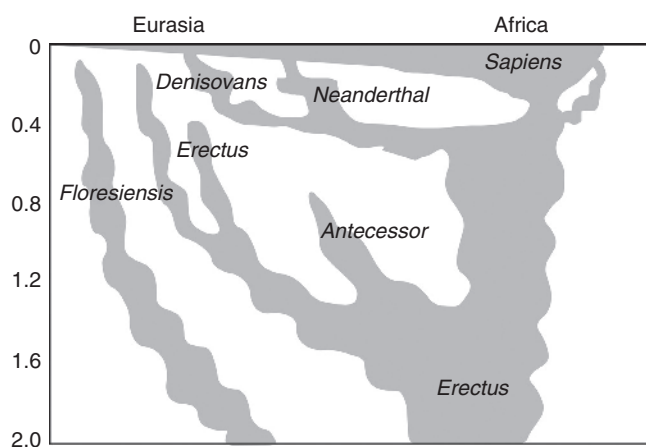


Figure 1.7. The latest phylogeny envisioned by Chris Stringer (after Stringer, 2011). The phylogeny incorporates reticulate evolution with Neandertals (Green et al., 2010), Denisovans (Reich et al., 2010), and archaic hominins within Africa (Wall et al., 2009; Hammer et al., 2011).

Acknowledgments

Thanks to Fred Smith and Jim Ahern for the invitation to contribute to this volume, to Fred Smith and Frank L'Engle Williams for comments and criticisms on a draft of the manuscript, and to my wife, Amy Farnbach Pearson, for her forbearance and encouragement as I wrote it.

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