Chapter 17

The Late Quaternary Hominins of Africa: The Skeletal Evidence from MIS 6-2

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Abstract The late Quaternary African hominin fossil record provides a tantalizing glimpse into considerable temporal and geographic morphological diversity within the genus *Homo*. A total of 50 sites that can be constrained from MIS 6-2 have yielded specimens ranging from isolated teeth to nearly complete skeletons. However, only a dozen or so provide particularly informative or interesting evidence spanning this period of nearly 200 kyr. In addition to the rather paltry nature of the record, one of the seemingly more intractable problems that bedevil its interpretation is the nature of the chronometric record for many of the sites. The Late Pleistocene terrestrial climatic record for Africa is also rather patchy, making continent-wide generalizations difficult. Attempts to link large-scale environmental perturbations in Africa to patterns of human evolution and behavior are even more problematic. Although the African fossil (and archaeological) record is most often viewed from the perspective of a single lineage culminating in the appearance of *Homo sapiens* and thence modern humans, the degree of morphological diversity evident even in this meager assemblage can be rather striking. Some of this diversity may be related to geographic and/or temporal differences, but in other instances, there are noticeable differences among remains that are contemporaneous, or at least penecontemporaneous. The Late Pleistocene African hominin fossil record, despite its manifestly incomplete nature, finds consistency with an impressive array of genetic evidence that points to an African origin for our species, and it also has consilience with genetic data that indicate a coalescence of lineages to the common ancestor of *Homo sapiens* at around the beginning of MIS 6. Although multiple lines of genetic evidence indicate a deep separation of lineages, with the ancestors of the southern African Khoesan diverging early on from that which gave rise to all other groups, there is a notable paucity of human remains that predate MIS 2 that exhibit strong phenetic resemblance to recent African populations. A number of the human dental samples from Late Pleistocene South African sites possess morphological variants that characterize the teeth of the recent inhabitants of sub-Saharan Africa, but these similarities do not necessarily signify a close evolutionary relationship with any of these populations because they appear to be plesiomorphic.

Keywords Cranium • Dentition • Postcranial skeleton • Middle Stone Age • Later Stone Age • Middle Paleolithic • Upper Paleolithic

Introduction

Stable isotope studies have provided the basis for constructing global and regional climatic scales against which the human paleontological and archaeological records can be assessed (Behrensmeyer 2006). These paleoclimatic interpretations may be based on stable carbon isotopes extracted from paleosols (Cerling and Quade 1993; Wynn 2006), or the oxygen isotope records obtained from the calcitic shells produced by marine organisms such as foraminifera (McCrea 1950; Epstein et al. 1951, 1953; Emiliani 1966). In either case, these isotope studies are based on the same basic principles of chemistry. All atoms of an element have the same number of protons (i.e., they have the same atomic number), but they may differ in their numbers of neutrons (i.e., they differ in atomic mass). Elements such as carbon have two principal, or common isotopic forms (i.e., ^{12}C or ^{13}C), whereas oxygen has three (i.e., ^{16}O, ^{17}O and ^{18}O). In each instance the isotope is identified by a superscript number, which is the sum of the number of protons and neutrons in the nucleus. The higher mass isotopes are considerably more rare in nature, such that 98.9% of stable

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carbon in the atmosphere (in the form of CO_2) consists of ^{12}C and 99.7% of oxygen consists of ^{16}O.

The mass, or weight, differences of these elemental isotopes translate to different thermodynamic and kinetic properties (Hoefs 2009). Molecules that contain the more rare (higher-mass) isotope are thermodynamically more stable and slower to react in chemical reactions as well as in physical and biological processes such as the precipitation of calcium carbonate from water, photosynthesis and digestion. In such instances, the weaker bond formed by the lighter isotope affects molecular reaction kinetics; molecules with the lighter isotope react faster (using less energy), which results in its enrichment relative to the parent isotope ratio. Thus, for example, during the process of photosynthesis ^{12}C is enriched relative to ^{13}C as a kinetic effect of the lighter isotope proceeding more rapidly through the process. The enrichment, or fractionation of one isotope relative to another is expressed as a ratio represented as delta (δ) values that represent the difference between the observed isotope ratio and that within an internationally recognized standard in parts in parts *per mille* (or *permil* = *per thousand*).

In other instances, however, the heavier isotope can become enriched, such as in the precipitation of calcium carbonate from water. In this case, because ^{18}O is two neutrons heavier than ^{16}O, the latter takes less energy to vaporize and diffuse from water, resulting in the remaining water being enriched in ^{18}O. Because the physical process of evaporation results in an enrichment of ^{16}O relative to ^{18}O in atmospheric water vapor (hence rain and snow), and a concomitant increase of ^{18}O water, any precipitate from the water will be relatively enriched in the heavier ^{18}O. Since this process is temperature dependent, the changes in the light isotope ratios of oxygen can be used to determine the temperature of the water in which the precipitation of calcium carbonate occurred (Urey 1947). Thus, increased temperature results in progressively higher $^{18}O/^{16}O$ ratios in marine carbonate precipitates (Dansgaard 1964). This is the basis for the reconstruction of oceanic paleotemperatures and the recognition of oxygen isotope stages (OIS) or marine isotope stages (MIS) from the analyses of shells secreted by marine organisms (McCrea 1950; Epstein et al. 1951, 1953; Emiliani 1955, 1966).

Oxygen isotope ($\delta^{18}O_{calcite}$) records obtained from planktonic foraminifera from deep-sea cores in the Caribbean Sea and the Atlantic and Pacific Oceans revealed a cyclic temporal pattern that enabled Emiliani (1955) to recognize seven most recent climatic (paleotemperature) cycles or stages. He numbered these from the most recent (Holocene) downwards, with the odd-numbered stages representing warm periods (interglacial intervals) and the even-numbered designating cold episodes (glacial intervals). A decade later, Shackleton (1967) provided evidence that this $\delta^{18}O$ record is dominated by oceanic changes related to ice-sheet volume. Hence, Emiliani's oxygen isotope stages (OIS) are now widely referred to as Marine Isotope Stages (MIS). Importantly, Shackleton (1967) also observed that this record could be employed to construct a global stratigraphic framework for marine sediments. Since these pioneering studies, considerable advances have been made in refining the $\delta^{18}O$-based temporal/climatic record, providing an increasingly accurate geochronological calibration extending back several Ma, and the identification of short-term (i.e., c. 1 kyr), high-resolution and high-frequency Dansgaard-Oeschger events in the Pleistocene.[1] The isotope record has been extended to astronomically based models of orbital insolation and precession, resulting in the radiometrically calibrated spectral mapping project (SPECMAP) $\delta^{18}O$ record (Hays et al. 1976; Imbrie et al. 1984; Bond et al. 1993; Cramp and O'Sullivan 1999; Thompson and Goldstein 2006; Imbrie and McIntyre 2006).

Over one hundred marine isotope stages have been identified extending into the Miocene, but the most thoroughly documented and well-dated cover the latter half of the Quaternary (Imbrie et al. 1984, 1993; Martinson et al. 1987; Williams et al. 1988; Bassinot et al. 1994; Shackleton et al. 1990; Aitken and Stokes 1997; Andrews 2000; Wright 2000; Tzedakis 2003; Landais et al. 2004; Lisiecki and Raymo 2005; Lang and Wolff 2011). A number of studies have compiled stacked records from various sources and have used these data to refine the SPECMAP dates initially identified by Imbrie et al. (1984) for the isotope stages extending over the past 500 ka or beyond (Table 17.1). For example, the duration of the peak of the last Interglaciation (MIS 5e) has been determined between 124 and 111 ka by Martinson et al. (1987), 122 and 106 ka by Bassinot et al. (1994), and 130 and 119 ka by Hearty et al. (2007). The latter range comfortably accommodates the MIS 5e peak dates of 122 and 123 ka proposed by Wright (2000) and Lisiecki and Raymo (2005). For the most parts, such modifications have resulted in differences among various age determinations that are on the order of about 2%.

The marine paleotemperature signatures of the MISs and their dates of their onset over the past 0.3 Ma are provided in Fig. 17.1. The dates employed here to define stage boundaries are those of Lisiecki and Raymo (2005).

Marine records also have been interpreted in relation to Quaternary environmental changes in Africa (Hilgren 1991; deMenocal 1995, 2004; Camp and O'Sullivan 1999;

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[1] Since the mid-1980s, the lower boundary of the Pleistocene Epoch (i.e., the beginning of the Quaternary Period) has been regarded as corresponding with the base of the Calabrian stratotype at 1.81 Ma. Recently, however, the International Union of Geological Sciences has recognized the base of the Gelasian stratotype, which corresponds to the Matuyama (C2r) chronozone, or the Gauss-Matuyama boundary, as defining the Pliocene-Pleistocene boundary at 2.588 Ma (Gibbard and Head 2009). This change is significant for discussions of hominin paleontology. Pending the outcome of appeals to this ruling, I continue to regard the base of the Pleistocene at 1.81 Ma.

Table 17.1 Dates (ka) determined for the onset of Mid-Late Pleistocene MIS stages by different workers

MIS	Stage					
	A	B	C	D	E	F
MIS 1	12	12	11	11	12	14
MIS 2	24	24	24	24	24	29
MIS 3	59	59	57	60	59	57
MIS 4	71	74	71	71	71	71
MIS 5a	80	79	79	79	82*	82*
MIS 5b	87	91	86	–	–	87*
MIS 5c	99	99	97	–	105*	96*
MIS 5d	107	111	106	–	–	109*
MIS 5e	122	124	122	–	122*	123*
MIS 5	128	139	127	130	128	130
MIS 6	(186)	190	186	190	186	191
MIS 7	(245)	244	242	244	245	243
MIS 8	(303)	–	301	301	303	300
MIS 9	(339)	–	334	334	339	337
MIS 10	362	–	364	364	362	374
MIS 11	(423)	–	427	427	423	424
MIS 12	(478)	–	474	474	478	478

Sources: *A* Imbrie et al. (1984: Table 6) SPECMAP with ages in parentheses interpolated between adjacent ages with reference to the stratigraphic level of the corresponding event in core V28-238; *B* Martinson et al. (1987: Table 2); *C* Bassinot et al. (1994: Table 4); *D* Aitken and Stokes (1997: Table 1.2); *E* Wright (2000: Fig. 4); *F* Lisieck and Raymo (2005)

*Dates are for the *peaks* of the MIS 5 substages; the other dates for MIS substages represent their onset

deMenocal et al. 2000; Schefuß et al. 2003, 2005; Weldeab et al. 2005; Adkins et al. 2006; Kröpelin et al. 2008). Undoubtedly, oceanic temperatures in the Northern Hemisphere affect the Southern Hemisphere as well (Crowley 1992), where reduced North Atlantic temperatures weaken African monsoonal circulation and tend to reduce rainfall. However, changes in Southern Hemisphere temperatures may precede changes in Northern Hemisphere ice volume, and although oceanic patterns are generally confirmed by terrestrial records, there are differences between them with regard to aspects of timing and intensity (Partridge et al. 1997; deMenocal et al. 2000; Drake and Bristow 2006; Armitage et al. 2007; Trauth et al. 2003, 2005, 2007).

While considerable attention has been paid to developing detailed terrestrial records in Europe (e.g., van Andel and Tzedakis 1996; Tzedakis et al. 1997; Watts et al. 2000; Voelker et al. 2002), there are comparatively few detailed terrestrial records for Africa (e.g., Pokras and Mix 1985; Stokes et al. 1997; Gasse 2000; Salzmann et al. 2002; Thomas and Shaw 2002; Zhao et al. 2003; Tierney et al. 2008, 2011; Bruch et al. 2012; Scholz et al. 2007, 2011). As noted by Tryon et al. (2010), we have, at best, an incomplete understanding of the spatial and temporal patterns of climatic change in Pleistocene Africa. Indeed, noticeable differences have been recorded for terrestrial responses within Africa even for very recent periods of time.

Thus, for example, the terminal Pleistocene to early Holocene "African Humid Period" (AHP) saw abundant North and East African lakes that were much higher than present; whereas lakes in South Africa stood at considerably lower levels (Hoelzmann et al. 2002; Schefuß et al. 2005; Weldeab et al. 2005; Kuper and Kröpelin 2006; Tierney et al. 2011). Additional evidence for time-transgressive terrestrial changes in the AHP has been documented even *within* the Sahara (e.g., deMenocal et al. 2000; Kuper and Kröpelin 2006; Cole et al. 2009), as well as between northern and southern Africa (Gasse 2000).

Moreover, while Trauth et al. (2003) claim that the MIS 6/5 boundary ("Termination II") is roughly synchronous across Africa, their own data (Trauth et al. 2003: Fig. 4) suggest otherwise. Furthermore, the data presented by Scholz et al. (2007) and Cohen et al. (2007) demonstrate multiple episodes of extreme hyperaridity in the Late Pleistocene, but that Lakes Malawi and Tanganyika experienced "mega-drought" conditions out of phase with the arid intervals elsewhere in the eastern Rift Valley system let alone sub-Saharan Africa. These differences suggest that climate changes within different areas of continental sub-regions (e.g., East Africa) were out of phase. Such discrepancies would have resulted in different parts of the same sub-region experiencing very different climate regimes.

This renders continent-wide generalization difficult if not perilous (Mitchell 2008; Chase 2010; Marean 2010). Scenarios that attempt to link large-scale environmental perturbations in Africa to patterns of human evolution and behavior (e.g., Scholz et al. 2007; Blome et al. 2012; Thomas and Burrough 2012; Ziegler et al. 2013) are even more problematic.

The hominin fossil record for the late Quaternary – especially the latter part of the Pleistocene – provides a tantalizing glimpse into considerable morphological diversity, temporally and geographically, within the genus *Homo*. Some of this almost certainly translates to potential lineage splitting and attendant taxonomic diversity. Considerable heed has been paid to the morphological and/or molecular evidence for later Pleistocene lineages in Eurasia, such as our relationships with *H. neanderthalensis* (e.g., Ponce de León and Zollikofer 2001; Harvati et al. 2004; Green et al. 2008, 2010; Noonan et al. 2006; Gunz et al. 2010; Hodgson et al. 2010; Currat and Excoffier 2011; Lalueza-Fox and Gilbert 2011) and the "Denisovans" (e.g., Krause et al. 2010; Reich et al. 2010, 2011; Meyer et al. 2012; Sawyer et al. 2015). Attention has been directed also to Southeast Asia in relation to the existence of late surviving *H. erectus* (Yokoyama et al. 2008; Indriati et al. 2011) and *H. floresiensis* (Brown et al. 2004; Aiello 2010).

By comparison, however, relatively little attention has been directed toward the morphological diversity that is evident within Africa in the later Pleistocene and Holocene (Manica et al. 2007; Crevecoeur et al. 2009; Gunz et al.

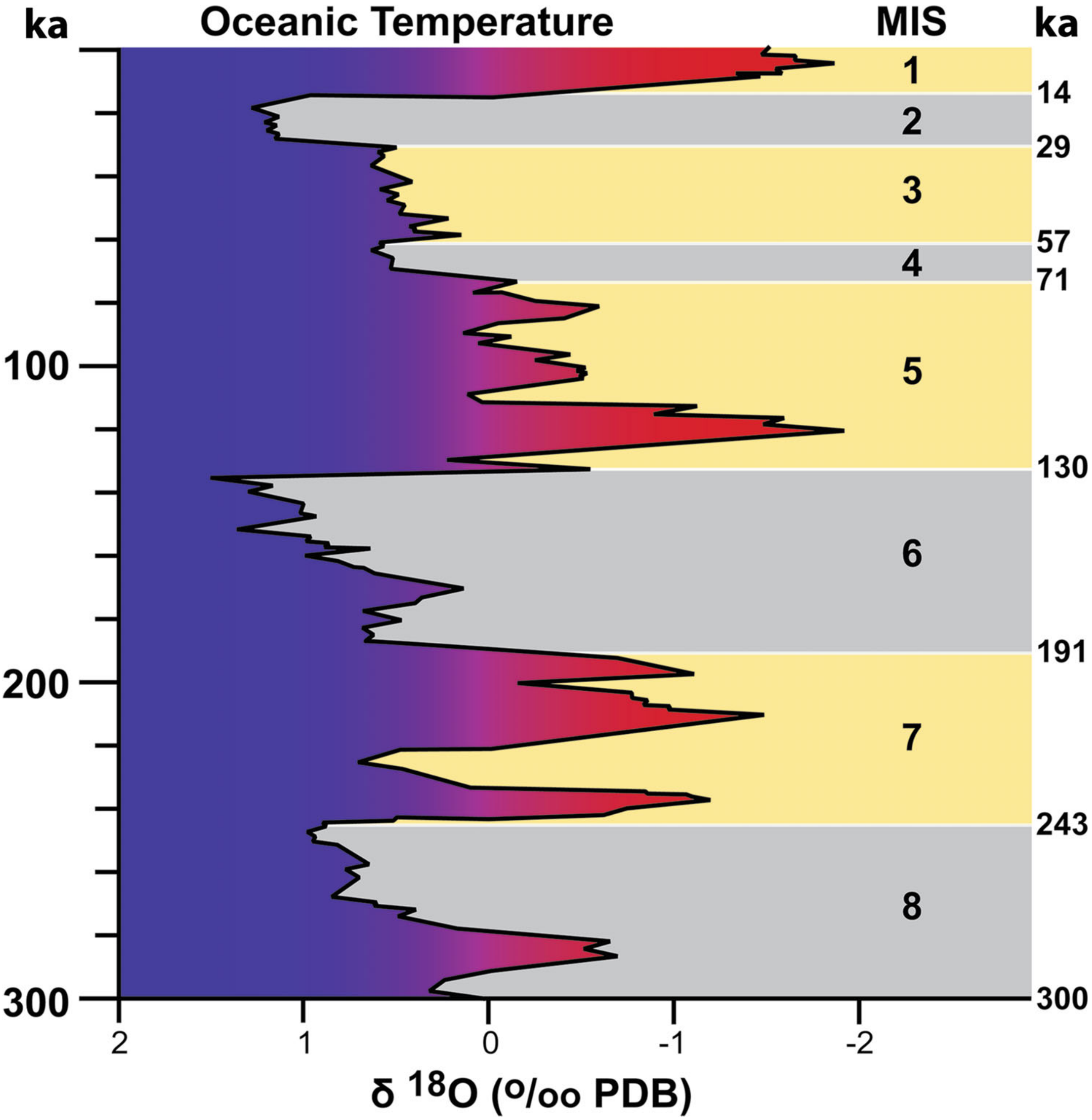

Fig. 17.1 Marine paleotemperature signatures reflecting global ice volume compiled from stacked oxygen isotope records of benthic foraminifera from deep-sea cores over the past 300 kyr. The $\delta^{18}O$ record reflects variation in parts *per mille* from the global reference standard (Vienna PeeDee Belemnite [VPDB]), which was obtained initially from the calcitic internal rostrums of the Cretaceous cephalopod, *Belemnitella*, preserved in the PeeDee Formation marine limestone of South Carolina (PDB). This has since been recalibrated by a laboratory in Vienna to the original sample (Coplen 1988, 1996). The standard is defined as zero (0‰). The other standard for oxygen ($^{18}O/^{16}O$) is Vienna Standard Mean Ocean Water (VSMOW), although this is somewhat of a misnomer since it now refers to pure water rather than the original seawater standard (Coplen 1988, 1996). PDB rather than VSMOW is used as the standard in this instance because the oxygen isotope data for benthic foramina derive from the calcium carbonate of their shells. The isotope plot and its relationship to the marine isotope stages is adapted from Martinson et al. (1987: Fig. 18), Porter (1989: Fig. 1), Kennett et al. (2000: Fig. 4) and Crosta and Shemesh (2002: Fig. 5). It is based upon data from an equatorial Pacific Core (V19-30) reported by Shackleton and Pisias (1985). The dates that correspond to the MIS stage boundaries are those of Lisiecki and Raymo (2005)

2009; Harvati et al. 2011). Rather, the African fossil (and archaeological) record is most commonly viewed from the perspective of a single lineage culminating in the appearance of *Homo sapiens* and thence modern humans (e.g., Bräuer 1984b, 2008; Smith 2002; Stringer 2002; Rightmire 2008, 2009; Pearson 2011). Thus, hominin fossils that date to perhaps 700–400 ka from sites such as Kabwe (Broken Hill), Elandsfontein, Bodo, Ndutu, Olduvai Gorge (OH 11), and Garba III (Melka Kunturé) have been viewed as representing a form that is related to us through a morphologically more derived intermediate. The latter is held to be represented by specimens such as the cranium from Florisbad.

This scheme remains the dominant one by which human evolution in Africa is interpreted, even if the names and hypodigms accorded these "grades" or "stages" differ somewhat among workers (e.g., Bräuer 1989a, 1992, 2008; Foley and Lahr 1997; Rightmire 1998, 2001, 2008, 2009; Kuman et al. 1999; McBrearty and Brooks 2000; Haile-Selassie et al. 2004). Some view these more "archaic" forms as representing separate species, with *Homo rhodesiensis* (or, arguably, *H. heidelbergensis*) being the appellation for the earlier, and *Homo helmei* the preferred name for the latter. Others view them as "grades" of *Homo sapiens* (i.e., "early archaic" *H. sapiens*, and "late archaic" or "pre-modern" *H. sapiens*). Regardless of the names that are applied, they are still viewed as representing "stages" of morphological evolution in a lineage leading inextricably to anatomically modern humans.

Fossils that are universally (or at least almost universally) recognized as being attributable to *Homo sapiens* – as defined by the possession of a number of morphological apomorphies that we see in ourselves – appear for the first time in Africa in the temporal span between MIS 7 and MIS 6, on the order of some 200 ka (Weaver 2012). However, at this time, as subsequently in the Pleistocene, the degree of morphological variation can be rather striking, and its significance continues to be a subject of discussion (e.g., Stringer 2007; Hammer et al. 2011).

One of the seemingly more intractable problems that bedevils the rigorous analysis and interpretation of the fossil evidence relating to the origin of *Homo sapiens* and the emergence of fully anatomically modern human morphology in Africa in the Late Pleistocene is the nature of the chronometric record for many of the potentially more interesting specimens (Millard 2008).

Despite various attempts to provide absolute ages for many African fossils that extend from MIS 6-2, a number of these have been dated solely by notoriously fallible techniques, such as the application of electron spin resonance (ESR) to mammalian tooth enamel (e.g., Grün 2006). ESR is problematic because variables such as background dose rate and sediment moisture history must be known or assumed; open systems (such as tooth enamel) only compound these troubles. Depending upon the uranium uptake model that is preferred (often preferred for less than compelling scientific reasons), just about any "date" is feasible. Indeed, Zhao et al. (2001) found significant differences in U-series dates obtained from speleothems and tooth enamel samples, indicating that uranium uptake history is "far more complex than existing models can handle." They cautioned that great care must be taken in the interpretation of ESR "dates" for fossil teeth. Similarly, Grine et al. (2012) have observed that dating studies based on ESR of tooth enamel from the South African Early Pleistocene karst cave site of Swartkrans have produced a bizarre range of age estimates: 4.38 Ma–36 ka. Another example of the malleability of ESR dating of more proximate interest relates to the age determinations that were made on two parts of a single bovid tooth excavated from adjacent stratigraphic levels (4–5 and 6) at the Late Pleistocene site of Die Kelders, South Africa. The initial assessment found these two conjoining pieces to be separated by ~10 kyr in a site that likely dates to only ~70 ka (Avery et al. 1997), but subsequent reanalysis found them to have identical Early Uptake and Linear Uptake ages (Schwarcz and Rink 2000).

Unfortunately, the validity of dates obtained by alternative methods, such as U-series analyses of open systems (e.g., vertebrate bone, dentine, and enamel), may be problematic (Hinz and Kohn 2010). Finally, the dates obtained by optically stimulated luminescence (OSL) of sediment particles of unknown moisture history are clearly open to question (Guérin et al. 2013; Tribolo et al. 2013). It is lamentable that many (if not most) of the Late Pleistocene sites and fossils of Africa owe their geochronological placement to such questionable and sometimes seemingly idiosyncratic methods. As a result, the ages of many of these fossils are loosely constrained, and this may render a number of evolutionary scenarios suspect. This imprecision necessarily complicates attempts to deduce possible relationships among demographic, cultural, morphological, and climatic variables.

The Late Pleistocene African human fossils that are reasonably constrained between MIS 6-2 are reviewed here (Table 17.2). A total of 50 sites that can be attributed to this interval have yielded hominin remains, ranging from isolated teeth to nearly complete skeletons. While this number might seem rather impressive, only a dozen or so have provided particularly informative or interesting specimens.

In this review, the sites and/or specimens are grouped geochronologically, insofar as possible, in relation to the marine isotope stages to which they pertain. For a number of

Table 17.2 African hominin-bearing sites dating from MIS 6 through MIS 2

Within MIS	Site/specimen	Site sge (ka)	Human remains
7–6	Omo (Kibish Fm.)	195	**Cranium; fragmentary skull and partial postcranial skeleton**
7–6	Kébibat	200–130	Skull fragments
6	Twin Rivers	178–139	Humerus fragment
6	Mumbwa Caves	172	Two teeth; two radius fragments; possible femoral diaphysis
6	Jebel Irhoud	160	**Two crania, juvenile mandible; fragmentary postcrania**
6	Herto	160–150	**Cranium; fragmentary cranial remains of five individuals**
6	Singa	145–133	**Calvaria**
6–3	Border Cave	170–56	Postcranial fragments
5e	Ngaloba Beds	129	**Cranium**
5e	Blind River	124–112	Femur
5e–4	Klasies River	115–58	**Multiple cranial, mandibular and postcranial fragments**
5e–5a	Sea Harvest	110–71	Manual distal phalanx; tooth
5d–5c	Grotte des Contrebandiers	110–92	Cranial fragments
5e–5c	Dar es-Soltan II	125–92*	**Incomplete skull; cranial fragments**
5c	Eyasi	104–92	**Partial cranium; mandibles; cranial fragments; teeth**
5c–3	Equus Cave	103–30	Eight teeth
5c–5a	Aduma	105–80	**Cranium; cranial fragments**
6–5c	Pinnacle Point	162–90	Parietal; tooth
5c–5a	Blombos	102–70	Nine teeth
5c–3	Ysterfontein 1	130–50	Three teeth
5c–3	Witkrans	100–50	Three teeth
5a–4	Plovers Lake	89–62	Postcranial fragments
5a	Haua Fteah	80–68	Two mandibular fragments
5a	Mumba Shelter	78–60	Teeth
4–3	Porc-Épic	78–36	Mandibular fragment
4	Die Kelders	74–59	24 teeth; mandibular fragment; 2 phalanges
4	Klipdrift Shelter	72–52	Isolated tooth
3	Sibudu	77–38	Phalanx; distal fibula
3	Diepkloof	61–48	Two toe bones; tooth
3	Mugharet el 'Aliya	57–27	Juvenile maxilla; isolated teeth
3	Nyamita	55–45	Partial humerus
3	Magubike Rock Shelter	42	Six isolated teeth
3	Nazlet Khater	38	**Skulls and postcranial skeletons**
3	Hofmeyr	36	**Cranium**
3	El Harhoura I	41–26	Mandible; isolated tooth
2	Ishango 11	26–20	Fragmentary crania and postcrania
2	Taramsa 1	70–24	Child skeleton
2	Leopard's Hill Cave	24–21	Isolated parietal
2	Lukenya Hill	24–22	**Partial calotte**
2	Tuinplaas	<20–11	Skull and partial postcranial skeleton
2	Deir El-Fakhuri (E71K1)	18	Two partial skeletons
2	Taza Cave I	16–14	Skull
2	Afalou-bou-Rhummel	15–11	**63 partial crania and skeletons**
2	Gebel Silsila 2A	14–13	Isolated frontal bone
2	Jebel Sahaba (117)	14–12	**58 partial skeletons**
2	Wadi Halfa (6B28 & 6B36)	14–10	Mandible (6B28); 37 partial skeletons (6B36)
2	Ifri n'Baroud	17–11	Single postcranial skeleton
2	Bushman Rock Shelter	13–12	Single infant mandible
2	Mlambalasi Rock Shelter	13–12	Partial postcranial skeleton (? *in situ*)
2	Grotte des Pigeons (Taforalt)	13–11	**200 skeletons**
2	Iwo Eleru	13–11	Incomplete skeleton and calvaria

The age ranges provided for a site are the maximum and minimum estimates for the site and do not include the confidence intervals for individual sample averages. The age ranges for the human specimens in a site when they do not extend throughout the thickness of the deposit, but are rather restricted to specific dated horizons within the site, are recorded in Tables 17.3, 17.4, 17.5 and 17.6. See text for details. The more significant specimens are designated in boldface type

*The Aterian- and hominin-bearing strata at Dar es-Soltan II have not been directly dated; these estimates are those that have been reported for the Aterian at proximate localities. The older date is likely too old; the range is more likely 107–96 ka sites, the hominin fossil-bearing strata may overlap two (or more) isotope stages. In other instances, the stratigraphic derivation of the fossils is unclear, such that it is not possible to assign a given specimen to a particular MIS with certainty. In these cases, I have referred the sites and/or fossils to the geochronologically oldest possible stage simply for purposes of organization. Thus, it should be stressed that the order of appearance of the sites on the pages that follow does not necessarily imply their strict geochronological seriation.

Human Specimens Not Considered: The Undated and the Redated

A number of human specimens that have been regarded at one time or another as being of Late Pleistocene age are not considered here. These specimens fall into one of two categories that serve to exclude them from consideration. The first comprises those that are undated, but have been thought to date to the Late Pleistocene on less than adequate morphological criteria or on highly questionable geochronological evidence. The second category consists of specimens that were once thought to be related to the Middle Stone Age (MSA), but are demonstrably Holocene in age. It is reasonable to briefly discuss these specimens insofar as all have been regarded at one time or another as relevant to discussions of Late Pleistocene human evolution in Africa.

Specimens that May or May Not Be Relevant: The Undated

Specimens that comprise this category are the calvaria from Oranjemund, Namibia; Boskop, South Africa; Eliye Springs, Kenya, and the KNM-ER 999 femur and KNM-ER 3884 cranium from Ileret, Kenya. In addition, the sites of Mumbwa Caves, Zambia and Lukenya Hill, Kenya contain human bones for which radiocarbon and/or amino acid racemization dates pertaining to MIS 2 have been reported (Protsch 1975, 1977). Unfortunately, the veracity of these age determinations is extremely doubtful; the human remains could well relate to the Holocene. However, the Mumbwa Caves also preserve human specimens associated with the MSA that likely relate to MIS 6.

Oranjemund, Namibia

The Oranjemund calotte was found in 1988 on the beach between the Orange River and the Atlantic Ocean (28°36′ S, 16°26′ E) following an exceptional flood (Senut et al. 2000). Although Senut et al. (2000) acknowledge that the specimen is “difficult to date, having been found out of its geological context,” they opine that it likely originated from an undated black clay horizon that outcrops along the banks of the river approximately 100 m away. The “main evidence” presented concerning the calotte’s age is its morphology, which was said to “compare well with other African archaic sapients [sic] aged between 100,000 and 50,000 years” (Senut et al. 2000: 813). However, this assessment is based on comparisons of measurements of overall cranial size for three recent human population samples and of several frontal bone dimensions with fossils from Ngaloba (Tanzania), Florisbad (South Africa), and Zuttiyeh (Israel). In no instance do the cranial metrics align the Oranjemund specimen with fossils dated to c. 100–50 ka in preference to recent humans. Moreover, the Oranjemund calotte evinces no morphology than can be regarded as archaic. Its noticeably separate medial superciliary eminence and lateral supraorbital trigone do not, contrary to Senut et al. (2000), constitute a “well-marked supraorbital torus,” but rather define a fully modern configuration.

Boskop, South Africa

The Boskop calotte was recovered in 1913 by workers digging a trench on a farm along the banks of the Mooi River in Gauteng Province, South Africa. The specimen was found at a shallow depth in disturbed riverine sediments (Haughton 1917). Subsequent finds included a mandibular fragment, a temporal bone, and parts of a poorly preserved skeleton. The specimen was initially thought to be of considerable antiquity, and was believed to be associated with the MSA on the basis of a single artifact reported to have come from the same site (van Riet Lowe 1954). Wells (1952) intimated this when he wrote that although the precise antiquity of the cranium had not been established, “there is now good evidence that the skull was derived from a Middle Stone Age horizon.” Broom (1918) proposed that Boskop represented a distinct species, *Homo capensis*, which he diagnosed primarily on the basis of a poorly preserved fragment of mandibular corpus. However, with the possible exception of its comparatively large endocranial cavity, the specimen preserves no morphology that can be considered unusual for modern humans; indeed, a number of studies have concluded that Boskop (though perhaps suggestive of a distinct “physical type” to some) has discernible features in common with the recent Khoe-San (e.g., Broom 1923; Pycraft 1925; Wells 1959). The lack of any solid geological or archaeological context for these remains, and the fact that other animal bones from the same deposits were judged to have been secondarily redeposited by fluvial action (Haughton 1917) suggest that Boskop is best regarded as undated.

Eliye Springs, Kenya

The heavily mineralized human calvaria from Eliye Springs has featured prominently in discussions of the Middle to Late Pleistocene hominin fossil record, although it is wholly undated. The cranium lacks any primary geological context, having been discovered in 1985 by two German tourists who were "beach combing" along the western shore of Lake Turkana near the Eliye Springs resort (Bräuer and Leakey 1986a, b). Immediate investigation of the site by R.E. Leakey revealed that the specimen was unlikely to have been found in primary context, but rather to have been reworked by wave action from sediments that outcrop nearby. A few isolated faunal remains which exhibit the same heavily mineralization as the hominin cranium were collected in the immediate vicinity, but they provide no evidence of antiquity.

Although the calvaria from Eliye Springs lacks an absolute geochronological date, its morphological resemblance (or lack thereof) to other African specimens has led some workers to associate it with a date. Thus, in their initial assessment, Bräuer and Leakey (1986a: 251) concluded that because the cranium "exhibits clear relations to archaic *Homo sapiens* – in particular to the later representatives, i.e., to late archaic *Homo sapiens* – a late Middle to early Upper [sic] Pleistocene age for this hominid is a very probable assumption." This age was taken to encompass a span between 200 and 100 ka (Bräuer and Leakey 1986a, b), as illustrated by Bräuer (1989b: Fig. 8.2). Subsequently, Bräuer et al. (2003: 200) revised its presumed age. They concluded that "based on the morphological similarities to absolutely dated archaic *Homo sapiens* specimens, an age of about 200,000–300,000 years can be assumed for the Eliye Springs hominid." This range was expanded when Bräuer et al. (2004: 114) wrote, "comparisons of the cranium have shown close affinities to later Middle Pleistocene archaic *H. sapiens*, which, according to recent dating, might have existed between 300,000 and 150,000 years BP." Four years later, however, it was cited as having an age between Omo II at c. 200 ka and Florisbad at c. 260 ka (Bräuer 2008). In an interesting turn of phrase relating to its age, Bräuer (2008: 25) stated, "although it is not as well dated [as KNM-ER 3884, LH 18 and Florisbad], the cranium from Eliye Springs…might also belong to this group based on its combination of archaic and derived conditions." Thus, in the space of just over two decades, this cranium transmogrified from an unprovenanced and undated fossil to one with a rather secure placement between 260 and 200 ka. This was achieved wholly on the basis of morphological comparisons. As such, the use of this "date," or of the earlier date of 200–100 ka, as by Senut et al. (2000) in their assessment of the Oranjemund calvaria, in any discussion of human evolution in Africa is wholly circular.

Ileret, Kenya

Two hominin specimens of potential relevance from Ileret, Kenya also fall into the category of being poorly constrained geochronologically. These are the KNM-ER 999 femur and KNM-ER 3884 cranium. Although they are bracketed by age constraints, the brackets are so broad as to render the estimates of little meaning.

The KNM-ER 999 femur is essentially modern in appearance, with a high neck-shaft angle and a pronounced linea aspera (Day and Leakey 1974; Trinkaus 1993). Indeed, Trinkaus (1993) drew favorable comparisons between it and early *Homo sapiens* femora from Skhul and Qafzeh, noting that this pilastric configuration is unknown in the femora of archaic members of the genus. KNM-ER 999 was recovered in 1971 on the surface in locality 6A at Ileret, and was considered to have eroded from a horizon originally described as comprising part of the Guomde Formation (Bowen and Vondra 1973). These strata are now assigned to the Chari Member of the Koobi Fora Formation (Brown and Feibel 1986).

The KNM-ER 3884 cranium seems to evince a mixture of archaic morphology (e.g., a relatively receding frontal with a supraorbital region described as "torus-like") with more derived features such as a rounded occipital bone (Bräuer et al. 1992b; Bräuer 2001). KNM-ER 3884 was discovered in 1976 in Area 5 at Ileret. Most of the pieces were recovered from the surface, although some parts were excavated *in situ* from sediments also initially described as comprising part of the Guomde Formation. These too are now assigned to the Chari Member.

The strata from which these two fossils derive are some 8–10 m (or less) above the Chari Tuff, which defines the base of the Chari Member of the Koobi Fora Formation. The Chari Tuff is equivalent to Tuff L of the Shungura Formation, dated by ^{40}Ar/^{39}Ar to 1.38 Ma (McDougall and Brown 2006). The Chari Member extends to the base of the Holocene Galana Boi Beds. Unfortunately, the Chari stratigraphy remains one of the least well understood of any member of the Koobi Fora Formation because its lithological facies are extremely localized (Gathogo and Brown 2006). The fossils do not derive from the Holocene Galana Boi Formation because the sediments do not contain equivalent mollusk shells, and it is not certain where the sediments from which KNM-ER 999 and KNM-ER 3884 derived should be placed within that member – that is, between 1.38 Ma and 10 ka (Feibel personal communication). An iron manganese oxide cemented shell bed that lies above the *probable* hominin-bearing level is probably equivalent to the "orange and black stained bivalve packed bed" described by Gathogo and Brown (2006); if this is so, then the hominin fossils lie above the Silbo and Kale Tuffs, which would suggest an age of less than 0.75 Ma

(McDougall and Brown 2006). The strata from which these specimens came were tilted to the west and eroded before deposition of the overlying sediments of the Galana Boi Formation (Brown personal communication).

In the Omo-Turkana Basin, there are few exposures of strata that can be assigned to the time interval between the Galana Boi Formation and the upper part of the Chari Member of the Koobi Fora Formation. The best known of these is the Kibish Formation in southern Ethiopia, which ranges in age from 200 to ~6.5 ka (Brown and Fuller 2008). Although the Kibish Formation strata are separated from the Ileret region by some 125 km, it is perhaps noteworthy that they have not been structurally deformed and are still flat lying. This might be taken as evidence that the deformation that affects the Chari Member predates the Kibish Formation, and the fossils from the upper part of the Chari Member are greater than 200 ka (Brown personal communication).

Bräuer et al. (1997) reported direct U-series for KNM-ER 3884 and KNM-ER 999; the two cranial samples provided U-Th dates of 279 and 272 ka with minimum ages of 160 ka, and the single femoral sample yielded a U-Th age of 301 ka with a minimum of 205 ka. The U-Pa determinations for all three samples provided ages in excess of 180 ka. However, the older confidence limit for the U-Th estimates includes infinity, thus extending the method beyond its actual limits. The U-series estimates provided by Bräuer et al. (1997) accord with their stratigraphic derivation above the Silbo Tuff, and with their derivation from tilted strata. It is likely that they are between 750 and 200 ka. At present, It is not possible to place these specimens more precisely than this and, in any case, they are very likely beyond the geochronological scope of this contribution.

Specimens Once Thought to Be Relevant: The Redated

The second category of human remains excluded from consideration here includes those from South African sites such as Peers Cave, Cape Flats, and Canteen Kopje. The South African sites of Tuinplaas and Bushman Rock Shelter once considered to be of considerable antiquity have also been redated, and while both may ultimately prove to date to the Holocene, they are here (tentatively) attributed to MIS 2.

The Peers Cave rock shelter, also known by the name Skildergat, is located near the town of Fish Hoek on the Cape Peninsula of South Africa. It was the subject of a series of excavations by V.P. and B. Peers in the late 1920s. They uncovered a number of human skeletons of clear LSA origin, and one specimen (Fish Hoek 1, or Peers Cave 4) described as coming from the late MSA levels (Peers and Goodwin 1953). An uncalibrated conventional radiocarbon date of some 36.0 ^{14}C kBP was obtained for charcoal that lay beneath the burial (Anthony 1967; Vogel and Beaumont 1972), and Protsch (1974) reported a date of 35.0 ^{14}C kBP for bone from the level from which the human skeleton was believed to have derived. As a result, the specimen has featured in several studies as an example of Late Pleistocene human morphology (e.g., Rightmire 1978; van Vark 1984; Bräuer and Rosing 1989). However, a recent AMS assessment of the Peers Cave 4 cranium itself found that it actually dates to only 7,457–7,145 ^{14}C BP (Stynder et al. 2009).

In 1929, a human cranium and femoral fragment were found eroding from a sand dune in Philippi (the Cape Flats), near Cape Town. Drennan (1929) described this specimen as having "Australoid" affinities, and argued that the stone artifacts found eroding out with the bones attested to their MSA derivation. At the same time, however, Goodwin (1929) noted that these artifacts appeared to be a mixture of MSA (i.e., Still Bay) and LSA (i.e., Wilton) lithics and that "no valid proof" of the association of the MSA with the cranium was available. Nevertheless, Drennan (1929) persisted in reasoning that "in the light of the evidence afforded by the bones themselves it is difficult to escape the conclusion that this individual represents one of the human links between Mousterian and modern man." In particular, Drennan was struck by the relatively low, receding frontal – "it is not an exaggeration to describe the forehead as 'Neanderthaloid'" (1929: 422) – as attesting to its antiquity and its physical difference from the crania of the recent inhabitants of southern Africa. Drennan's assessment of the specimen's morphology and antiquity worked its way into the literature, with some workers accepting its morphological distinctiveness (e.g., Wells 1952, 1959). Although other workers expressed doubts about Drennan's assessment of the cranium's morphology (e.g., Brothwell 1963) or its MSA association (Klein 1970), some (e.g., Lahr 1996) have persisted in referring to its "late Pleistocene" age, despite Singer's (1993) observation that the specimen has been radiocarbon dated to 150 ± 60 ^{14}C BP. It is particularly interesting to note the emphasis that Drennan (1929) had placed on the low, receding frontal of the Cape Flats specimen in view of the recent conclusions that have been proffered by Harvati et al. (2011) about the affinities of the Iwo Eleru cranium from the terminal Pleistocene of Nigeria.

Several other isolated and variably mineralized specimens, such as the fragmentary cranium from Canteen Kopje, South Africa at one time regarded as being of MSA antiquity (Broom 1929b), are likely to be of recent derivation, although their absolute ages cannot be determined at present (Smith et al. 2012). These specimens have rightly fallen into obscurity.

Human Fossils Associated with MIS 6 (191–130 ka)

The earliest fossils that have been securely attributed to *Homo sapiens* appear during the transition from MIS 7-6 at ~195 ka. Marine isotope stage 6 was one of the longest and coldest glacial periods of the Northern Hemisphere (Petit et al. 1999) and, as such, is generally considered to have witnessed increased aridification in Africa, with desert environments – especially the Sahara, Namib, and Kalahari – expanding across the continent (Hetherington et al. 2008; Carto et al. 2009; Castañeda et al. 2009; Marean 2010). Marean (2010) has suggested that this may have hampered the movement of humans and other mammals between and even within subcontinental regions, but notes that this downturn in global temperature was likely to have had variable effects on the ecosystems of sub-Saharan Africa, with pulses of increased rainfall (see also Blome et al. 2012).

Some of the most complete and therefore informative crania and postcranial skeletons derive from sites that are dated to the transition to and within the early part of MIS 6. Eight hominin-bearing sites are grouped here as being associated with MIS 6 (Fig. 17.2; Table 17.3). The Omo Kibish fossils derive from the transition between MIS 7-6, and the Kébibat cranial fragments are possibly of this antiquity. The Border Cave postcranial bones, which are here judged likely to be the only MSA human remains from that site, may date anywhere from MIS 6-3. The eight sites are discussed below in the order in which they appear in Fig. 17.2 and Table 17.3.

Omo (Kibish Formation), Ethiopia (5°23′ N, 35°56′ E)

In 1967, a team led by R.E. Leakey discovered three fossil hominin specimens in the Member I sediments of the Kibish Formation along the Omo River in southern Ethiopia (Leakey 1969; Day 1969; Butzer 1969; Butzer et al. 1969). These fossils, which were described as contemporaneous, comprise an incomplete skull and associated partial postcranial skeleton (Omo I), a well-preserved calvaria (Omo II), and fragments of a neurocranium and face (Omo III). Some of the Omo I remains were reported to have been recovered *in situ* during an excavation of the site (Shea et al. 2007).

Although both Omo I and Omo II were found in the upper part of Member 1 of the Kibish Formation and below the KHS Tuff at the base of Member 2, the Omo II calvaria presents an overall more archaic morphology than the cranial remains of Omo I. Some have held this to signify a population with considerable individual variation (Day 1969; Rightmire 1976; Trinkaus 2005), or perhaps two different contemporaneous populations (Day and Stringer 1982, 1991). Others have suggested that Omo I is younger, and perhaps intrusive (e.g., Chavaillon 1982; Bräuer et al. 1997; Bräuer 2001; Klein 2009). Subsequent fieldwork between 1999 and 2003 led by J. G. Fleagle resulted in the discovery of a partial tibia and fibula of a fourth individual at another site in Member I (AHS-Kib-158-1; Pearson et al. 2008b). Importantly, this also led to the discovery of additional parts of the Omo I skeleton that had weathered out of the level excavated in 1967 at KHS. Some of these actually refitted bones discovered in 1967 (Pearson et al. 2008a). These discoveries, together with more comprehensive stratigraphic and geochronological analyses of the site (McDougall et al. 2005, 2008; Brown and Fuller 2008; F. Brown et al. 2012) have provided ample evidence for the contemporaneity of the Member 1 hominin specimens.

Table 17.3 African hominin-bearing sites and hominin fossils associated with MIS 6

Site/specimen	Country	Coordinates	Age (ka)
Omo (Kibish Fm.)	Ethiopia	05°23′ N, 35°56′ E	195
Kébibat	Morocco	34°02′ N, 06°51′ W	200–130
Twin Rivers Kopje	Zambia	15°31′ S, 28°11′ E	178–139
Mumbwa Caves	Zambia	15°01′ S, 26°59′ E	172
Jebel Irhoud	Morocco	31°56′ N, 08°52′ W	160–150
Herto	Ethiopia	10°15′ N, 40°33′ E	160–150
Singa	Sudan	13°00′ N, 33°55′ E	145–133
Border Cave	South Africa	27°01′ S, 31°59′ E	170–56

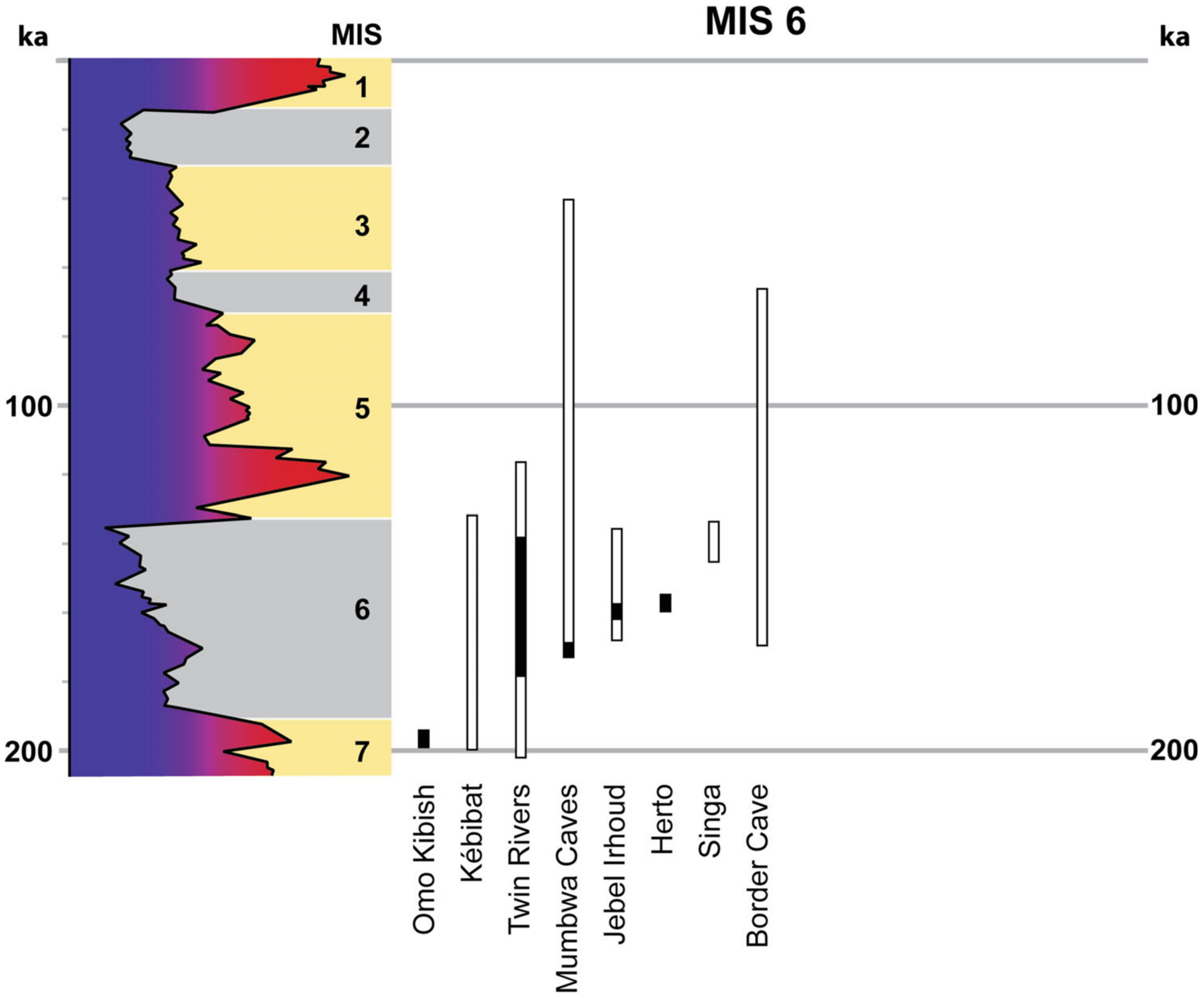

Fig. 17.2 Distribution of age determinations and/or estimates for hominin fossils and hominin-bearing sites that are most reasonably related to Marine Isotope Stage 6. *Open rectangles* represent possible age ranges deduced for a site or specimen; *solid rectangles* represent well-established dates for the hominin fossils

Member I of the Kibish Formation formed, probably in a short period of time, during a period of high water level in Lake Turkana correlated with Mediterranean sapropel 7 at c. 197 ka (McDougall et al. 2008). Ar–Ar dating of the Nakaákire Tuff just below the level of the fossils and the Aliyo Tuff well above to 196 and 104 ka, respectively, serves to bracket the fossils (McDougall et al. 2005, 2008; Millard 2008). More recently, F. Brown et al. (2012) have presented additional evidence that the KHS Tuff at the base of Member 2, which overlies the recovery sites of Omo I and Omo II, is best dated by correlation with other tuffs in East Africa to 172 ka. This more tightly brackets the Kibish Formation hominins between 197 and 172 ka, and their stratigraphic position within Member 1 places them much closer to 195 ka. In addition, Aubert et al. (2012) have conducted U-series dating on a fragment of the Omo I cranium, which yielded a minimum age of some 187–155 ka.

Kébibat, Morocco (34°02′ N, 6°51′ W)

Dynamite blasting in 1933 in the Mifsud-Guidice Quarry in a suburb of Rabat, Morocco resulted in the discovery of a fragmentary mandible, maxilla, and cranial vault of a juvenile individual (Rabat 1). Uranium-series (Th^{230}/U^{234}) dates on overlying seashells suggest an age in excess of 130 ka (Stearns and Thurber 1965). Although Millard (2008) has argued that nothing more precise than a Middle Pleistocene age can be assigned to the hominin remains, the biostratigraphic data are consistent with an age of some 200–130 ka (Hublin 2001).

The dentition, mandible, and cranial remains, that comprise Rabat I, have been described by several workers (e.g., Vallois 1945; Thoma and Vallois 1977; Saban 1975, 1977). This fossil was initially regarded as representing "evolved *Homo erectus*" by Saban (1975, 1977), but a more recent interpretation (Hublin 2001) attributes it to *Homo sapiens*.

Twin Rivers Kopje, Zambia (15°31′ S, 28°11′ E)

The site of Twin Rivers in eastern Zambia consists of several fissures filled with speleothem-cemented sediments that contain animal bones as well as MSA and LSA lithics. The fissures formed in a hill located between the Chikupi and Nangombi rivers, some 24 km southwest of Lusaka. The site was excavated by J.D. Clark in the 1950s (Clark and Brown 2001) and by L. Barham in the 1990s (Barham et al. 2000). Uranium-series and thermoluminescence (TL) dates from the speleothems have placed the MSA breccias in the range of c. 226–117 ka; the LSA material dates to between 60 ka and the Holocene (Barham et al. 2000).

The only human bone from the site is a fragment of humeral diaphysis described by Pearson (2000). Its sole noteworthy feature is its cortical thickness, which has been described as "strikingly thick relative to recent humans but similar to the thick-walled bones of other Pleistocene hominins" (Pearson 2000: 281).

The humeral fragment, which was recovered in the 1999 excavation, comes from sediments "within and beneath" an 8–10 cm thick ferro-manganese "crust" covering the top of Block F (Barham 2002). Uranium-series dates for two speleothem samples from Block F range between c. 178 and c. 139 ka (Barham et al. 2000: Table 10.1), but the presence of small lithic segments, which are a distinctive feature of the LSA in Zambia, may imply the possibility of intrusive contamination. Alternatively, as suggested by Barham (2002), they may simply attest to technological variability in the Lupemban. Given the striking thickness of the humeral cortex, it would seem unlikely to be intrusive from the LSA, so a date of c. 178–139 ka for it is accepted here as not being unreasonable.

Mumbwa Caves, Zambia (15°01′ S, 26°59′ E)

This site takes its name from the multiple cave entrances to a deep cavity formed in a large dolomite outcrop near the township of Mumbwa in the Central Province of Zambia, some 180 km northwest of Lusaka. The infilling of this cavity has been the object of excavation by a series of workers since 1925, when F.B. Macrae investigated the entrance of Cave I for its archaeological potential. Macrae dug a test trench of some 3 m depth that produced artifacts ranging from the historic/Iron Age through the LSA into the MSA. This was followed by excavations by Raymond Dart in 1930 and by J. Desmond Clark in 1939.

Dart's expedition recovered a number of fragmentary human skeletons that were buried at various depths into MSA-bearing deposits from overlying Late Pleistocene or Holocene horizons (Dart and del Grande 1931). Dart and del Grande (1931) recorded evidence of at least 16 individuals, but only four of these specimens (designated Mumbwa 1-4) have been preserved (Jones 1940; Gabel 1963). Clark (1942) found 17 teeth in the Holocene levels.

Subsequent excavations were undertaken in the early 1970s by D.K. Savage (1983) and in 1993–1996 under the direction of L.S. Barham (Barham 1995, 2000). Barham's expeditions yielded a small number of isolated human teeth and postcranial fragments, some of which come from the Holocene LSA strata (Pearson et al. 2000).

Although Protsch (1975, 1977) published a series of radiocarbon dates of between 20,450 ± 340 ^{14}C BP and 18,000 ± 370 ^{14}C BP for animal bones in apparent association with the four human specimens recovered by Dart, and a date of 19,780 ± 130 ^{14}C BP for bone collagen from Mumbwa 1, these dates are of very questionable validity. The LSA specimens could derive from MIS 2, as suggested by Protsch (1975, 1977), but they could equally derive from the Holocene. As such, Mumbwa Caves is not discussed below with reference to human skeletal remains associated with MIS 2 in sub-Saharan Africa.

However, the latest and most detailed excavations led by Barham recovered at least two teeth and two fragmentary radii that certainly derive from the MSA deposits – a third tooth is of possible MSA derivation and a partial femoral diaphysis is of probable MSA origin (Pearson et al. 2000). The MSA human remains are generally unremarkable. The teeth are somewhat large by comparison with modern southern African homologues, while the postcranial bones suggest individuals of comparatively small body size.

Thermoluminescence determinations on sand grains, burnt quartz, and calcite as well as ESR measurements on mammalian tooth enamel fragments suggest an age for the intermittent MSA occupations of the site of between 40 ka and somewhat greater than 172 ka (Barham and Debenham 2000). The MSA human remains derive from the lower units (X and XII), which are believed to date to ~172 ka.

Jebel Irhoud, Morocco (31°56′ N, 8°52′ W)

Mining operations in 1961 and subsequent excavations from 1963 to 1969 of this cave site some 60 km southeast of Safi, Morocco resulted in the recovery of the skeletal remains of several individuals in association with MSA (Middle Paleolithic) artifacts. The first specimen (Irhoud 1) is represented by a nearly complete cranium, the second (Irhoud 2) by a calvaria, and the third (Irhoud 3) is a juvenile mandible. Excavations in 1969 uncovered a juvenile humeral diaphysis (Irhoud 4), and Hublin (2001) has more recently identified a fragmentary pelvis of another adolescent individual in a sample of breccia collected in 1969 by J. Texier.

Irhoud 1 and 2 were initially thought to have Neandertal affinities (Ennouchi 1962, 1963, 1968; Howell 1978; Bräuer 1984b), but other analyses have suggested instead a mixture of plesiomorphic traits and features shared with modern humans (Stringer 1974, 1978; Hublin 1992, 2001). When compared with the Skhul-Qafzeh group of fossils, the Irhoud specimens are only slightly more primitive (Hublin 2001). The teeth of the juvenile individual (Irhoud 3), which was also initially interpreted as belonging to a Neandertal (Ennouchi 1969), have been argued to represent the earliest evidence for slow, modern human-like development (Smith et al. 2007).

Electron spin resonance (ESR) spectroscopy on three artiodactyl teeth from a level immediately overlying one of the human specimens provided age ranges of 125–90 ka assuming an early uptake model, or 190–105 ka assuming a linear-uptake model (Grün and Stringer 1991). As noted by Millard (2008), however, these would appear to be ranges for the midpoint estimates rather than confidence ranges. More recent U-series and ESR dates on a tooth from the Irhoud 3 juvenile suggest an age of c. 160 ka (Smith et al. 2007). This is close to the maximum age of c. 150 ka suggested by Amani and Geraads (1993) on the basis of faunal comparisons.

Herto, Ethiopia (10°15′ N, 40°33′ E)

Six hominin specimens were initially recovered from the Upper Herto Member of the Bouri Formation in the Middle Awash of Ethiopia by a team led by J.D. Clark, T.D. White, B. Asfaw, and G. Wolde-Gabriel (White et al. 2003; Clark et al. 2003). Two of the specimens (BOU-VP-16/1 and, BOU-VP-16/2) comprise complete and partial adult crania, and a third (BOU-VP-16/5) is the cranium of a child. The other three specimens are isolated, fragmentary cranial bones, or teeth. The more complete fossils represent some of the most significant discoveries of early *Homo sapiens* made thus far, owing not only to the morphological information they possess, but also to their well-constrained geochronology and archaeological context. All of the specimens display evidence of human modification, such as cut marks, and the discoverers have interpreted this as resulting from mortuary practices that may or may not have included cannibalism.

The cranium is very large and shares with more ancient African fossils a wide interorbital breadth, a prognathic maxilla, and a short and angulated occipital. On the other hand, it displays a moderately domed forehead, a low and flat mid-face, and a globular calvaria, features that are more widely shared with more recent humans. White et al. (2003) attributed the Herto specimens to the "paleosubspecies" *Homo sapiens idaltu*.

These fossils have been dated between 160 and 154 ka on the basis of volcanic clasts from the fossil bearing unit, and by geochemical correlation of the overlying Waidedo Vitric Tuff (WAVT) with an unnamed tuff underlying the Konso Silver Tuff. Millard (2008) has recomputed the ages from the supplementary data provided in Clark et al. (2003) with stratigraphic ordering using OxCal, and has obtained an age constraint of 161–150 ka for the Herto fossils. Clark et al. (2003) and Morgan et al. (2009) have obtained ^{40}Ar/^{39}Ar ages ranging from 110 to 253 ka for obsidian clasts within the Herto Member. Although Brown et al. (2012a, b) have argued that the stratigraphic relation between the WAVT, which they observe as being probably near 172 ka, and the sedimentary sequence containing the Herto fossils has not been determined satisfactorily, a correlative age of c. 160 ka for the Herto hominin fossils seems likely pending further investigation.

Singa, Sudan (13°00′ N, 33°55′ E)

Singa 1 is a heavily mineralized partial human cranium. It was discovered in 1924 together with MSA artifacts eroding from a calcified hardpan (caliche) deposit on the west bank of the Blue Nile River some 320 km south of Khartoum.

The calcrete matrix that encrusted the cranium was dated by U-Th to c. 133 ka, which is within the ranges of ESR estimates from mammalian tooth enamel, being 159 and 89 ka on the basis of a late uptake and early uptake models, respectively (McDermott et al. 1996). Because the calcrete formed after the deposition of the calvaria, its age must constitute a minimum for the fossil (Millard 2008). However, the degree of preservation of the specimen would seem to suggest that it was not deposited too far in advance of the calcrete formation; thus, an age range of c. 145–133 ka would seem reasonable for Singa 1 (Millard 2008).

The cranium presents a number of modern features together with more archaic traits, such as a well-developed supraorbital torus. Its accentuated parietal bossing, which some early workers identified as being suggestive of Khoe-San affinities (Woodward 1938; Wells 1951), may be unduly developed as a result of cranial asymmetry and possibly some unidentified underlying pathology (Stringer et al. 1985; Spoor and Stringer 1998).

Border Cave, South Africa (27°01′ S, 31°59′ E)

This large cave is situated high on the steep western side of the Lebombo Mountains in KwaZulu-Natal, some 400 m from the border with Swaziland. It was discovered and first excavated in 1934 by R. Dart, who dug a thin, shallow trench into the deposit (Cooke et al. 1945). This was followed in 1940 by extensive digging for bat-guano by miners led by W.E. Horton, who discarded stone tools and bones in their dumps. B.D. Malan and colleagues renewed archaeological excavations in 1941–1942, and P. Beaumont undertook more extensive work in the 1970s. A deposit of nearly 5 m depth records MSA, LSA, and Iron Age occupations. In the upper part of the sequence, two layers dated to 44.0–42.0 ^{14}C kBP by AMS and conventional ^{14}C appear to mark the beginning of the LSA in South Africa (Bird et al. 2003; Villa et al. 2012), although this is some 20 ka earlier than evidenced at other dated sites (Deacon 1995; Vogel 2001; Bousman 2005). These early LSA layers have not yielded any human remains.

The cave contains thick deposits that preserve MSA 1, Howiesons Poort and MSA 3 artifacts (Butzer et al. 1978a). Estimates of the ages of the MSA-bearing horizons have been based on ESR of tooth enamel (Grün et al. 1990a, 2003; Grün and Beaumont 2001; Millard 2008) and/or amino acid racemization of eggshell (Miller et al. 1999). A series of unpublished luminescence dates cited by Grün and Beaumont (2001) also exist. These various estimates place the MSA sequence from perhaps 171–152 ka at the base to ~56 ka for MSA 3.

There are eight human specimens from Border Cave that have been said to derive from the MSA levels. A partial cranium (BC1) and an edentulous partial mandible (BC2) were found by Malan and colleagues in 1941 in the dumps created by Horton's guano diggings (Cooke et al. 1945). Although Beaumont (Beaumont et al. 1978; Beaumont 1980) has argued that these specimens derive from the MSA deposit – either layer 4BS or layer 5BS (BS = Brown Sands) – below the Howiesons Poort on the basis of tiny bits of adhering sediment, other workers (e.g., Klein 1983; Parkington 1990) have cited factors pertaining to their state of preservation which indicate that they may not derive from an MSA context. In particular, they are much better preserved than the faunal remains that have been excavated *in situ* from the MSA. Sillen and Morris (1996) obtained conflicting results in their assessment of the mineral crystallinity of BC2 bone, but their own sample provided a "young" signal in relation to the known MSA animal bones. While they obtained elevated crystallinity values for powdered samples of the BC 1 cranium taken by Kenneth Oakley, they had cause to doubt their validity in light of the mixed results they obtained from a similarly powdered sample from BC 2.

A nearly complete skeleton of a very young (c. 3-month-old) infant (BC 3) buried in a shallow grave was recovered in 1941 from the base of the Howiesons Poort sequence by Malan and colleagues (Cooke et al. 1945). It was posited to derive from a MSA layer immediately above. However, the state of preservation of the very fragile bones together with the fact that Sillen and Morris (1996) found the "splitting factor" of samples from BC 3 to differ noticeably from that of the *in situ* MSA fauna certainly indicate it to be intrusive from much younger levels. Sillen and Morris (1996) suggested that the BC3 infant is "associated with the Holocene" and given its clear association with grave goods in the form of a perforated *Conus* shell, they noted that it "would be archaeologically consistent with other [Holocene] sites in the region." Protsch (1975) reported one of his infamous isoleucine racemization dates for the BC 3 infant, but this estimate of c. 60 ka can be wholly disregarded.

An adult mandible (BC 5) was found by C. Powell, working with Beaumont in 1974. The jaw, which is nearly complete, is said to have come from a depression in the base of Layer 3WA (de Villiers 1975), and to be associated with fauna dated to c. 66 ka on the basis of ESR (Beaumont et al. 1978; Beaumont 1980; Grün and Beaumont 2001). It is stated to have been "recovered" while "collecting sediment samples… from the south face of Excavation 3A" (Grün et al. 2003: 155). More precisely, however, it was actually dislodged from the south face of the previous excavation wall during the process of cleaning it prior to the removal of sediment samples. It was *not* recovered using controlled excavation techniques. Sillen and Morris (1996) noted that BC 5 is very well preserved, with "both poor crystallinity and elevated nitrogen when compared with faunal bones from the 3WA" layer. In view of the discrepancies between BC 3 and BC 5, on the one hand, and the *in situ* MSA fauna on the other, Sillen and Morris (1996) concluded that these two human specimens cannot be connected to the MSA with any confidence.

Subsequent analysis by Grün et al. (2003) from a piece of tooth enamel from BC 5 yielded an ESR date of 74 ± 5 ka, which was held to corroborate their earlier assertions regarding its antiquity. However, this argument rests substantially (if not entirely) on the fact that their ESR date for BC 5 fits "exactly into the ESR age sequence of the faunal material" from the stratigraphic sequence that was determined by them (Grün et al. 2003: 165). In actual fact, examination of their data (see Grün et al. 2003: Fig. 9) reveals that the BC 5 value does not differ significantly from specimen 537c from Layer 2 BS, and that several of the faunal tooth enamel values from Layer 3WS cannot be differentiated from those for fragments from Layer 2 BS or even layer 1WA (said to be between 47 and 36 ka).

Almost all studies to date have concluded that the BC 1 cranium and the BC 2 and BC 5 mandibles are fully modern in morphology (de Villiers 1973, 1975; Rightmire 1979, 1984; de Villiers and Fatti 1982; Bräuer 1984a; Smith 1985; Fatti 1986; Smith et al. 1989). The only exceptions relate to the multivariate morphometric analyses undertaken by Cambell (1984), Ambergen and Schaafsma (1984) and van Vark et al. (1989). Cambell (1984) and Ambergen and Schaafsma (1984), who employed Rightmire's (1979) data in their analyses, indicated that BC-1 is statistically atypical for the modern southern African samples that were employed by Rightmire. van Vark et al. (1989), who included larger samples of modern humans from different geographical regions, argued that although BC-1 may look modern, it is "quite different from recent *Homo sapiens*." This same study also concluded that BC-1 is perhaps "only slightly more distinct from Asiatic *Homo erectus* than it is from recent *Homo sapiens*" (van Vark et al. 1989: 54)! As noted by Grine et al. (1991), such a patently absurd conclusion cannot but detract from the credibility of this kind of analysis.

Indeed, Rightmire (1979) has demonstrated distinct morphometric similarities of the Border Cave cranial and mandibular remains to the recent indigenous peoples of South Africa. This, in itself, is most unusual for cranial remains elsewhere in Africa that are in indisputable Late Pleistocene MSA contexts.

On the other hand, Morris (1992) briefly described several postcranial fragments – a humeral shaft, proximal ulna, and two metatarsals (from rays IV and V) – that had been discovered by P. Beaumont in 1987 from sediments that had slumped into the 1941–42 excavation pit. Because they derive from a disturbed context, they cannot be attributed to any particular stratum within the cave. Nevertheless, these bones, which have been referred to as BC 6, 7, and 8 (Grün and Beaumont 2001; Villa et al. 2012: SI page 2), are the most likely of all of the human remains from Border Cave to actually derive from the MSA (although where in the MSA sequence is impossible to determine at present). The reason for this is threefold.

In the first instance, they are generally more fragmentary that the other human remains and have the same macroscopic preservation as indisputable MSA faunal elements (Sillen and Morris 1996). In the second instance, samples from the humerus and ulna have the same degree of crystallinity and low nitrogen as the MSA fauna (Sillen and Morris 1996). Finally, unlike the other human remains, both the humerus and ulna display archaic features in common with other undeniable MSA hominins from South Africa (Pearson and Grine 1996; Pfeiffer and Zehr 1996). In particular, the proximal ulna is comparable to one from the MSA at Klasies River and to more ancient African homologues in the archaic pattern of the relative heights of the coronoid and olecranon processes (Pearson and Grine 1996), and the humeral diaphysis has thick cortical bone (Pearson and Grine 1996; Pfeiffer and Zehr 1996). Although morphology cannot be used to "date" a fossil, it is nonetheless noteworthy that these fragmentary postcranial bones are the only human specimens from Border Cave to differ in any notable manner from those of the Holocene (including the Iron Age and current) inhabitants of South Africa.

Human Fossils Associated with MIS 5 (130–71 ka)

Marine Isotope Stage 5 represents the penultimate interglacial period. Shackleton (1969) proposed its informal division into five substages. The first of these (5e) represents the interglacial maximum, when sea levels stood c. 6 m above the present and global temperatures were some 2 °C higher than today (Shackleton 1987; Jouzel et al. 1987). In sub-Saharan Africa, MIS 5 is thought to have been characterized by generally warm and wet conditions with a general expansion of forest over savannah regions (Pokras and Mix 1985). However, this stage is characterized by rather wide swings in oceanic temperature (Fig. 17.1), which must have been accompanied by significant climatic fluctuations across parts of Africa. Thus, while MIS 5 represents a humid interval in northern Africa (Castañeda et al. 2009), Lake Malawi experienced a lowstand for much of this time (Lyons et al. 2011; Scholz et al. 2011). Moreover, as noted above, regional differences in response to these global oceanic patterns of temperature fluctuation must have varied quite widely across different parts of Africa, making sweeping, continent-wide generalizations very difficult if not meaningless.

Fifteen hominin-bearing sites are grouped here as being associated or likely associated with MIS 5 (Fig. 17.3; Table 17.4). Some, such as Pinnacle Point appear to extend from MIS 6-5 (in this instance through to MIS 5c), but their human fossils derive from the latter. In other cases, such as Klasies River Main Site, the sequence and human remains

Table 17.4 African hominin-bearing sites and hominin fossils associated with MIS 5

Site/specimen	Country	Coordinates	Age (ka)
Ngaloba Beds (Laetoli)	Tanzania	03°13′ S, 35°11′ E	129
Blind River	South Africa	27°01′ S, 33°00′ E	118
Klasies River Main Site	South Africa	34°06′ S, 24°24′ E	115–58
Sea Harvest	South Africa	33°01′ S, 17°57′ E	110–71
Grotte de Contrebandiers	Morocco	33°55′ N, 07°00′ W	107–96
Dar es-Soltan II	Morocco	33°57′ N, 06°35′ W	?125–96
Eyasi	Tanzania	03°32′ S, 35°16′ E	104–92
Equus Cave	South Africa	27°37′ S, 24°38′ E	?103–30
Aduma	Ethiopia	10°25′ N, 40°31′ E	100–80
Pinnacle Point	South Africa	34°12′ S, 22°05′ E	90
Blombos	South Africa	34°25′ S, 21°13′ E	100–73
Ysterfontein 1	South Africa	33°20′ S, 18°09′ E	105–71
Witkrans	South Africa	27°37′ S, 24°38′ E	100–50
Plovers Lake	South Africa	25°58′ S, 27°46′ E	89–63
Haua Fteah	Libya	32°55′ N, 22°05′ E	80–68
Mumba Shelter	Tanzania	03°32′ S, 35°19′ E	78–60

extend upwards beyond MIS 5 (in this instance, into MIS 4). Other sites, such as Equus Cave, Ysterfontein 1, and Witkrans entail more loosely constrained dates that may extend from MIS 5-3. The 15 sites are discussed below in the order in which they appear in Fig. 17.3 and Table 17.4.

Ngaloba, Tanzania (3°13′ S, 35°11′ E)

In 1976, fossilized human cranial fragments were discovered *in situ* eroding out of the Ngaloba Beds at Laetoli, northern Tanzania (Day et al. 1980). The reassembled fragments formed a nearly complete adult cranium (LH 18) that displays a mixture of archaic and modern features (Day et al. 1980; Magori and Day 1983; Cohen 1996). In particular, the expanded parietals, rounded occiput, and low position of inion are seen as modern traits, while the receding frontal, large supraorbital tori, and thick vault bones are seen as archaic. It has been likened to specimens such as Omo I and Eyasi I (Magori and Day 1983).

The cranium derives from a horizon that includes a trachytic tuff that has been correlated with the "marker tuff" in the lower unit of the Ndutu Beds at Olduvai Gorge. Magori and Day (1983) stated that this has provided an estimate of some 120 ka for the cranium, but gave no basis for this assertion. Subsequently, Hay (1987) provided an age estimate of the "marker tuff" of 129 ± 4 ka on the basis of a U-Th date of bone from it. Manega (1993, 1995) revised the date to ~200 ka on the basis of amino acid racemization of ostrich eggshell. However, the dependency of this technique on temperature, as well as the moisture and pH histories of the matrix renders amino acid dating of material with unknown environmental histories a very perilous undertaking.

Blind River, South Africa (27°1′ S, 33°0′ E)

A nearly complete human femur lacking its proximal end was found by P. Laidler in 1933 just upstream from the mouth of the Blind River canyon, which opens to the Indian Ocean in East London, South Africa. The bone is fundamentally modern in morphology, and most of its features are compatible with those of indigenous South African populations (Wells 1935; Wang et al. 2008).

The specimen is an isolated find that is said to have come from an estuarine calcarenite of an old raised beach platform. Optically stimulated luminescence (OSL) assessments of two samples of sedimentary quartz grains extracted from just below the level from which the femur is said to have derived provided a weighted mean age of 118 ± 6 ka (Wang et al. 2008). This date gains some apparent support from the presence below the femoral horizon of marine/estuarine deposits at c. 10 m above current sea level. According to Wang et al. (2008), these deposits would correspond to the maximum marine transgression of MIS 5e.

Klasies River Main Site, South Africa (34°06′ S, 24°24′ E)

The "site" of Klasies River, also referred to as Klasies River Mouth (Singer and Wymer 1982), comprises five caves or rock shelters located between 0.5 and 2 km east of the mouth of the Klasies River on the Tsitsikamma Coast of South Africa. Its significance derives from the abundant archaeological debris and the 40 or so fragmentary human fossils from the thick MSA deposits of what has become known as

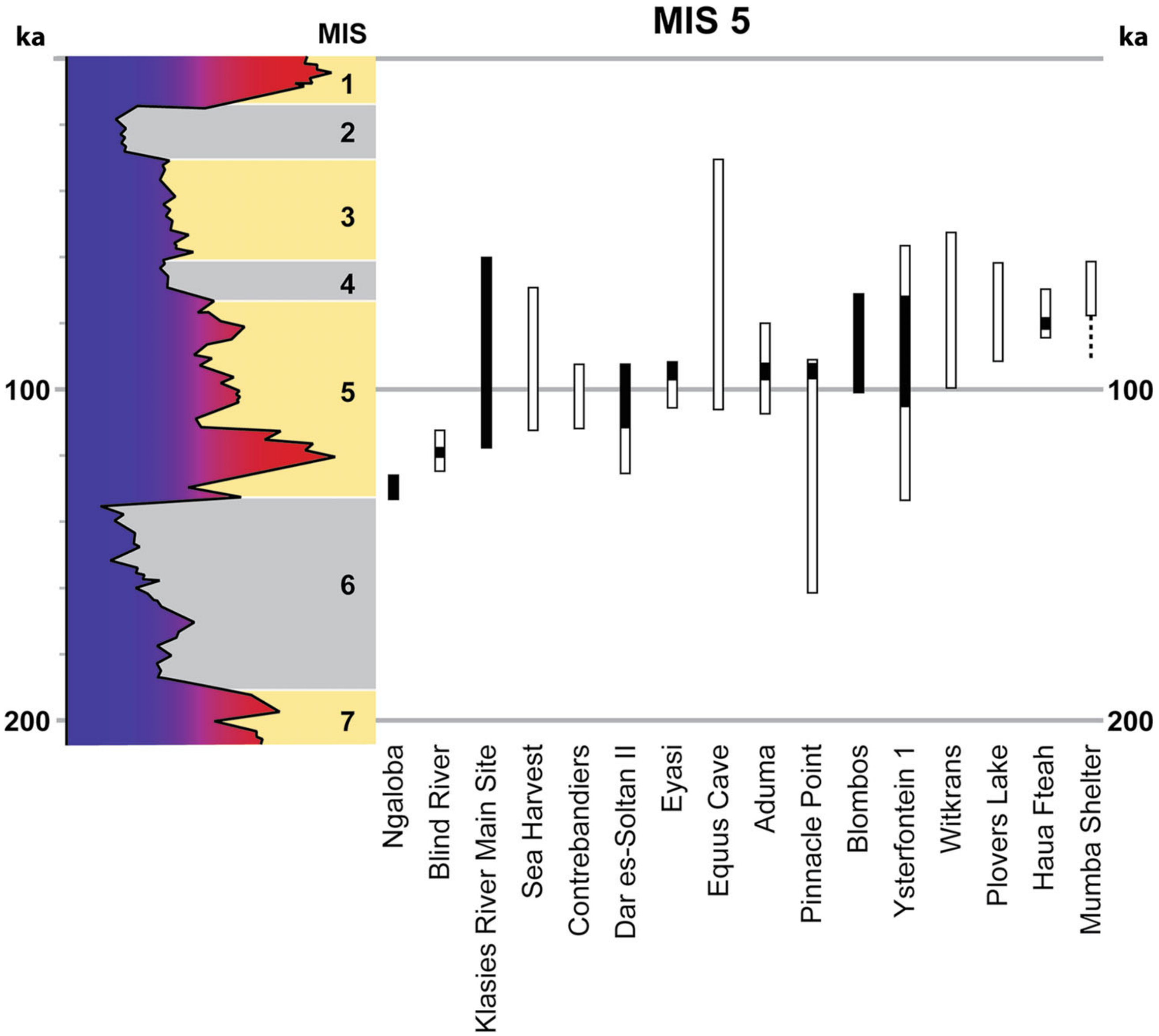

Fig. 17.3 Distribution of age determinations and/or estimates for hominin fossils and hominin-bearing sites that are most reasonably related to Marine Isotope Stage 5. *Open rectangles* represent possible age ranges deduced for a site or specimen; *solid rectangles* represent well-established dates for the hominin fossils; *dotted lines* indicate possible but not probable dates

the "Main Site." These artifacts and faunal remains have featured prominently in discussions over the emergence of modern human behaviors (e.g., Klein 1976, 1989; Deacon 1992; Klein and Cruz-Uribe 1996; Milo 1998; Wurz 1999, 2008; McCall 2006; Dusseldorp 2010; d'Errico et al. 2012). The hominin fossils, despite their generally fragmentary nature, have played a significant role in interpretations of human evolution (e.g., Singer and Wymer 1982; Smith 1992; Bräuer et al. 1992a; Frayer et al. 1993; Stringer and Bräuer 1994; Bräuer and Singer 1996; Churchill et al. 1996; Lam et al. 1996; Ahern and Smith 2004; Royer et al. 2009).

The Main Site consists of a c. 21 m deep deposit of sediments spread across a series of interrelated recesses referred to as Caves 1, 1A, 1B, and 2. Most of the work has focused on the Cave 1 and Cave 1A deposits. The first systematic excavation of the Main Site was undertaken by J. Wymer in 1967–1968. This resulted in the recovery of abundant stone tools and animal bones and the bulk of the human fossils found thus far (Singer and Wymer 1982). Subsequent excavations by H. Deacon in 1984–1995 provided an improved stratigraphic framework and a reasonable geochronology of the MSA deposits, together with some additional human fossils. The stratigraphic scheme provided by Deacon and Geleijnse (1988) recognized a number of members, and they managed to place most of the units described by Singer and Wymer (1982) into this context.

The lowermost sedimentary unit, which overlies bedrock, was referred to as the LBS ("Light Brown Sand") Member by Deacon and Geleijnse (1988). Shackleton (1982) and Deacon et al. (1988) have argued that it was most likely deposited c. 115–105 ka during MIS 5d, when sea level was very close to that at present, following the Last Interglacial transgression of MIS 5e. A U-series date of c. 108 ka obtained by Vogel (2001) for speleothem carbonates is consistent with this interpretation, as are optically stimulated luminescence dates of 115–110 ka recorded by Feathers (2002) for sand from Cave 1A. The two maxillae recovered by Deacon from the LBS Member are the oldest hominin fossils from the site (Rightmire and Deacon 1991; Bräuer et al. 1992a).

The LBS Member is overlain by the SAS ("Shell and Sand") Member, which comprises the bulk of the thickness of the deposit in Caves 1 and 1A (Deacon and Geleijnse 1988). It appears to have begun accumulation during MIS 5c at 105–92 ka (Shackleton 1982; Deacon et al. 1988),[2] and several dating methods have produced results consistent with an age of c.100–80 ka (Grün et al. 1990b; Vogel 2001; Feathers 2002). Although Millard (2008) has recalibrated the ESR ages from data in Grün et al. (1990a, b) to produce a wider range of dates, his recalibration is at odds with all other results. The vast majority of the human fossils recovered by Singer, Wymer, and Deacon derive from the SAS Member, and most are from its lower units (Deacon 2008).

In Cave 1A, the relatively thin RF ("Rock Fall") Member overlies the SAS Member. The oxygen isotope profile of the RF Member correlates with MIS 5a (84–74 ka) (Deacon et al. 1988). Vogel (2001) and Feathers (2002) have reported concordant U-series and luminescence dates of some 77 and 80–70 ka, respectively, for what seems to be the lower part of this unit. The stratigraphic sequence in Cave 1A is capped by the Upper Member. The majority of its thickness contains Howiesons Poort lithics, while the artifacts from its uppermost portion have been categorized as conforming to a distinctive post-Howiesons Poort MSA III by Singer and Wymer (1982; see also Wurz 2002; Villa et al. 2010). The oxygen isotope profile of the Upper Member is consistent with its deposition during MIS 4 at some 71 ka (Deacon et al. 1988). Several methods have produced dates between 65 and 40 ka (Grün et al. 1990b; Vogel 2001; Feathers 2002), but Jacobs et al. (2008a) obtained somewhat earlier dates of c. 65.5–63.4 ka for the Howiesons Poort, and a date of 57.9 ka for the post-Howiesons Poort. The RF and Upper Member deposits have yielded two human parietal fragments (Singer and Wymer 1982) and three isolated teeth (Rightmire and Deacon 1991).

In Cave 1, the WS ("White Sand") Member caps the SAS (Deacon and Geleijnse 1988), but this unit is devoid of human fossils.

Singer and Wymer recovered nearly 40 human fossils from Klasies River Main Site, and almost all of these were documented in their 1982 monograph. Four others (a lumbar vertebra, a fragment of temporal bone, a partial atlas, and a left hallucial metatarsal) were identified subsequently by Richard Klein from among the faunal remains recovered from those excavations. These have been documented by Grine et al. (1998) and Rightmire et al. (2006). Deacon's excavations recovered another dozen human fossils. These have been described by Rightmire and Deacon (1991, 2001), Bräuer et al. (1992a), Churchill et al. (1996), Rightmire et al. (2006) and Grine (2012). Many of the human fossils display manifestly modern morphologies, while others exhibit somewhat more archaic traits, and the degree of modernity or primitiveness of still others has been a matter of debate (Singer and Wymer 1982; Rightmire and Deacon 1991, 2001; Bräuer et al. 1992a, b; Smith 1992; Frayer et al. 1993; Bräuer and Singer 1996; Churchill et al. 1996; Lam et al. 1996; Pearson and Grine 1997; Grine et al. 1998; Pearson et al. 1998; Rightmire et al. 2006; Royer et al. 2009; Grine 2012).

A number of these fossils exhibit arguably archaic traits, and the degree of size dimorphism seems unmatched among recent people. The limited evidence, however, seems to suggest a pattern of general, albeit incomplete morphological modernity. As observed by Smith (1992: 148), the "somewhat primitive aspects of certain features in some specimens" might be expected in an otherwise morphologically modern population of this geological antiquity. The mosaic nature of human evolution is perhaps manifest by the Late Pleistocene representatives of the human lineage from Klasies. Alternatively, it is possible that these specimens do not represent individuals from a single population, but attest to different populations who utilized the site at different times.

Sea Harvest, South Africa (33°01′ S, 17°57′ E)

This locality comprises a dozen or so "pockets" of fossiliferous deposits overlain by MSA shell middens on the Atlantic coast of South Africa just north of Cape Town. These pockets, which were first investigated in 1969 by Q.B. Hendey (1984), most likely represent shallow solution cavities that were utilized as dens by hyenas. From them, G. Avery and R.G. Klein recovered a premolar and manual distal phalanx, which are morphometrically compatible with homologues of recent indigenous South Africans (Grine and Klein 1993).

The faunal (biochronological) and geological evidence are consistent in suggesting deposition during the relatively

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[2] The ages for MIS 5c employed by Shackleton (1982) and Deacon et al. (1988) correspond to the SPECMAP dates recorded in Imbrie et al. (1984).

cool and moist conditions of MIS 5, corresponding perhaps to MIS 5c or MIS 5a (Hendey 1984; Grine and Klein 1993; Butzer 2004). Butzer (2004), however, has suggested that the Sea Harvest sequence is “an essentially complete record of MIS 5.”

La Grotte des Contrebandiers à Témara, Morocco (33°55′ N, 7°00′ W)

This site, also known Smugglers’ Cave, or simply as Témara (after the closest town), is located on the Atlantic coast of Morocco, some 17 km southwest of Rabat. It was discovered in 1955, and excavated in 1955–1957, 1967–1975, 1994, and 2007–2009 by different workers. The 1956 excavations yielded a mandible that was initially mistakenly thought to be associated with the Acheulean (Vallois and Roche 1958). The 1975 field season produced the back of a cranium in association with Aterian artifacts (Roche and Texier 1976; Debénath et al. 1986). A skull and partial skeleton of a child were discovered in these same strata in 2010 (Balter 2011). All of the human remains recovered thus far appear to derive from the Aterian layers, and they are, overall, morphologically modern, although the teeth are comparatively large (Ferembach 1976a, 1998; Debénath 2000; Hublin et al. 2012).

The antiquity of the human remains from the Aterian levels, as established by Jacobs et al. (2011) on the basis of single grain OSL determinations that average to 95.9 ± 4.1 and 107 ± 3.5 ka, are generally concordant with the bulk (multigrain) OSL estimates reported by Schwenninger et al. (2010). Scerri (2013: Table 2) has tabulated a very wide range of U-series, TL, and OSL dates reported for Aterian assemblages elsewhere in North Africa: from c. 145 ka at Ifri n’Ammar, Morocco (Richter et al. 2010) to c. 61 ka at Uan Tabu, Libya (Cremaschi et al. 1998). The OSL determinations for the Aterian at La Grotte des Contrebandiers à Témara fall very nearly in the middle of this range.

Dar es-Soltan II, Morocco (33°57′ N, 6°35′ W)

This cave site, situated on the Atlantic coast some 6 km southwest of Rabat, was first excavated in 1969 by A. Debénath. It has a deep (c. 8 m) archaeological deposit that comprises three Aterian horizons below Neolithic/Epipaleolithic occupations.

The remains of five hominin individuals reportedly come from the middle and lower Aterian strata. Unfortunately, most of these are not described. The most complete comprises a partial adult cranium and associated mandible (H 5) recovered from a sterile marine sand deposit (level 7) immediately below a layer containing Aterian artifacts (Debénath 1976, 1980). Ferembach (1976b) assigned the specimen to *Homo sapiens sapiens*, although noted that it has a relatively wide face and robust supraorbital relief. Bräuer and Rimbach (1990) have pointed out multivariate morphometric similarities with earlier specimens from North Africa and with later (Upper Paleolithic) specimens from Eurasia. Harvati and Hublin (2012) have argued on the basis of a 3D geometric morphometric analysis of the face that the H 5 specimen is similar to penecontemporaneous specimens from the Levantine site of Qafzeh. The teeth from this and the other Aterian specimens at the site (H4, NN, H6, H9, and H10) are comparatively large in relation to some modern human samples (Hublin et al. 2012).

Although there are no published dates for Dar es-Soltan II, the Aterian layers in the nearby (c. 200 m distant) Dar es-Soltan I cave have been dated by OSL to ∼125 ka (Barton et al. 2009). This date is close to the oldest recorded for this industry (c. 145 ka at Ifri n’Ammar, Morocco [Richter et al. (2010)]), and is substantially older than the OLS dates of 107–96 ka (Schwenninger et al. 2010; Jacobs et al. 2011) for the Aterian at the nearby site of La Grotte des Contrebandiers à Témara. It is also significantly older than the ESR dates (Wrinn and Rink [2003], revised by Millard [2008]) of 57–27 ka for the Aterian at the proximate cave site of Mugharet el ‘Aliya. Because the Aterian levels in Dar es-Soltan II are themselves undated, it might be reasonable to place them within the limits of other Aterian deposits nearby at between 145 and 96 ka, with a somewhat greater probability of being in the range of 125–96 ka.

Eyasi, Tanzania (3°32′ S, 35°16′ E)

This “site,” from which the remains of a number of hominin individuals have been recovered, comprises several fossil-bearing localities on the shore of Lake Eyasi. The first human cranial remains (Eyasi 1-3) were recovered in the 1930s by Margit Kohl-Larsen, and subsequent discoveries, culminating in that by Dominquez-Rodrigo and colleagues, have brought the number of specimens to seven. All are fragmentary, with Eyasi 1 being the most complete; all appear to derive from strata (Member C of the Eyasi Beds) associated with the MSA (Mehlman 1987). Although earlier analyses of these fragments (e.g., Bräuer 1984b, Bräuer and Mabulla 1996) tended to emphasize their “archaic” qualities, Domínguez-Rodrigo et al. (2008) have stressed their more modern features, suggesting similarities to other early *Homo sapiens* specimens from sites such as Omo Kibish and Herto. It is perhaps noteworthy, however, that even Domínguez-Rodrigo et al. (2008) regard Eyasi 1 and 6 to show primitive features in a period where “other areas have yielded…substantially more modern-looking specimens.”

Initial dates for the Eyasi hominin fossils by Protsch (1981) using amino-acid racemization have been discredited (Mehlman 1984). Domínguez-Rodrigo et al. (2008) obtained ESR and U-series (^{230}Th/^{234}U) estimates of some 104 and 92 ka, respectively, for a bovid tooth found within reasonable proximity of the Eyasi 6 hominin frontal. Domínguez-Rodrigo et al. (2008) consider that the earlier finds could be similar or even older in age depending on whether they were over, or belonged to the top of, the red soils unit from which Eyasi 6 derives.

However, as noted by Millard (2008), ESR dates on tooth enamel cannot be relied upon without investigation of its uranium uptake history. As such, he has argued that these results most likely underestimate the true age; but by how much is uncertain.

Equus Cave, South Africa (27°37′ S, 24°38′ E)

This karst cave formed in the face of the Oxland tufa fan that built out from the Gaap Escarpment near Taung, some 193 km north of Kimberly, in the Northern Cape Province of South Africa. The site contains a rich record of vertebrate remains found in association with MSA artifacts. The bones appear to have been accumulated by hyenas (Klein et al. 1991). A number of isolated human teeth were recovered from these deposits during excavations led by P. Beaumont in 1978 and 1982, and a mandibular fragment found by C.K. Brain in 1971 on a scree slope below the cave may come from the same MSA horizons. The specimens are morphometrically unremarkable by comparison with recent homologues (Grine and Klein 1985), and the molars display enamel thickness and formation rates consistent with those of recent humans (Smith et al. 2006).

The Equus Cave fauna is dominated by grazing species, which suggests an open grassland, while pollens from coprolites indicate the environment to have been cooler and moister; this would perhaps correspond to the last glaciations (MIS 4-2) or to the colder intervals of MIS 5 (i.e., 5d and 5b) (Butzer et al. 1978b; Klein et al. 1991; Scott 1987). Millard (2008) reviewed the evidence pertaining to the geochronological age of the deposit, and concluded that it most likely belongs to the period between 103 and 30 ka.

Aduma, Ethiopia (10°25′ N, 40°31′ E)

Five human specimens were discovered on the surface of the MSA-bearing Ardu Beds at Aduma and Bouri along the Awash River of Ethiopia (Haile-Selassie et al. 2004). One partial cranium (ADU-VP-1/3) found partially *in situ* has the globular appearance of modern human homologues. The other four pieces from Aduma and the one from Bouri (BOU-VP-5/1) confirm this overall pattern of morphological modernity, although there is some resemblance as well to "premodern" specimens such as LH 18 (Haile-Selassie et al. 2004). Although Haile-Selassie et al. (2004) describe the presence of a suprainiac fossa in the Aduma specimen, this feature is not unique to (although it occurs in high frequencies in) Neandertals; similarly located depressions are observable on the occipitals of Middle Paleolithic *Homo sapiens* from Skhul and Qafzeh (Nara 1994), and in recent Khoe-San crania from the LSA of South Africa (personal observation).

A variety of dating methods (e.g., U-series, TL, and OSL) have been applied in attempts to determine the age of the Aduma deposits, but there are some inconsistencies in the results (Haile-Selassie et al. 2004). Argon-argon determinations on underlying pumice demonstrate that the deposits are younger than 180 ka (Yellen et al. 2005). Optically stimulated luminescence determinations of 91–93 ka are considered to be the most reliable, and are concordant with U-series estimates on associated bone of 105–79 ka (Yellen et al. 2005). An age range of c.100–80 ka is probable for these specimens, although Millard (2008) has placed little confidence on this estimate.

Pinnacle Point, South Africa (34°12′ S, 22°05′ E)

The locality of Pinnacle Point consists of a series of caves and rock shelters cut into cliffs around a small promontory that extends into the Indian Ocean near the town of Mossel Bay on the southern coast of South Africa. Survey work and excavations initiated by C. Marean and P. Nilssen explored three sites (PP 5-6, PP 9, and PP 13B), with the focus of the work being PP 13B. Pinnacle Point is perhaps best known for providing the oldest evidence (from PP 5-6) for heat treatment of rock to produce stone tools (Brown et al. 2009) and microlithic technology dating between 71 and 60 ka (Brown et al. 2012a, b), and (from PP 13B) the use of scraped and ground ochre and the early systematic exploitation of marine resources at c. 164 ka (Marean et al. 2007; Jerardino and Marean 2010; Watts 2010). It is one of the few archaeological sites in Africa with a depth of deposits to sample MIS 6.

The artifact- and faunal-bearing sediments at PP 13B do not comprise a deep, continuously stacked series, but rather a series of horizontally disconnected set of occupations that seem to span the period of time from c. 162 to 90 ka (Jacobs 2010; Bar-Matthews et al. 2010). PP 5-6 has a ~14 m vertical sequence of sediments dating from about 90 to 50 ka (K. Brown et al. 2009, 2012).

The only human remains recovered so far – a parietal fragment and a mandibular central incisor – likely derive from the upper part of the sequence in PP 13B. They were found in 2000 in deposits that had been disturbed, probably by fishermen or campers digging to produce a flat surface in the cave (Marean et al. 2004). The disturbed sediment was mostly from the MSA Brown Sand facies, which is almost certainly the source of the fossils (Marean et al. 2004). There is no LSA deposit above the areas where the fossils were found, and the cave appears to have been sealed to human occupation from 90 to 40 ka by a dune, as were most of the caves on the western side of the point (Bar-Matthews et al. 2010). Thus, there is reason to be confident that the human remains date to "at least 90 ka, but probably not much older than that" (Marean personal communication). The parietal fragment is thin, whereas the incisor is relatively large in comparison to recent African homologues (Marean et al. 2004).

Blombos Cave, South Africa (34°25′ S, 21°13′ E)

Blombos Cave is situated adjacent to the Indian Ocean along the southern Cape coast of South Africa, some 300 km east of Cape Town. This wave-cut shelter contains LSA deposits overlying some 2 m of stratified MSA deposits. The site has been excavated since 1992 under the leadership of C. Henshilwood (Henshilwood et al. 2001). The MSA-bearing layers have been designated M1, M2, and M3 from top to bottom.

The site is best known for the artifacts from the M1 and M3 phases. In the uppermost M1, these include pressure flaked bifacial Still Bay foliate points fashioned on heat treated stone, pierced gastropod shell beads, pieces of engraved ochre, and formal bone tools (Henshilwood et al. 2002, 2004; Mourre et al. 2010; Henshilwood 2012). The M3 phase has produced evidence of engraved ochre and abalone shells that appear to have been used to store and/or produce a pigment-rich mixture (Henshilwood et al. 2009, 2011).

Nine isolated human teeth have been recovered from the MSA strata: three from level M1, one from level M2, and five from the lowermost M3 (Grine et al. 2000; Grine and Henshilwood 2002). About half of the tooth crown diameters exceed those of recent Africans, while the rest fall among modern African sample means. The specimens are morphologically similar to those of recent Africans and to penecontemporaneous homologues from sites such as Die Kelders (Grine et al. 2000; Grine and Henshilwood 2002).

The upper part of the M1 Still Bay phase has been dated by OSL to 72.7 ± 3.1 ka (Jacobs et al. 2003a, b, 2013), with TL dates of 78 ± 6 and 74 ± 5 ka for this phase of occupation (Tribolo et al. 2006). The OSL dates for the M2 phase fall between 84.6 ± 5.8 and 76.8 ± 3.1 ka (Jacobs et al. 2006). The M3 phase dates to c. 100–94 ka on the basis of OSL and U-Th determinations (Henshilwood et al. 2009, 2011). Thus, the human remains from the MSA strata at Blombos would seem to date to between about 100 and 73 ka; that is from MIS 5c to the end of MIS 5a.

Ysterfontein 1, South Africa (33°20′ S, 18°09′ E)

This rock shelter on the Atlantic Coast of the Western Cape Province of South Africa contains nearly 4 m of stratified sands with classic MSA artifacts. The site was first visited in the early 1980s by G. Avery, and a series of excavations the late 1990s and early 2000s led by R.G. Klein, R. Yates and D. Halkett recovered evidence for the early exploitation of coastal resources (Halkett et al. 2003; Klein et al. 2004; Avery et al. 2008). This site has yielded the largest lithic assemblage attributable to MIS 5 from any site on the southwestern coast of South Africa, and this technocomplex is dominated by quadrilateral flakes and blades (Wurz 2012). Three unpublished human teeth have been recovered from these MSA deposits (Klein personal communication).

Although four OSL dates of 132–120 ka have been obtained from sand samples (Jacobs personal communication, cited in Avery et al. 2008), Avery et al. (2008) have argued that the site must have formed after the high sea level stand of MIS 5e (i.e., after 123 ka), and suggest that it was occupied sometime during MIS 5c to 5a (i.e., between 105 and 71 ka). Another perhaps somewhat less likely possibility discussed by Avery et al. (2008) is that it was occupied in MIS 3 between c. 59 and 50 ka.

Witkrans Cave, South Africa (27°37′ S, 24°38′ E)

This site, like Equus Cave, formed as a karst feature in a travertine apron that built out from the Gaap Escarpment near Taung, some 193 km north of Kimberly, in the Northern Cape Province of South Africa. Excavations by F. Peabody in 1947–1948 resulted in the recovery of a large number of MSA artifacts and faunal remains and, in association, three isolated human mandibular molars from Layer C. The teeth are similar in size and morphology to homologues from other South African MSA sites such as Die Kelders and Klasies River Main Site (McCrossin 1992).

Clark (1971) likened the fauna to the Florisian (Land Mammal Age), and the artifacts to the MSA 2 (pre-Howiesons Poort) of Klasies River Main Site. This would suggest an age of c. 100–80 ka (MIS 5c-4). Volman (1984), however, has argued that the Witkrans artifacts are attributable to the post-Howiesons Poort, MSA 3, and this, in turn, would suggest an age of c. 52 ka or less (i.e., attribution to MIS 3).

Plovers Lake, South Africa (25°58′ S, 27°46′ E)

The "internal deposit" of the Plovers Lake karst feature consists of loosely calcified sediments with faunal remains and MSA artifacts that are constrained by underlying and capping flowstones (de Ruiter et al. 2008). The human remains from this deposit comprise several isolated teeth and seven postcranial pieces from a single individual, of which only the tibia has been afforded either description or illustration, and this only in relation to its state of preservation (Backwell et al. 2012).

The age of the "internal" deposit is constrained by U-series dates of 88.7 ± 1.6 and 62.9 ± 1.3 ka for the underlying and capping flowstones, respectively. A single isochron ESR date of 75.6 ± 5.6 ka is consistent with this constraint (Backwell et al. 2012).

Haua Fteah, Libya (32°55′ N, 22°05′ E)

This large cave is situated on the Mediterranean coast of northeastern Libya (Cyrenaica). It was recognized by C.T. Houlder and C. McBurney in 1948 and excavated by the latter from 1951 to 1955. These excavations, which extended to a depth of some 13 m, uncovered levels that span occupations from recent centuries through the Holocene into the Middle Paleolithic (McBurney 1967; Barker et al. 2010; Hunt et al. 2010). McBurney (1967) recognized 35 archaeologically rich levels overlying what he referred to as the "Phase A" basal "Pre-Aurignacian." He divided the "Phase B" or "Levalloiso-Mousterian" occupation layers, which constitute the bulk of the Pleistocene deposit, into four units. This is overlain by "Phase C" Upper Paleolithic "Dabban" deposits and three subsequent occupation phases extending into the Graeco-Roman period. Current excavations at the site were initiated in 2007 under the direction of G. Barker, C. Hunt, and T. Reynolds (Barker et al. 2007, 2010, 2012; Hunt et al. 2010; Reynolds 2013; Jones et al. 2016). This work has provided an improved appreciation of the stratigraphy, archaeology, and age of the site.

Two human mandibular fragments – one young adult (Haua Fteah I) and one juvenile (Haua Fteah II) – were recovered in 1952 and 1955 from Layer XXXIII, one of the lower "Levalloiso-Mousterian" levels (McBurney et al. 1953a, b; McBurney 1958, 1967; Tobias 1967). Initial assessment of these jaws suggested similarities to the "Tabun group" of "Neandertaloids" (McBurney et al. 1953a, b; McBurney 1958). Tobias (1967) agreed with this assessment, viewing them as "part of an advanced Neandertaloid population" where the "Neandertaloids" represented a phase in the evolution of humans pertaining not only to Eurasia but also to sub-Saharan Africa. Tobias (1967) also saw some similarities to "remains described as a primitive variant of Neanderthal man (*Homo sapiens rhodesiensis*)." Rak (1998), however, astutely observed that both rami are symmetric in appearance with equal-sized condylar and coronoid processes separated by a deep and symmetrical notch, and that this "anatomy is diagnostic enough to confidently rule out the possibility that they are Neanderthals and strongly suggests that they are *Homo sapiens*." Hublin (2000) subsequently pointed out some additional features (e.g., the lack of a retromolar space and the shape of the mandibular foramen) that argue against their Neandertal affinity.

McBurney (1967) estimated the "Phase A" basal "Pre-Aurignacian" layers to be 80–65 ka on the basis of climatic reconstructions. Some workers (e.g., Meignen 2007; Foley et al. 2013) have seemingly accepted McBurney's (1967) description of this as a blade-artifact assemblage, which would most closely resemble the "Amudian" at sites such as Qesem and Tabun in Israel (Garrod 1970; Jelinek 1990; Copeland 2000; Meignen 2000; Barkai et al. 2005). The relevant level at Tabun (Layer Ea of Garrod and Unit XI of Jelinek) has been dated by TL to some 264 ka (Mercier and Valladas 2003), and the Acheuleo-Yabrudian, of which the Amudian is a facies at Qesem has been dated by ^{230}Th/^{234}U TIMS to between 382 and 152 ka (Barkai et al. 2003). However, Reynolds' (2013) analysis of the "Pre-Aurignacian" lithics from Haua Fteah indicates that all of its "typological elements" can be found with variable degrees of expression in the overlying Levalloiso-Mousterian, and that it has closer affinities to the overlying Middle Paleolithic assemblage at Haua Fteah than to anything else. As such, the "Pre-Aurignacian" provides no information relating to the age of the human jaws that overlie it.

The lowermost "Levalloiso-Mousterian" layers (XXX–XXXVI) were interpreted as possibly representing the early cooler phase of the last glaciation on the basis of paleotemperature reconstructions from marine mollusk shells (Emiliani et al. 1964; McBurney 1967). Klein and Scott (1986), however, have argued that layers XXII–XXXV may equally well belong to MIS 4 and/or MIS 3 on the basis of faunal composition.

Vogel and Waterbolk (1963) obtained a conventional radiocarbon date for burnt bone from Layer XXXIII of 45,050 ± 3200 ^{14}C BP. Employing this date, McBurney (1967) considered this BII phase of occupation to have begun ~55 ka, and to have been followed by a stage (Phase

BIII) of "probably Aterian character." However, the validity of this radiocarbon date has been discounted by some workers (e.g.; Klein and Scott 1986; Hublin 2000; Klein 2009). Indeed, Lowe et al. (2012) have recently identified Campanian Ignimbrite deposits that date to 39.28 ± 0.11 ka (DeVivo et al. 2001; Fitzsimmons et al. 2013) in Haua Fteah. These ashes are within a continuous sequence of Upper Paleolithic ("Dabban") deposits that clearly overlie the "Levalloiso-Mousterian" layers from which the human jaws derive (Lowe et al. 2012). Thus, the mandibles must predate 40 ka; Klein (2009) has suggested that the jaws may be anywhere between 50 and 130 ka.

Although Hublin (2000) states that the hominin-bearing level underlies the Aterian, which might establish the upper age limit for it, Haua Fteah does not preserve an Aterian assemblage (Scerri 2013; Reynolds 2013). Indeed, even if the Aterian was evident in Haua Fteah (as Phase BIII overlying the jaws in Phase BII), dates for the Aterian in North Africa (synthesized in Scerri 2013) range from c. 145 ka at Ifri n'Ammar, Morocco (Richter et al. 2010), to c. 61 ka at Uan Tabu, Libya (Cremaschi et al. 1998).

More recent work at Haua Fteah, however, indicates that the lower "Levalloiso-Mousterian" levels at the site date to the latter part of MIS 5 (MIS 5a) or the earlier part of MIS 4 (Lane et al. 2011; Reynolds 2013; Douka et al. 2014). Lane et al. (2011) obtained an age of c. 67.5 ka for a sample of hidden, diminutive volcanic ash layers (cryptotephra) just above the level from which the human jaws were extracted; this tephra layer now has a more secure varve date of 68,620 ± 2060 BP (Douka et al. 2014). Additional work has suggested that these early Levalloiso-Mousterian levels at Haua Fteah date to ~80 ka (Douka et al. 2014). In particular, the human mandibles are likely to date to this interval (Barker personal communication).

Mumba Shelter, Tanzania (3°32′ S, 35°19′ E)

This rock shelter is located in close proximity to Lake Eyasi. It has yielded three isolated, comparatively small human molars in an MSA context (Bräuer and Mehlman 1988). The molars derive from the basal deposits (Bed VI-B) for which uranium-thorium and uranium-protactinium measurements on bone have yielded average estimates of some 132 and 109 ka, respectively (Bräuer and Mehlman 1988). However, as noted by Millard (2008), U-series dates on bone cannot be relied upon without investigation of their uranium uptake history. More recently, Gliganic et al. (2012) have obtained both optically stimulated and infrared stimulated luminescence (OSL and IRSL) measurements on single grains of quartz and multigrain aliquots of potassium feldspar from the MSA horizons. These have provided dates of 63.4 ± 5.7 and 73.6 ± 3.8 ka respectively for the Bed VI-A deposits that overlay the human teeth. The MSA human remains are unlikely to be much older given their degree of stratigraphic separation from the dated horizons.

Human Fossils Associated with MIS 4 (71–57 ka)

A major shift in global climatic conditions occurred from the warmer, interglacial conditions of MIS 5 to the significantly cooler glacial conditions of MIS 4. Some have speculated that this shift, at ~71 ka, coincides with the Toba super-eruption, which would have caused a long-lasting "volcanic winter" triggering the MIS 4 Ice Age due to the huge volume of gas and ash that it injected into the atmosphere (e.g., Rampino and Self 1992, 1993). However, this specific trigger event has been questioned by several studies, which found no evidence for persistent climatic perturbation associated with it (e.g., Zielinski et al. 1996; Schulz et al. 2002). In fact, the Mt. Toba eruption appears to precede the onset of MIS 4 by ~3 kyr or more (Mark et al. 2014). Moreover, ash from the Toba eruption (the Youngest Toba Tuff) has been identified in the sediment bed of Lake Malawi, and this is not accompanied by any change in sediment composition or evidence for substantial temperature change. This eruption does not seem to have significantly impacted the climate of East Africa (Lane et al. 2013).

In Africa, MIS 4 is generally asserted to have witnessed relatively dry conditions (e.g., Avery 1982; Dupont 2011), although there was almost certainly significant variation at the local scale (e.g., Chase 2010). Indeed, Adams (1997) has provided a model that predicts much of sub-Saharan Africa to have been covered in grassland at this time, and water levels in Lake Malawi varied throughout MIS 4 (Lyons et al. 2011; Scholz et al. 2011). Chase (2010) has argued that in southern Africa, there is a relationship between the climatic conditions of MIS 4 and the occurrence of archaeological traditions such as the Still Bay and Howiesons Poort.

Three sites in South Africa (Die Kelders, Klipdrift Shelter, and Sibudu) and one site in Ethiopia (Porc-Épic) have deposits that began to accumulate towards the onset of MIS 4. Deposition at Sibudu and Porc-Épic appears to have continued throughout much of the succeeding MIS 3. The human fossils from Die Kelders and Klipdrift Shelter most likely date to MIS 4, and the human jaw from Porc-Épic probably also dates to this interval (Table 17.5; Fig. 17.4). The human bones from Sibudu date to MIS 3.

Table 17.5 African hominin-bearing sites and hominin fossils associated with MIS 4

Site/specimen	Country	Coordinates	Age (ka)
Porc-Épic	Ethiopia	09°34′ N, 41°53′ E	78–36
Die Kelders	South Africa	34°32′ S, 19°22′ E	74–59
Klipdrift Shelter	South Africa	34°27′ S, 20°43′ E	64

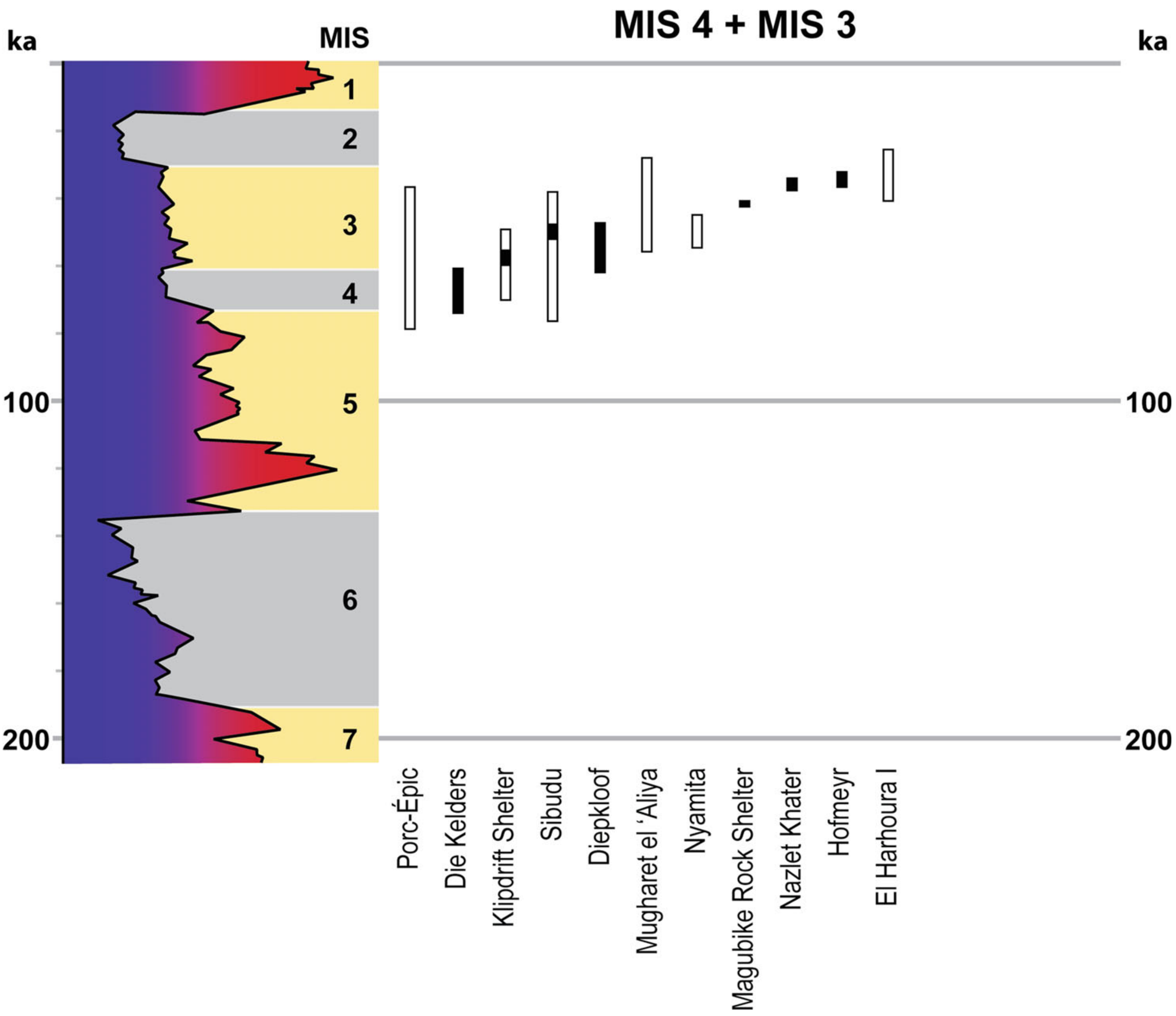

Fig. 17.4 Distribution of age determinations and/or estimates for hominin fossils and hominin-bearing sites that are most reasonably related to Marine Isotope Stages 4 and 3. *Open rectangles* represent possible age ranges deduced for a site or specimen; *solid rectangles* represent well-established dates for the hominin fossils

Thus, there are only three sites whose hominin remains are considered here as being associated (or likely associated) with MIS 4 (Fig. 17.4; Table 17.5). These three are discussed below in the order in which they appear in Fig. 17.4 and Table 17.5.

Porc-Épic, Ethiopia (9°34′ N, 41°53′ E)

This cave site is located in a steep cliff face some three km south of the town of Diré Dawa in southeastern Ethiopia. It was first excavated in 1929 by P. Teilhard de Chardin

(Teilhard de Chardin 1930). In 1933 a fragment of human mandible was recovered during excavations led by Teilhard de Chardin and P. Wernert (Breuil et al. 1951) The specimen was initially assessed by Vallois (1951) as an Ethiopian "neanderthaloid." Bräuer (1984a) described it as lacking specific Neandertal features (e.g., a retromolar gap), but he noted that it exhibits some archaic traits (e.g., a vertical symphysis without a chin).

Unfortunately, details of stratigraphy and specimen location from these early excavations were not well documented, and it is possible that some of the materials described as coming from the MSA strata are intrusive from the overlying LSA (Clark and Williamson 1984). In 1974, excavations were undertaken under the leadership of J. Desmond Clark with the object of reconstructing the stratigraphic sequence in the cave, and providing additional MSA artifacts (Pleurdeau 2005). Obsidian hydration dating provided ages for the MSA occupation of between 61.2 and 77.5 ka (Michels and Marean 1984). Unfortunately, the dated artifacts are from the 1933 excavation and lack adequate stratigraphic provenance, and AMS dating of gastropod shell yielded an age range of between >43.2 and c. 35.6 ^{14}C kBP (Assefa 2006). Although Millard (2008) concluded that a date no more precise that "later Pleistocene" can be attributed to the human mandible, it would seem likely to date to somewhere between 78 and 36 ka, and probably closer to the former if it does (as seems likely) come from the MSA levels.

Die Kelders, South Africa (34°32′ S, 19°22′ E)

This site, also known as Klipgat, consists of a pair of contiguous caves situated at sea level on the southeastern Atlantic coast of South Africa. Initial excavations by F. Schweizer between 1969 and 1973 revealed a rich LSA occupation and a thick series of MSA layers below. The bulk of the MSA is situated in Cave 1 (referred to as DK1). Schweitzer's excavations produced nine isolated human teeth from the MSA levels (levels 4–17), with most deriving from level 6 (Grine et al. 1991). Subsequent excavations of DK1 between 1992 and 1995 led by C.W. Marean, R.G. Klein, G. Avery and F.E. Grine resulted in the recovery of an additional 18 human specimens comprising isolated teeth, a small mandibular fragment and two manual phalanges (Grine 1998, 2000). These are distributed from level 4 through level 15, but most come from level 6.

As might be expected for teeth of this antiquity, most of the crowns tend to be large in comparison to recent African homologues. However, the majority of morphological variants displayed by the DK1 teeth characterize those of recent sub-Saharan Africans, and they resemble recent African homologues in a number of traits that have been used to define a sub-Saharan African regional complex. These morphological similarities, however, do not necessarily signify a close evolutionary relationship between them, because the crowns variants appear to be plesiomorphic (Grine 2000). The teeth also evince a modern human pattern of crown development (Smith et al. 2006).

Luminescence and early uptake model ESR dates place the deposits in the range of ~70–60 ka (Feathers and Bush 2000; Schwarcz and Rink 2000), and sedimentological considerations suggest an age for the entirety of the MSA in DK1 between some 74–59 ka, that is, within MIS 4 (Grine 2000). Millard (2008) has employed a Bayesian stratigraphic model incorporating the luminescence and early uptake ESR dates published by Feathers and Bush (2000) and Schwarcz and Rink (2000) to deduce a considerably wider range of possible ages of 85–48 ka. This is certainly within the realm of possibility, although the close proximity of the cave mouth to the present shoreline would seem to argue against deposition during MIS 5a, as the rise in sea level at this time would have scoured the cave (Grine et al. 1991; Grine 2000; Goldberg 2000).

Klipdrift Shelter, South Africa (34°27′ S, 20°43′ E)

This site, together with Klipdrift Cave and Klipdrift Cave Lower, comprises the Klipdrift Complex located in the De Hoop Nature Reserve, southern Cape Province, South Africa. The complex is situated some 12–15 m from the Indian Ocean coast. Test excavations under the leadership of C. Henshilwood and K. van Niekerk in 2011 in the Klipdrift Shelter revealed a c. 1.6 m deep deposit of horizontally stratified MSA deposits immediately below a steeply sloping, eroded surface. Subsequent excavations in 2012 and 2013 showed these layers to contain marine shells, terrestrial faunal remains (dominated by tortoise and small mammals), ash lenses and hearths, ochre, engraved ostrich eggshells, and lithic artifacts (Henshilwood et al. 2014).

The MSA levels at Klipdrift Shelter have been dated by single-grain optically stimulated luminescence (OSL). The artifacts in the uppermost level appear to relate to a post-Howiesons Poort industry, and these are associated with an OSL date of 51.7 ± 3.3 ka. The lowermost stratigraphic level at the site, which contains no anthropogenic material, has been dated to 71.6 ± 5.1 ka. The middle layers contain abundant artifacts attributed to the Howiesons Poort, and are dated to between 65 and 60 ka.

An isolated human mandibular second deciduous molar crown was recovered from one of the lowermost HP layers (designated PBE), and would appear to be most closely

Table 17.6 African hominin-bearing sites and hominin fossils associated with MIS 3

Site/specimen	Country	Coordinates	Age (ka)
Sibudu	South Africa	29°31′ S, 31°05′ E	48
Diepkloof Rock Shelter	South Africa	32°25′ S, 18°30′ E	61–48
Mugharet el ‘Aliya	Morocco	35°45′ N, 05°56′ W	57–27
Nyamita	Kenya	00°24′ S, 34°10′ E	55–45
Magubike Rock Shelter	Tanzania	07°45′ S, 35°28′ E	42
Nazlet Khater	Egypt	26°47′ N, 31°21′ E	38
Hofmeyr	South Africa	25°58′ E, 31°34′ S	36
El Harhoura I	Morocco	33°57′ N, 06°55′ W	41–26

associated with a date of c. 64 ka (Henshilwood et al. 2014). Unlike penecontemporaneous homologues from Die Kelders, where most of the crowns tend to be large in comparison to recent African homologues, the Klipdrift molar is comparable in size to recent South African dm_2s. Like the other deciduous teeth that have been recovered from the Howiesons Poort levels at sites such as Klasies River Main Site (Grine 2012) and Diepkloof Rock Shelter (Verna et al. 2013), the Klipdrift Shelter crown is comparatively small (Harvati et al. 2015). The majority of morphological variants displayed by the Klipdrift molar also characterize those of recent sub-Saharan Africans, and it resembles recent African homologues in a number of traits that have been used to define a sub-Saharan African regional complex. These morphological similarities, however, appear to be plesiomorphic (Grine 2000). The sole exception pertains to the presence of a “mid-trigonid” crest on the Klipdrift crown; this variant is not unknown among modern San and South African populations, but it is comparatively rare (at some 3–8%).

Human Fossils Associated with MIS 3 (57–29 ka)

During the last glacial period of MIS 3, global climate underwent strong millennial-scale fluctuations. The Northern Hemisphere experienced repeated abrupt warming phases (Dansgaard-Oeschger events), characterized by shifts of up to 16 °C between stadial (cold phase) and interstadial (warm phase) climates that occurred sometimes on the order of a few decades (Dansgaard et al. 1993). These abrupt climatic shifts, although best expressed in the North Atlantic, were almost certainly important on a global scale, with effects seen in the South Atlantic as well (Crowley 1992; Stocker 1998; Compton 2011; Hessler et al. 2011). However, in the context of the abrupt climatic perturbations that characterized MIS 3, only sparse terrestrial paleoecological information is available, and much of this comes from sites located in Mediterranean Europe (Voelker et al. 2002; Ziegler et al. 2013).

North Africa experienced a generally humid period (Castañeda et al. 2009) and Lakes Malawi and Tanganyika experienced highstands throughout most of MIS 3 (Trauth et al. 2003; Lyons et al. 2011; Scholz et al. 2011), but evidence from Lake Tanganyika also reveals changes in lake water temperature and precipitation, indicating pulses of aridity that are consistent with Northern Hemisphere Heinrich events (Tierney et al. 2008). Vegetation and climatic changes for at least some of MIS 3 in South Africa have been recorded from fossil plant material in Sibudu Cave (Bruch et al. 2012). This work has shown that climatic changes were reflected most pronouncedly by winter temperatures (especially minimum winter temperatures), and to a lesser extent by changes in summer precipitation. Ecological trends seem to be affected mainly by the former.

Mitchell (2008) has reviewed the available paleoecological information for South Africa during MIS 3, and while he has identified a good number of archaeological sites that he argues date to MIS 3, the human paleontological record for this period in southern Africa – indeed, throughout Africa – remains woefully small. There are eight sites throughout the entire continent whose human remains date to MIS 3 (Table 17.6; Fig. 17.4). These are discussed below in the order in which they appear in Fig. 17.4 and Table 17.6.

Sibudu Cave, South Africa (29°31′ S, 31°05′ E)

This rock shelter, located some 15 km inland from the Indian Ocean in KwaZulu-Natal, was discovered and first excavated by A. Mazel in 1983. Current excavations, under the direction of L. Wadley, began in 1998 and these have demonstrated a stratified sequence of intermittent occupation with Still Bay, Howiesons Poort and final MSA phases (Wadley and Jacobs 2004, 2006; Wadley 2007). Indications are that the site was occupied throughout MIS 3, but during its wetter rather than its drier phases (Jacobs et al. 2008b). Wadley’s efforts have provided evidence for the earliest recorded bow and arrow technology, as well as for bone needles (Backwell et al. 2008; Lombard and Phillipson 2010), the use of a heat-treated glue compound (Wadley et al. 2009), bedding (Wadley et al. 2011) and possible shell beads (d'Errico et al. 2008) in MSA context.

Despite its spectacular archaeological record, Sibudu Cave is virtually lacking in human remains. Two specimens thought to probably derive from a single individual have been recorded as possibly coming from the final MSA (Plug 2004). These bones comprise a distal fibula and a manual phalanx. Although some Iron Age pits had been dug into the final MSA deposits in the cave, extreme care was taken to clear these before commencing work in the MSA strata, and no human bone was ever recorded as coming from the Iron Age pits. Thus, although Plug (2004) considered that these two human bones were intrusive owing to their "relatively fresh" appearance, this possibility would seem to be reasonably remote (Wadley personal communication).

A series of OSL dates from various levels in Sibudu place occupation of the site from ~77.2 to 38.0 ka (Wadley and Jacobs 2006; Jacobs et al. 2008a, b). The levels of the horizons from which the human remains derive within the final MSA strata would indicate an age of c. 48 ka for these two bones (Wadley personal communication).

Diepkloof Rock Shelter, South Africa (32°25′ S, 18°30′ E)

This rock shelter is located approximately 180 km north of Cape Town and some 17 km from the Atlantic Ocean at Elands Bay in the Western Cape Province of South Africa. The site was first excavated by J. Parkington and C. Poggenpoel in 1973, and subsequent work has uncovered a deep record of MSA occupation – including Still Bay and Howiesons Poort horizons – that dates from MIS 5-3 (Parkington and Poggenpoel 1987). The site is perhaps best known for fragments of engraved ostrich eggshell from the Howiesons Poort levels (Texier et al. 2010).

Excavations in 2002 recovered a mandibular deciduous molar in the latest Howiesons Poort levels and two pedal phalanges from post-Howiesons Poort strata (Verna et al. 2013). The toe bones are indistinguishable from those of recent humans; the molar is morphologically unremarkable but comparatively large in relation to recent homologues.

Thermoluminescence dates of the Howiesons Poort levels yielded a weighted average of some 52 ± 5 ka, but with high environmental dose rate variability (Tribolo et al. 2009). In the sector where the human toe bones were found, OSL dates give consistent ages of between 61.3 ± 1.9 and 58.1 ± 1.9 ka and for this Howiesons Poort occupation, and the layer from which the tooth was extracted is dated by OSL to 60.5 ± 1.9 ka. The post-Howiesons Poort layers located above the layer that yielded the toe bones has been dated by OSL to between 55.4 ± 2.0 and 47.7 ± 1.7 ka (Tribolo et al. 2009, 2013).

Mugharet el 'Aliya, Morocco (35°45′ N, 5°56′ W)

This cave site, situated some 11 southwest of Tangier on Cap Ashakar, was first excavated in the 1930s by C. Coon, who recovered a juvenile human maxilla (Tangier 1) *ex situ*. Two isolated molars discovered subsequently likely belong to the same individual, and another isolated upper molar derives from a second individual (Minugh-Purvis 1993). The site, also referred to simply as Tangier or as Dar el 'Aliya, contains a thick accumulation of fauna and Aterian artifacts. The human remains are believed to derive from one of the uppermost Aterian levels (Layer 5). Although initial assessment of the remains suggested their Neandertal affinities (Şenyürek 1940), the maxilla shares features with those from other North African Aterian contexts (Hublin 1993), and these are of modern appearance (Minugh-Purvis 1993).

Although none of the human specimens was recovered *in situ*, they are all believed to have come from layer 5. Electron spin resonance dates from one mammal tooth each from layers 9, 6, and 5 have produced estimates of between 56 and 39 ka (Wrinn and Rink 2003). However, Millard (2008) has argued that the gamma dose rate from the sediment seems to have been miscalculated by Wrinn and Rink (2003), which would revise the dates for the human remains to 46–21 ka assuming early uranium uptake, and 57–27 ka assuming linear uptake. These age estimates are significantly younger than the OSL dates of 107–96 ka obtained by Schwenninger et al. (2010) and Jacobs et al. (2011) for the Aterian levels at the nearby Smugglers' Cave, and they are also substantially younger than the youngest TL and OSL dates of c. 61 ka recorded for *in situ* Aterian artifacts at Uan Tabu, Libya (Cremaschi et al. 1998).

Nyamita (Wasiriya Beds), Kenya (0°24′ S, 34°10′ E)

The artifact and bone-bearing Late Pleistocene Wasiriya Beds, which are discontinuously exposed around the perimeter of Rusinga Island on the northeastern edge of Lake Victoria, have been known since the 1940s (van Couvering 1972; Pickford 1986). However, the first systematic archaeological surveys and excavations of these exposures were initiated only in 2009 (Tryon et al. 2010). This work has focused on the recovery of artifacts and fossils from several localities along the southern margin of the island, including Wakondo and Nyamita. The MSA artifacts recovered from the Wasiriya Beds are typologically distinct from Lupemban assemblages in the region around Lake Victoria, and include Levallois flakes and very small bifacially flaked points that are similar to those from other tropical grassland MSA localities in the East African Rift (Tryon et al. 2010, 2012). Alcelaphines (e.g., wildebeest) and equids dominate the faunal assemblages, indicating the presence of an open grassland that is distinct from the historic vegetation. Several extinct bovids are represented, and these are characterized by dental or postcranial adaptations to grazing in open habitats (Faith et al. 2016).

A series of AMS radiocarbon dates of between c. 45 and 33 ka obtained from the carbonate fractions of intrusive gastropod shells at the Nyamita 2 and Nyamita 3 localities indicate that the Wasiriya beds predate MIS 2 (Tryon et al. 2010). The maximum age of the Wasiriya Beds would appear to be constrained by the geochemistry of the basal phonolitic tephra deposits at Nyamita and Wakondo, which suggest derivation from the Logonot and/or Suswa volcanoes that began erupting at ~100 ka (Tyron et al. 2010).

The only human fossil that has been recovered from the Wasiriya Beds to date is a partial right humeral diaphysis. It was found during surface collecting at Nyamita in 2010 and identified as human in 2013 by J.T. Faith. The proximal end is missing, probably as a result of carnivore damage, and there is an old break approximately mid-shaft, just distal to the deltoid tuberosity (Faith personal communication). It is currently under study by O.M. Pearson. A combination of OSL, ESR, and U-Series age estimates of 75–55 ka for the stratigraphically lower Wakondo locality (Blegen et al. 2015; Faith personal communication) constrains the lower age limit for the specimen, and its upper limit is established by the radiocarbon dates for the intrusive snails at Nyamita. Thus, the specimen almost certainly dates to MIS 3, and an age between 55 and 45 ka would seem to be a reasonable estimate.

Magubike Rock Shelter, Tanzania (7°45′ S, 35°28′ E)

This rock shelter is located close to the village of the same name in the Iringa Region of southern Tanzania. Test excavations were undertaken by Pamela Willoughby in 2005, and these revealed a sequence containing historic/Iron Age and LSA artifacts separated by some 30 cm of mixed MSA and LSA artifacts from underlying MSA strata (Biittner et al. 2007; Biittner 2011; Collins and Willoughby 2010; Willoughby 2012). A half dozen isolated human maxillary teeth were recovered from the MSA deposits; four of the teeth derive from a 10 cm deep level just below the disturbed horizon, and the other two were separated by a further 10 cm of deposit (Willoughby 2012). Some of the teeth exhibit traits found in moderate to high frequencies in recent sub-Saharan African human samples (Willoughby personal communication), but this is to be expected since other Late Pleistocene human teeth from southern Africa do as well (Grine and Klein 1985, 1993; Grine 2000; Grine et al. 2000; Grine and Henshilwod 2002).

A radiocarbon date of 41,790 ± 690 ^{14}C BP, calibrated to 43,020 ± 830 cal BP (using CalPal), has been obtained from snail shells from the same level as the human teeth (Willoughby 2012), although which level was not specified. More recently, ESR determinations on snail shells from this layer suggest an age in excess of 200 ka (Willoughby personal communication). However, the extremely porous nature of gastropod shell makes it of highly questionable utility in uranium-based age assessments (Schellmann and Radtke 1999; Feathers 2002). This, together with other factors such as the incredible discrepancy between the ESR and ^{14}C determinations suggests that little reliance can be placed on these supposedly more ancient dates.

Nazlet Khater, Egypt (26°47′ N, 31°21′ E)

Nazlet Khater comprises eight geographically proximate archaeological sites associated with intermittent Middle and Upper Paleolithic chert-mining activities close to the Nile River in Egypt. The locality takes its name from a nearby village. Excavations in 1980–1982 recovered two burials (Nazlet Khater 1 and Nazlet Khater 2) in Upper Paleolithic context at the locality known as Boulder Hill. The burials are associated with the Upper Paleolithic chert-mining site of Nazlet Khater IV (Vermeersch 2002).

Nazlet Khater 1 (NK 1) is a very poorly preserved skeleton of an adult female associated with fetal bones (Vermeersch 2002). Owing to its state of preservation, the bones of NK 1 were never subjected to any morphometric analysis before they were submitted for ^{14}C dating. Nazlet Khater 2 is a nearly complete adult male skeleton (Vermeersch et al. 1984). Considerable attention has been paid to it (Thoma 1984; Pinhasi and Semal 2000; Bruner and Manzi 2002; Pinhasi 2002; Crevecoeur and Trinkaus 2004; Crevecoeur 2008a, 2009, 2012; Bouchneb and Crevecoeur 2009). Despite its overall modern appearance (the cranium is described as "robust," but it lacks a supraorbital torus and displays a projecting chin, rounded cranial form and modest dental dimensions), several archaic features are noteworthy. These include thick cranial vault bone, the broad ramus and robustness of the mandibular corpus, and the inner ear, which presents features that are unusual among recent humans, but occur with some frequency among Middle and Upper Paleolithic specimens from Eurasia (Crevecoeur and Trinkaus 2004; Bouchneb and Crevecoeur 2009; Crevecoeur 2012). The postcranial skeleton exhibits a few traits that may be plesiomorphic, such as the marked angulation of the radial neck and shaft (Crevecoeur 2012). Comparative morphometric analyses of Nazlet Khater 2 and other Late Pleistocene specimens paint a picture of variation that is distinctly elevated relative to that among recent humans (Crevecoeur et al. 2009).

The two burials are dated to the latter part of MIS 3 by AMS ^{14}C, OSL, and ESR (Stokes and Bailey 2002). In particular, the NK 1 skeleton is AMS-dated to 37,600 ± 350 ^{14}C BP, and NK 2 is dated to c. 38 ± 6 ka on the basis of ESR on tooth enamel fragments (Crevecoeur 2008a; Crevecoeur et al. 2009).

Hofmeyr, South Africa (25°58′ E, 31°34′ S)

The Hofmeyr skull was discovered in 1954 by a farmer digging for sand in a dry channel bed of the Vlekpoort River near the town of the same name, in the Eastern Cape Province of South Africa. This isolated partial human skull is without any associated archaeological or faunal evidence, and it lacks clear geological context. When it was discovered, the cranium was nearly complete, but subsequent mishandling has resulted in the loss of much of the lower face and occipital. The specimen has been partially reconstructed using mirror imaging, clay modeling, and reference-based methods from photographs and measurements recorded prior to the damage (Grine et al. 2010).

The cranium is overall morphologically modern, but it possesses a moderately strong supraorbital torus and projecting glabella as well as marked alveolar prognathism (Grine et al. 2007, 2010). Morphometric analyses showed it to have close affinities to penecontemporaneous Upper Paleolithic specimens from Eurasia and to reside at the edge of the range of variation for recent sub-Saharan Africans (Grine et al. 2007). Comparisons of it with penecontemporaneous remains from Egypt (Nazlet Khater) and Europe (Peştera cu Oase) point to a greater range of variability in Late Pleistocene human crania than may be evident today (Crevecoeur et al. 2009), although aboriginal Australians were not included in that analysis. The reconstructed cranium (Grine et al. 2010), which has yet to be studied in a comparative phenetic context, may reveal additional or novel insights into its morphometric affinities.

No excavation was undertaken at the time of the discovery, and within a decade the channel from which it came had become filled by silt following the construction of an anti-erosion dam downstream. This precludes any possibility of locating the original position of the skull or of directly dating the surrounding sediments. The bone lacks sufficient collagen to be amenable to direct AMS ^{14}C dating. As a result, the heavily indurated carbonate sand matrix that largely filled the endocranial cavity was analyzed using a combination of OSL and U-series dating methods to estimate the burial time of the skull at 36.2 ± 3.3 ka (Grine et al. 2007).

El Harhoura I, Morocco (33°57′ N, 6°55′ W)

The cave of Zouhrah at El Harhoura 1 is situated between Dar es-Soltan and Grotte des Contrebandiers. It was excavated in the 1970s by A. Debénath, who recovered a canine from the Aterian level. In 1977, a mandible and an isolated canine were found during a salvage operation; while their provenance is uncertain, it is believed that they also derive from the Aterian strata (Debénath 1979, 1980).

The lower Aterian level (Niveau 2), which is the source for the excavated human canine, has been dated to between 41.2 and 25.5 ka by thermoluminescence on the basis of material that derives from the superjacent level (Niveau 3) (Aouraghie and Abbassi 2002). These dates are in keeping with Millard’s (2008) revised estimates for the Aterian at Mugharet el ‘Aliya (i.e., 57–21 ka). However, they are younger than the dates for the aforementioned Aterian levels at Smugglers’ Cave and Uan Tabu.

The teeth from the Aterian at El Harhoura I have been studied by Hublin et al. (2012), who commented upon their very large size.

Human Fossils Associated with MIS 2 (29–14 ka)

During the last part of MIS 3, global climate underwent strong millennial-scale fluctuations. The Northern Hemisphere experienced repeated and abrupt warming and cooling phases, which also affected the African climate. The end of MIS 3 witnessed the growth of ice sheets to their maximum positions between 33.0 and 26.5, and almost all were position at their maximum (the Last Glacial Maximum, or LGM) between 26.5 and 20 ka (Clark et al. 2009).

The growth of these ice sheets had a profound impact, causing desertification in many regions of Africa – especially an expansion of the Sahara and Kalahari/Namib deserts – and a drop in sea level that exposed variably wide swaths of land. Paleovegetation (pollen and plant macro-remains) and lake-level data suggest overall drought conditions in East

Table 17.7 African hominin-bearing sites and hominin fossils associated with MIS 2

Site/specimen	Country	Coordinates	Age (ka)
Ishango 11	Democratic Republic Congo	00°08′ S, 29°36′ E	26–20
Taramsa 1	Egypt	26°06′ N, 32°42′ E	24
Leopard's Hill Cave	Zambia	15°36′ S, 28°44′ E	24–22
Lukenya Hill	Kenya	01°29′ S, 37°04′ E	24–22
Tuinplaas	South Africa	25°00′ S, 28°36′ E	<20–11
Deir El-Fakhuri (E71K1) (Esna)	Egypt	25°22′ N, 32°28′ E	18
Taza Cave I	Algeria	36°42′ N, 05°32′ E	16–14
Afalou-bou-Rhummel	Algeria	36°29′ N, 03° 00′ E	15–11
Gebel Silsila 2A (Kom Ombo)	Egypt	24°28′ N, 32°57′ E	14–13
Jebel Sahaba (Site 117)	Sudan	21°59′ N, 31°20′ E	14–12
Wadi Halfa (Sites 6B28 & 6B36)	Sudan	21°57′ N, 31°20′ E	14–10
Ifri n'Baroud	Morocco	34°53′ N, 03°20′ E	13
Bushman Rock Shelter	South Africa	24°35′ S, 30°38′ E	13
Mlambalasi Rock Shelter	Tanzania	07°35′ S, 35°30′ E	13–12 (? *in situ*)
Grotte des Pigeons (Taforalt)	Morocco	34°48′ N, 02°24′ W	13–11
Iwo Eleru	Nigeria	07°26′ N, 05°08′ E	11

Africa (Farrera et al. 1999; Barker and Gasse 2003; Filippi and Talbot 2005). In South Africa, cooler and potentially wetter conditions prevailed (Partridge et al. 1999; Mills et al. 2012), and there is evidence for an expanded winter rainfall zone (Chase and Meadows 2007). In North Africa, the Maghreb appears to have been relatively cool and arid with expanded steppe and lower water levels in Lake Chad during the LGM; this was followed at ~15 ka by an increase of pollens indicative of higher humidity – the so-called "African Humid Period," or AHP (Close and Wendorf 1990; deMenocal et al. 2000). Recent evidence from the Gulf of Aden indicates that the AHP was very abrupt both in its initiation and termination (i.e., occurring within centuries) in the Horn of Africa (Tierney and deMenocal 2013).

However, while the terminal Pleistocene-early Holocene AHP witnessed abundant North African lakes and a variable rise in Central and East African lake levels, those in South Africa stood at considerably lower levels (Hoelzmann et al. 2002; Johnson et al. 2002; Thomas and Shaw 2002; Schefuß et al. 2005; Weldeab et al. 2005; Kuper and Kröpelin 2006; Garcin et al. 2009; Thomas et al. 2009; Tierney et al. 2011; Foerster et al. 2012; Lebamba et al. 2012). Moreover, time-transgressive terrestrial changes during the AHP have been documented even *within* the Sahara (e.g., deMenocal et al. 2000; Kuper and Kröpelin 2006; Cole et al. 2009; Larrasoaña 2012), as well as between northern and southern Africa (Gasse 2000; Gasse et al. 2008).

During the Last Glacial Maximum (LGM) the Maghreb is believed by some to have been largely depopulated c. 20–18 ka (Lubell 1984, 2001; Close and Wendorf 1990; Larrasoaña 2012). Similarly, Wadley (1993) has speculated, "the harsh conditions of the LGM over much of southern Africa may have resulted in widespread resource shortages."

A number of sites in North Africa (especially in Algeria) that date to the terminal Pleistocene-early Holocene have yielded fragmentary human remains associated with the microliths and backed bladelets that characterize the Epipaleolithic (Iberomaurusian) tradition there. These sites include Alain, Cap Tenes, Champlain, Ifri n'Ammar, and La Mouillah. Other sites, such as Columnata, contain large assemblages of human skeletons (c. 60 individuals; Chamla 1970) or very poorly preserved human remains (e.g., Tushka Site 8905, Locality A) that clearly date to the beginning of MIS 1. None of these sites is included in the present review.

Fifteen sites spread across the length and breadth of Africa contain human remains in reasonably well-dated contexts that help to document aspects of skeletal and dental variability during the period represented by MIS 2 (Table 17.7; Fig. 17.5). These 15 are discussed below in the order in which they appear in Fig. 17.5 and Table 17.7.

Ishango 11, Democratic Republic of the Congo (0°8′ S, 29°36′ E)

This site is located on the bank of the Semliki River at its exit from Lake Rutanzige (formerly Lake Edward) on the western side of the Democratic Republic of the Congo. It was discovered by H. Damas in 1935. He found a human jaw and several bone harpoons in a partially cemented sand-gravel matrix (Damas 1940). The site was excavated in the mid-1950s under the direction of J. de Heinzelin, and the mid-1980s by A. Brooks, J. Yellen and K. Misago. Ishango 11 preserves horizons that relate to early LSA and Holocene (Neolithic) occupations, and both preserve human skeletal

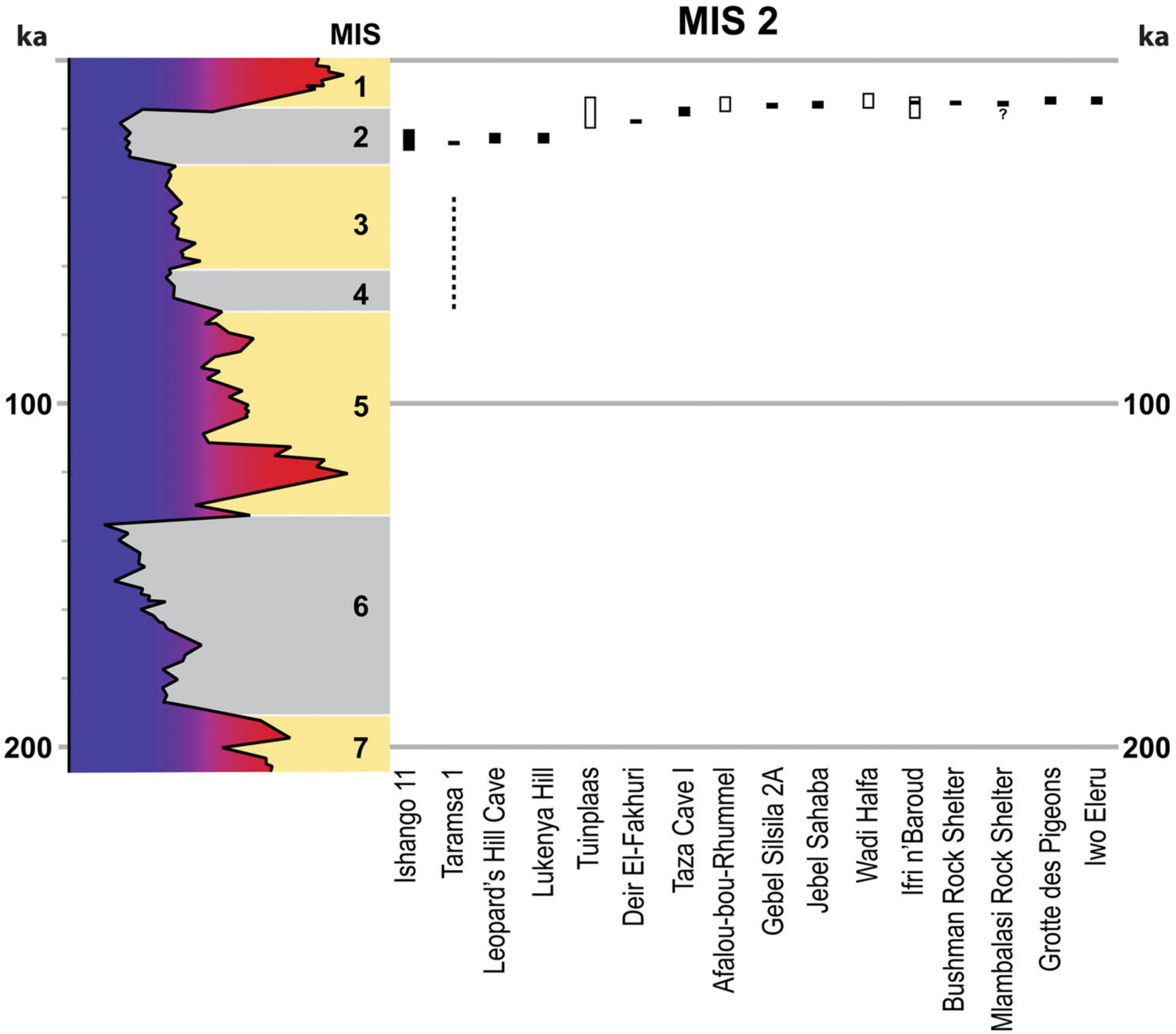

Fig. 17.5 Distribution of age determinations and/or estimates for human remains and human-bearing sites that are most reasonably related to Marine Isotope Stage 2. *Open rectangles* represent possible age ranges deduced for a site or specimen; *solid rectangles* represent well-established dates for the hominin fossils; *dotted lines* indicate possible but not probable dates; ? indicates likely disturbed context

remains. The LSA horizon, referred to as the Principal Fossiliferous Layer (Niveau Fossilifére Principal, or NFPr), contains a rich faunal assemblage and abundant archaeological debris, including quartz microliths, numerous barbed bone harpoon points, and engraved bone.

The human remains recovered by de Heinzelin from the NFPr comprise skull fragments, isolated teeth, and variably complete postcranial bones; 27 additional human fragments from this layer were uncovered by Brooks and collaborators (Twiesselmann 1958; de Heinzelin 1962; Boaz et al. 1990; Brooks et al. 1991). The entire collection represents five adults, one adolescent, three children, and two perinatal individuals (Crevecoeur personal communication). Various studies of these remains (e.g., Orban et al. 2001; Crevecoeur 2008b; Crevecoeur et al. 2010) indicate the crania to be comparatively robust, the teeth to be large, and the inner ear morphology to be unusual. The limb bone diaphyses are straight, and possess comparatively thick cortices. The appendicular remains exhibit considerable dimorphism in size and robustness, and considerable variation is also indicated by the crania and teeth (Crevecoeur et al. 2010).

A series of AMS dates on ostrich eggshell and mollusk shell from the NFPr layer range between 25,570 ± 350 ^{14}C BP and 19,920 ± 450 ^{14}C BP; these dates appear to be supported by amino acid racemization assessments on the same materials (Brooks and Smith 1987; Brooks et al. 1995; Brooks and Robertshaw 1990; Mercader and Brooks 2001; Brooks 2008).

Taramsa 1, Egypt (26 6′ N, 32°42′ E)

The site of Taramsa Hill is situated in the Nile Valley. It was discovered in 1985 and reported as site E85/2 in the earliest publications; it was subsequently referred to as Taramsa Hill (Van Peer et al. 2010). The hill is an isolated landform covered with chert cobbles, and the mining or extraction of chert for lithic tool production occurred here in what seems to have been five separate phases of activity in the Middle and Upper Paleolithic (Vermeersch et al. 1997). While surveying sector 91/01 of the hill for chert extraction sites in March 1994, a heavily weathered skull and very brittle partial skeleton of a child was discovered. Uniquely, it was found in a seated position in a collapsing ancient trench of phase 3 extraction debris.

The descriptions of the human child by Vermeersch et al. (1998) emphasized its anatomically modern affinities. This is particularly evident from the frontal bone, which exhibits a vertical squama and no supraorbital development, and the rounded occipital. At the same time, however, the face appears rather prognathic, and the teeth are comparatively large. The postcranial bones are slender rather than robust.

When the burial was first reported (Vermeersch et al. 1998), a weighted OSL average of 55.5 ± 3.7 ka from a wide range of imprecise estimates was given for it. Millard (2008) has remodeled these data to suggest a range of between some 73 and 41 ka. Most recently, Van Peer et al. (2010) have argued that the burial was covered by extraction waste for which an OSL date of 68.6 ± 8.0 ka is given. Interestingly, however, Van Peer et al. (2010) discount an OSL date of 24.3 ± 2.1 ka for sand grains that filled the endocranial cavity of the skull on the grounds that there are no other archaeological traces of this age on the hill. However, this sediment – as opposed to the disturbed sediments around the skeleton – would seem to be the most reasonable source for an age of the specimen itself inasmuch as the endocranial cavity would have filled within a reasonably short period of time after death. Thus, while an age of c. 70–40 ka is possible for this burial, it would seem that the discounted age of 24 ka is the most likely.

Leopard's Hill Cave, Zambia (15°36′ S, 28°44′ E)

This dolomitic cave is located approximately 55 km southeast of Lusaka, in south-central Zambia. It was initially explored in 1946 by J.D. Clark and R.P. Odendaal, who observed animal bones and stone tools in the dumps left behind by commercial guano miners. They recovered a fragment of human occipital from one of these dumps, but it is impossible to determine its archaeological derivation.

Subsequent excavations directed by L. Hodges and J.D. Clark in 1958 exposed some 3.2 m of Late Pleistocene and Holocene deposit overlying bedrock. Unfortunately, they dug in arbitrary spits rather than according to natural stratigraphic units. These excavations uncovered a number of animal bones and artifacts, which Miller (1971) divided into four LSA units extending from c. 23.5 ka into the mid-Holocene. A fragmentary human parietal bone was recovered from one of the lowermost units, and three charcoal samples that likely come from the same level have yielded conventional radiocarbon dates of 23,600 ± 360 ^{14}C BP, 22,600 ± 510 ^{14}C BP, and 21,550 ± 950 ^{14}C BP (Miller 1971; Klein 1984).

Lukenya Hill (GvJM/22), Kenya

This small rock shelter, designated GvJM/22, is one of five LSA archaeological "sites" located around the base of Lukenya Hill, some 37 km southeast of Nairobi. A test pit excavated by Richard Gramly in 1970 uncovered human frontal and parietal bones approximately 1.4 m below the surface in association with faunal remains and microlithic Later Stone Age (LSA) artifacts (Gramly and Rightmire 1973; Gramly 1976; Marean 1992; Kusimba 2001). The frontal is clearly of modern aspect, although the supraorbital torus is rather robust and the frontal "squame" (forehead) recedes somewhat more than is typical for modern sub-Saharan Africans (Gramly and Rightmire 1973). This is reminiscent of the condition described by Brothwell and Shaw (1971) for the terminal Pleistocene cranium from Iwo Eleru, Nigeria. Recent morphometric analysis of this partial calotte has shown it differ somewhat from recent African crania, but to have close affinity to some Neolithic specimens from North Africa (Tryon et al. 2015). This morphometric study demonstrates its relative distinctiveness from Iwo Eleru and Late Pleistocene African specimens such as those from Hofmeyr and Nazlet Khater.

Conventional dates of 17,700 ± 760 ^{14}C BP and 17,650 ± 800 ^{14}C BP were reported for collagen from associated animal bones, and an amino acid (aspartic acid) racemization date of c. 17.8 ka was reported for the parietal itself (Gramly and Rightmire 1973; Protsch 1975). However, the ^{14}C dates are considered questionable because of their reliance on collagen pretreatment techniques that have been shown to produce erroneous readings (Higham et al. 2006). The calotte derives from "occurrence E" and is associated with AMS ^{14}C dates determined from ostrich eggshell that indicated a modeled range of 23,576–22,887 years BP (Tryon et al. 2015).

Tuinplaas, South Africa (25°0′ S, 28°36′ E)

The fragmentary Tuinplaas skull and postcranial skeleton (TP 1) was discovered in 1929 at the Springbok Flats gravel quarry some 130 km north of Pretoria, in the Limpopo Province of South Africa. It was initially thought to be associated with MSA artifacts (Broom 1929a), and therefore a Late Pleistocene age seemed reasonable. However, van Riet Lowe (1929) observed that "linking of any of the implements…with the skeletal material is, in the absence of contributory evidence, wholly impossible." As noted by Pike et al. (2004), it was primarily the absence of LSA artifacts in the vicinity that led to the accepted consensus that the skeleton was associated with the MSA. Assessments of the human remains have stressed their similarities with the recent indigenous inhabitants of South Africa (Toerien and Hughes 1955; Hughes 1990; Pfeiffer et al. 1996; Houghton and Thackeray 2011), and U-series assessment of the TP 1 radius indicates it to be less than 20 ± 3 ka, and perhaps as young as 11.0 ± 0.7 ka (Pike et al. 2004).

Deir El-Fakhuri (Esna), Egypt (25°22′ N, 32°28′ E)

Five discrete surface concentrations of Late Paleolithic artifacts and faunal remains surround the abandoned Coptic monastery at Deir El-Fakhuri, some 11 km northwest of Esna, Egypt (Wendorf and Schild 1976). These sites were formed during the deposition of the sands and silts that comprise the Dibeira-Jer Formation, which represents an aggradation episode of the Nile River between c. 22–16 ka (Butzer and Hansen 1968; Wendorf et al. 1970, 1979). The microlithic flakes and blades at these sites have been attributed to the Fakhurian (Lubell 1974). Radiocarbon dates on shells of the aquatic bivalve *Unio* have been determined for some of the sites, and these range between 18,030 ± 330 ^{14}C BP for site E71K1, and 17,640 ± 300 ^{14}C BC for site E71K3 (Buckley and Willis 1969).

Two partial human skeletons were found weathering out of the western side of site E71K1 in the mid-1960s (Wendorf et al. 1970). One comprises the fragmentary pelvis and proximal femora of an adult male, and the other is represented by the fragmentary skull and partial postcranial skeleton of a late juvenile/young adult (Butler 1974).

Taza Cave I (Grotte de la Madeleine), Algeria (36°42′ N, 5°32′ E)

This small cave, situated on the Mediterranean coast in the Bédjaîa Bay of northern Algeria, was known originally as the Grotte de la Madeleine. It was first excavated by C. Arambourg in the 1920s (Arambourg et al. 1934). Its lowermost strata contain Middle Paleolithic artifacts, and the upper levels contain archaeological debris attributed to the Iberomaurusian. Excavations in 1990 under the direction of M. Medig and R. Meier uncovered a human skull in the lower part of the Iberomaurusian sequence (Medig et al. 1996). The skull, which is considered to be from an adult female, is rather diminutive in comparison with other Iberomaurusian specimens (Meier et al. 2003). A radiocarbon date of 16,100 ± 1400 ^{14}C BP is apparently associated with the human skull, although Barton et al. (2008) have questioned whether the specimen is in primary context. Even if it was buried from a higher level, radiocarbon dates for overlying Iberomaurusian strata constrain the specimen to at least 13,800 ± 130 ^{14}C BP.

Afalou-bou-Rhummel, Algeria (36°29′ N, 3°00′ E)

This large cave, located some 30 km east of Bédjaîa on the Mediterranean coast of Algeria, was first excavated by C. Arambourg in the late 1920s and subsequently by S. Hachi in the mid-1980s. A large number of human skeletons – some 53 in total with the majority represented by isolated crania – were uncovered by Arambourg (Arambourg et al. 1934; Camps 1969) in what he described as an "ossuary" in Level I. One more complete adult skeleton in association with the skull of an infant was recovered by him from the lowest level in the cave (Level III). Hachi's excavations uncovered an additional group of skeletons representing a minimum of eight individuals. The human remains are robust, and have been attributed by some workers to a distinctive cranial phenotype referred to as the "Mechta-Afalou" (Briggs 1955; Wendorf 1968; Vallois 1969; Ferembach 1985). These specimens have been the subject of a number of comparative studies (e.g., Irish 2000; Bruzek et al. 2004; Balzeau and Badawi-Fayad 2005), which concluded (unsurprisingly) that they share a distinct phenetic relationship with other North African Iberomaurusian people. Hachi (1996) obtained four dates between 15,000 and 11,000 ^{14}C BP that pertain to the human remains from the site.

Gebel Silsila 2A (Kom Ombo), Egypt (24°28′ N, 32°57′ E)

This open-air site is located on the eastern bank of the Nile River just north of the town of Kom Ombo. Later Pleistocene sands and gravels are exposed in this region of the Kom Ombo Plain in a series of channel complexes known as the Gebel Silsila Formation (Butzer and Hansen 1968). These complexes range from channel beds and point-bar sequences to levee and overbank deposits, and many contain Late Pleistocene lithic artifacts and animal bones (Vignard 1928; Sandford 1934; Churcher 1972; Butzer 1997). One such channel produced a human calvaria in 1926 in apparent association with Upper Paleolithic ("Sebilian") artifacts (Sandford 1934). Unfortunately, the specimen was never adequately described and has since been lost.

Subsequent exploration of the Kom Ombo deposits resulted in the discovery nearby of an isolated human frontal bone in 1963 in sediments related to an ancient branch of the Nile, the Fatira channel, which runs immediately to the east of the Gebel Silsila station (Reed 1965). The frontal bone is clearly of modern aspect, with fully separated medial and lateral superciliary eminences (Reed 1965). The specimen was found in direct association with "Middle Sebilian" artifacts, and two standard radiocarbon dates of 13,070 ± 160 ^{14}C BP and 13,560 ± 120 ^{14}C BP were obtained on charcoal and clam shell from the same layer (Reed 1965).

Soon after the discovery of the frontal bone, additional cranial fragments were found "immediately adjacent" to it but in a disturbed context. As such, it is not possible to relate these fragments to the frontal or the radiocarbon dates.

Jebel Sahaba (Site 117), Sudan (21°59′ N, 31°20′ E)

The "site" of Jebel Sahaba, which takes its name from a nearby hill, comprises two cemeteries on either side of the Nile River in northern Sudan, some 3 km north of the town of Wadi Halfa. A third penecontemporaneous cemetery situated close by is Tushka (Site 8905, Locality A), from which the very fragmentary remains of 12 adults and 1 child have been recovered.

Site 117 is the larger of the two cemeteries at Jebel Sahaba. It was discovered in 1962 by R. Paepe and J. Guichard during an archaeological survey of the region under the leadership of F. Wendorf for the UNESCO Aswan High Dam Salvage project. They discovered four human skeletons, and Wendorf returned 3 years later to begin extensive excavations that resulted in the recovery of 46 burials. In 1966, A. Marks excavated an additional eight burials, bringing the total from Site 117 to 58 skeletons (Wendorf 1968). Comprising this total are at least 24 adult females, 19 adult males, 3 adults of indeterminate sex, and a dozen juveniles ranging in age from infants to adolescents. Individual as well as multiple burials in shallow grave pits are present, and most were covered with sandstone slabs.

The skeletal assemblage from Site 117 is best known for its testament to violent death. About 40% of individuals exhibit some form of evidence for this in the form of "parry" fractures of the forearm bones, unhealed cut marks, or the not uncommon presence of lithic projectile points that would have been embedded in the bodies at time of death (Anderson 1968; Wendorf 1968; Wendorf and Schild 2004). Indeed, some bodies would have had between 15 and 30 projectile points embedded in them.

The skeletal assemblage has been widely studied (e.g., Anderson 1968; Irish and Turner 1990; Irish 2000, 2005; Franciscus 2003; Shackelford 2007; Starling and Stock 2007; Stock et al. 2011; Holliday 2015). Anderson (1968) concluded that the Jebel Sahaba skeletons were, as a group, quite homogeneous and that they were (as might be expected) most similar to presumably contemporaneous specimens from Wadi Halfa, and the Epipaleolithic and Mesolithic remains from the Maghreb sites of Afalou-bou-Rhummel and Grotte des Pigeons (Taforalt). He also argued that the crania exhibited features indicative of continuity with more recent (Holocene) skeletons from northern Africa (Anderson 1968). On the other hand, dental studies (Irish and Turner 1990; Irish 2000, 2005) have suggested that the Site 117 individuals were distinct not only from the Late Pleistocene Maghreb people but also from Holocene Nubians. These studies concluded that the skeletons from Jebel Sahaba showed phenetic affinities with recent West African populations. Franciscus (2003) also found similarities in maxillary morphology between the Jebel Sahaba sample and recent sub-Saharan Africans, and Holliday (2015) has suggested that the Jebel Sahaba sample was most similar in body form to recent sub-Saharan Africans, being distinct from penecontemporaries in other parts of North Africa or their successors in Nubia.

Although absolute (i.e., radiocarbon) dates for Site 117 were unavailable to Wendorf, he nevertheless was able to employ the artifacts (especially the microliths suggestive of the Qadan) and the geological setting of the site to suggest an age of 14–12 ka for the burials (Wendorf 1968). A single radiocarbon date of 13,740 ± 600 ^{14}C BP was subsequently obtained from bone of one of the skeletons (Close 1988), but poor collagen preservation at the site suggests that this determination may be somewhat unreliable. Most recently, Antoine et al. (2013) employed apatite radiocarbon dating on nine samples of bone, tooth enamel and dentine from four skeletons to suggest that the site dates to at least 11.6 ka.

Wadi Halfa (Sites 6B28 and 6B36), Sudan (21°57′ N, 31°20′ E)

The "site" of Wadi Halfa, which takes its name from the nearby town in northern Sudan, was excavated in the mid-1960s during archaeological work in the region under the leadership of Gordon Hewes of the University of Colorado for the UNESCO Aswan High Dam Salvage project. It is located only approximately 3 km from the penecontemporaneous (i.e., terminal Pleistocene-early Holocene) cemeteries at Wadi Tushka (Site 8905, Locality A), and Jebel Sahaba (Site 117).

Wadi Halfa Site 6B28 (21°57′ N, 31°20′ E) is a wind-eroded surface occupation site on the eastern bank of the Nile River. A single edentulous human mandible was found exposed on the surface by Eugene McCluney in 1963; it was associated with Upper Paleolithic artifacts and several fossilized bovid bones. The specimen was afforded a very brief description by Armelagos (1964). No direct radiocarbon value has been published for Site 6B28, but it is thought to date to c. 15 ka on the basis of a ^{14}C determination for the adjacent site of 6B29.

Wadi Halfa Site 6B36 (21°57′ N, 31°19′ E), which is located on the western bank of the Nile almost opposite the town, is a graveyard containing the cranial and postcranial remains of some 37 individuals (13 adult males, 15 adult females, and there juveniles). These specimens have been studied extensively (e.g., (Hewes et al. 1964; Greene and Armelagos 1972; Carlson 1976; Armelagos et al. 1984: Smith and Shegev 1988; Irish and Turner 1990; Turner and Markowitz 1990; Irish 2005; Shackelford 2007). Most studies have concluded that this sample has strong phenetic affinities to the one from the physically and (supposedly) chronologically proximate site of Jebel Sahaba Site 117. No direct radiocarbon dates have been published for Wadi Halfa Site 6B36, but it is thought to be penecontemporaneous with Jebel Sahaba Site 117 on the basis of shared microlithic (Qadan) assemblages. A terminal Pleistocene age of c. 14–10 ka is probably reasonable.

Ifri n'Baroud (Gunpowder Cave), Morocco (34°53′ N, 3°20′ E)

This cave site is located some 40 km south of the Mediterranean coast in eastern Morocco. It was discovered and excavated in the mid-1990s under the direction of A. Mikdad and J. Eiwanger, who documented a deep sequence (c. 3 m) of Iberomaurusian deposits (Mikdad and Eiwanger 2000; Nami 2007). A single human burial, comprising the postcranial skeleton of a tall adult female, was uncovered in the upper portion of the sequence (Ben-Ncer 2004). Radiocarbon dates for the Iberomaurusian deposits at Ifri n'Baroud range from 16,777 ± 83 ^{14}C BP to 11,639 ± 58 ^{14}C BP (Görsdorf and Eiwanger 1998; Nami 2007), and the skeleton is seemingly associated with a date of c. 12,500 ^{14}C BP (Ben-Ncer 2004).

Bushman Rock Shelter, South Africa (24°35′ S, 30°38′ E)

Bushman Rock Shelter is located near Origstad, Mpumalanga Province, South Africa. Excavations in the 1960s produced faunal remains together with LSA and MSA artifacts from a c. 2 m thick sequence of strata (Louw et al. 1969). In 1969, a tourist guide found the partial mandible of a 6–8-month-old human infant protruding from a witness section. The jaw was believed to have derived from one of the lower MSA levels (levels 16 or 17). A morphometric analysis by H. de Villiers revealed a cluster of features aligning it with those of the modern Bantu-speaking population of South Africa (Protsch and de Villiers 1974). A series of radiocarbon samples analyzed by Vogel dated the MSA at the site to between 53 and 12 ka (Louw et al. 1969), although the more recent age limit was thought to result from LSA disturbance of the underling MSA (Mason 1969). Subsequently, Protsch claimed to have undertaken a nitrogen analysis on the infant mandible, placing it in level 16 or 17, and to have produced radiocarbon dates of 29.5 ^{14}C kBP on bone from these levels (Protsch and de Villiers 1974). However, these chemical and dating analyses are highly suspect, if they were ever even conducted. Moreover, radiocarbon evaluations of charcoal taken from levels 16 through 18 have yielded dates of 12,950 ± 70 ^{14}C BP to 12,500 ± 120 ^{14}C BP (Vogel et al. 1986).

Mlambalasi Rock Shelter, Tanzania (7°35′ S, 35°30′ E)

This site is located midway up a large escarpment some 50 km northwest of Iringa in southern Tanzania. It was discovered and first excavated by Paul Msemwa in 2001–2002. Subsequent test excavations under the direction of P. Willoughby in 2006 (Biittner et al. 2007) and 2010 (Willoughby 2012) uncovered an archaeological sequence consisting of historic/Iron Age deposits overlying terminal Pleistocene and Holocene LSA levels.

The skeletal remains of two adults and one juvenile have been recovered, but only one of these (the most complete adult, numbered B-1) "can be confidently attributed to the LSA" (Sawchuk and Willoughby 2015). This specimen was excavated over the course of two field seasons; the elements of the lower body were recovered in 2006 and the skull and upper body in 2010. The specimen is of indeterminate sex and appears to be of interest owing to its comparatively small body size (Sawchuk and Willoughby 2015). The B-1 skeleton, which is reportedly *in situ*, is associated with an AMS date of 12,765 ± 55 ^{14}C BP from a sample of charcoal found next to its right shoulder. Additional dates on charcoal and land snail shells from levels above and below the skeleton have provided ages of 12,940 ± 90 ^{14}C BP and 11,710 ± 90 ^{14}C BP, respectively. Although these would seem to serve as brackets for the date most closely associated with the skeleton itself, it is disconcerting that the "brackets" are inverted. This would seem to indicate disturbance and reworking of Late Pleistocene sediments through interment of the individual in later LSA or even Iron Age times.

Grotte des Pigeons (Taforalt), Morocco (34°48′ N, 2°24′ W)

The large cave site of Grotte des Pigeons is located near the village of Taforalt in the Beni Snassen Mountains of northeastern Morocco. It is approximately 40 km inland from the Mediterranean coast. A series of excavations undertaken in the mid-1940s by Ruhlmann, the early 1950s and 1969–1977 by Abbé Roche (1953, 1963, 1969), and since 2003 under the direction of A. Bouzouggar and N. Barton (Barton et al. 2005; Bouzouggar et al. 2007, 2008) have revealed a deep sequence of archaeologically rich Middle Paleolithic and Epipaleolithic (Iberomaurusian) deposits. The site is perhaps best known archaeologically for the presence of perforated mud snail (*Nassarius*) shells in the c. 82 ka Aterian deposits (Bouzouggar et al. 2007). Although Roche (1953) initially reported some fragmentary human bones from the Aterian levels, these are almost certainly an intrusive burial.

Numerous human skeletons have been recovered from the final Iberomaurusian deposits in the cave (Ferembach 1962; Roche 1963; Mariotti et al. 2009; Humphrey et al. 2012). The remains of close to 200 adults and juvenile individuals constitute the burials in the so-called Iberomaurusian Necropolis I and II (Ferembach 1962, 1965; Mariotti et al. 2009; Humphrey et al. 2012). The burials represent both primary and secondary depositions, and some elements show evidence of intentional postmortem modification such as ochre staining and cut marks (Mariotti et al. 2009; Humphrey et al. 2012). In a number of instances it is clear that earlier burials were disturbed or truncated by subsequent internments. Antemortem evulsion of the maxillary central incisors is evidenced by nearly all of the adult cranial remains (Humphrey and Bocaege 2008). While the antemortem evulsion of the incisor teeth appears to have been a common practice by the Iberomaurusian people of northwestern Africa, the deliberate postmortem manipulation of human skeletal remains has not been documented at any other Iberomaurusian site (Humphrey and Bocaege 2008; Humphrey et al. 2012).

Charcoal from a level immediately above the burials excavated by Roche yielded a radiocarbon date of 11,900 ± 240 ^{14}C BP, and a series of charcoals from a continuous sequence in the burial-containing Grey Series deposits are constrained between 12,675 ± 50 ^{14}C BP and 10,935 ± 40 ^{14}C BP (Barton et al. 2007, 2013; Bouzouggar et al. 2008).

Iwo Eleru, Nigeria (7°26′ N, 5°8′ E)

This rock shelter is situated some 180 km from the Gulf of Guinea in southwestern Nigeria. It was excavated in 1965 by Thurstan Shaw, who uncovered a rich LSA archaeological assemblage, which was divided on the basis of artifact analyses into two periods and four "time vector planes" (Shaw and Daniels 1984). The earliest of these is associated with radiocarbon dates between 11,200 ± 200 ^{14}C BP and 8,685 ± 120 ^{14}C BP (Shaw and Daniels 1984). Shaw's excavations uncovered a human burial, which is almost certainly not intrusive, and is associated with a conventional date of 11.2 ^{14}C kBP (Shaw and Daniels 1984). This date could possibly calibrate to c. 13 ka (Allsworth-Jones et al. 2010; Harvati et al. 2011). A recent U-series analysis of a long bone cortical fragment provided a range of dates between c. 16.3 and 11.7 ka (Harvati et al. 2011). However, in view of the questionable reliability of highly alterable bone in U-series dating and its absolute reliance upon the uptake model (Millard and Hedges 1995; Zhao et al. 2001; Hedges 2002; Pike et al. 2002), these results should be regarded with some skepticism. At best, they can be regarded as simply corroborating the published radiocarbon date.

The human remains (Iwo Eleru 1) comprise a very fragmentary and poorly preserved postcranial skeleton and a partial skull of what was judged to be an adult male (Brothwell and Shaw 1971). The specimen exhibits a fairly weakly developed chin. Brothwell described the cranial vault as being relatively long and low, and observed that the frontal "shows a moderate degree of recession." Importantly, he noted, "this degree of frontal sloping is atypical of the fairly large West African series available in London, but does occur" (Brothwell and Shaw 1971: 222). Indeed, as noted above, this is reminiscent of the condition described for the LSA cranium from Lukenya Hill, Kenya (Gramly and Rightmire 1973). It is also interesting to note the emphasis that Drennan (1929) placed on the low, receding frontal of the Cape Flats specimen.

Unsurprisingly, Brothwell's initial observations have been borne out by subsequent multivariate morphometric analyses. In these studies, the receding frontal serves in some manner to align the cranium somewhat with more archaic human remains (e.g., Omo II), but the cranium also finds alignment with specimens from the Upper Paleolithic of Eurasia (Stringer 1974; Harvati et al. 2011). However, the Iwo Eleru I calvaria suffers from some distortion and considerable reconstruction (Brothwell and Shaw 1971), and 3D geometric morphometric (3DGM) analyses are very sensitive to such distortion. The failure to correct for (or recognize) this sort of distortion in 3DGM studies can lead to highly questionable results (Spoor et al. 2008). The conclusions of Harvati et al. (2011: e24024), who attempted to relate their results to the study by Hammer et al. (2011) in finding "suggestions of a deep population substructure in Africa and a complex evolutionary process for the origin of modern humans," are questionable at best. Indeed, it is unclear why the analysis by Harvati et al. (2011) failed to include either the Lukenya Hill or Cape Flats crania in light of the receding frontals that have been observed for both (Drennan 1929; Gramly and Rightmire 1973).

Any suggestion of a deep population substructure in Africa must clearly come from genomic rather than cranial morphometric data, but, as discussed below, even the genetic evidence that has been proffered for archaic admixture such as this is very much open to question.

Discussion

From the foregoing review, it should be evident that deterministic interpretations which attempt to correlate morphological features portending either the emergence of our species or the subsequent emergence of full-blown anatomical modernity with any of the climatic vicissitudes that characterize the various MIS over the past 200 kyr will be difficult, if not downright impossible, to achieve. The dominant scheme by which the later Pleistocene African hominin fossils have been interpreted envisions a single lineage culminating in the emergence of *Homo sapiens* and thence modern humans (e.g., Stringer and Andrews 1988; Hublin 2001; Smith 2002; Stringer 2002; Bräuer 2008; Rightmire 2008, 2009; Pearson 2011). However, increasing attention is being directed to the morphological diversity that is manifest even within this admittedly rather paltry assemblage (e.g., Manica et al. 2007; Stringer 2007; Rightmire 2009; Crevecoeur et al. 2009; Gunz et al. 2009).

This diversity may be manifest among penecontemporaneous (or potentially penecontemporaneous) sites that are located variously in southern, eastern, and northern Africa (e.g., among Klasies River Main Site, Dar es-Soltan II, Eyasi and Aduma, or between Hofmeyr and Nazlet Khater). In these instances, the diversity may be related to geographic and/or temporal differences between the specimens. In other instances, however, there is considerable diversity among contemporaneous (or, at least seemingly contemporaneous) specimens within a single site (e.g., between the Omo I and Omo II crania from the Kibish Formation, and among the human fossils from the lower part of the SAS Member at Klasies River Main Site).

Thus, for example, the four adult mandibles from the SAS Member at Klasies evince considerable differences in both size (Royer et al. 2009) and symphyseal morphology (Lam et al. 1996) (Fig. 17.6). While they derive from separate horizons[3] that may represent discrete occupation events, they are generally regarded as penecontemporaneous. These jaws, like some other elements from Klasies River Main Site, have been argued to demonstrate higher levels of sexual dimorphism than living humans (Rightmire and Deacon 1991; Smith 1992, 1994; Lam et al. 1996; Royer et al. 2009). As noted by Royer et al. (2009), high levels of mandibular variation – especially in corpus height – are also characteristic of some other Pleistocene samples (e.g., the Middle Paleolithic sample from Skhūl, the Upper Paleolithic sample from Dolní Věstonice, and the Middle Pleistocene sample from Sima de los Huesos). To the extent that size variation can be used as a proxy for sexual dimorphism, this suggests that the degree of dimorphism exhibited at Klasies was not unique among Middle and Late Pleistocene hominins. Although Wymer (1982: 139) opined that this sample comprises the mandibles of *Homo sapiens* and a "Neanderthal type," Lam et al. (1996) concluded that it simply attests to a high degree of intrapopulation variability. However, it should be noted that the analysis by Lam et al. (1996) entailed only two dimensions of what is manifestly a three-dimensional structure. The jury may still be out over this issue.

Similarly, as discussed above, the differences in calvarial morphology between Omo I and Omo II (Fig. 17.7) have been interpreted by different workers to mean different things. Some have argued that it attests to a population with

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[3] The best-represented element from the lower part of the SAS member is the mandibular corpus (n = 4). Of these four, the KRM 41815 jaw derives from the deposits in cave 1B (Layer 10 of Singer and Wymer 1982), while the others are from separate horizons in cave 1 (KRM 16424 from Layer 14+, KRM 13400 from Layer 14, and KRM 21776 from Layer 17 of Singer and Wymer 1982).

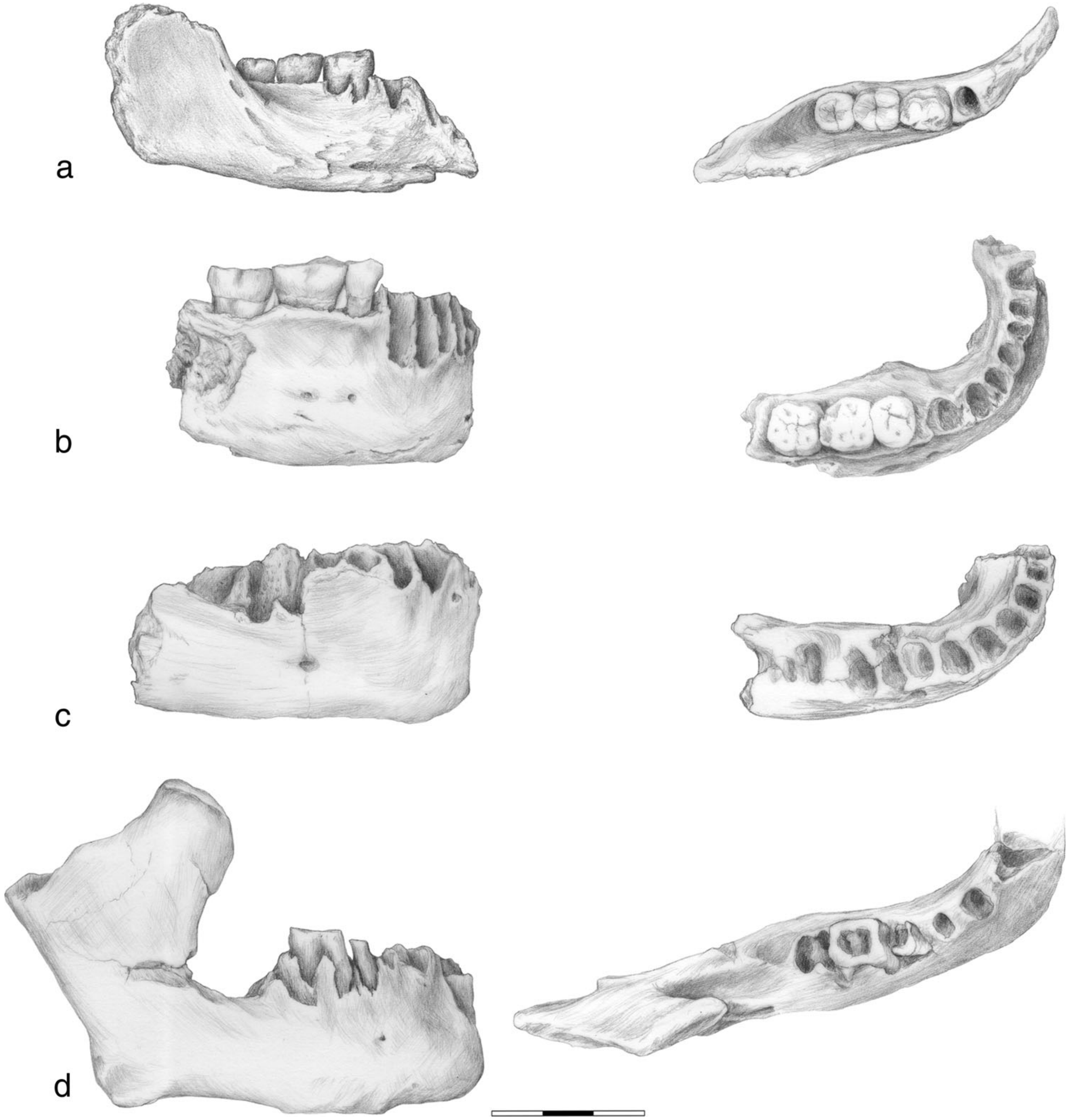

Fig. 17.6 Lateral and occlusal views of the hominin mandibles from the SAS Member at Klasies River Main Site illustrating the range of size and of symphyseal morphology in this penecontemporaneous sample. **a** = KRM 16424 (SAM AP 6225); **b** = KRM 13400 (SAM AP 6223); **c** = KRM 21776 (SAM AP 6101) reversed; **d** = KRM 41845 (SAM AP 6222). KRM 41815 derives from deposits in Cave 1B (Layer 10 of Singer and Wymer 1982). The others are from Cave 1 (KRM 16424 from Layer 14+, KRM 13400 from Layer 14, and KRM 21776 from Layer 17 of Singer and Wymer 1982). Scale bar in cms. Illustrations by Luci Betti-Nash from casts. Reproduced from Royer et al. (2009: Fig. 1)

considerable individual variation (Rightmire 1976; Trinkaus 2005), or two different contemporaneous populations (Day and Stringer 1982), while others have suggested that Omo I is a substantially younger specimen (e.g., Bräuer et al. 1997; Bräuer 2001; Klein 2009).

The contemporaneity of specimens that seemingly possess more archaic morphologies with those that display more derived attributes, and/or the presence of specimens with an apparent mosaic of primitive and derived features have been interpreted as being consistent with at least three different

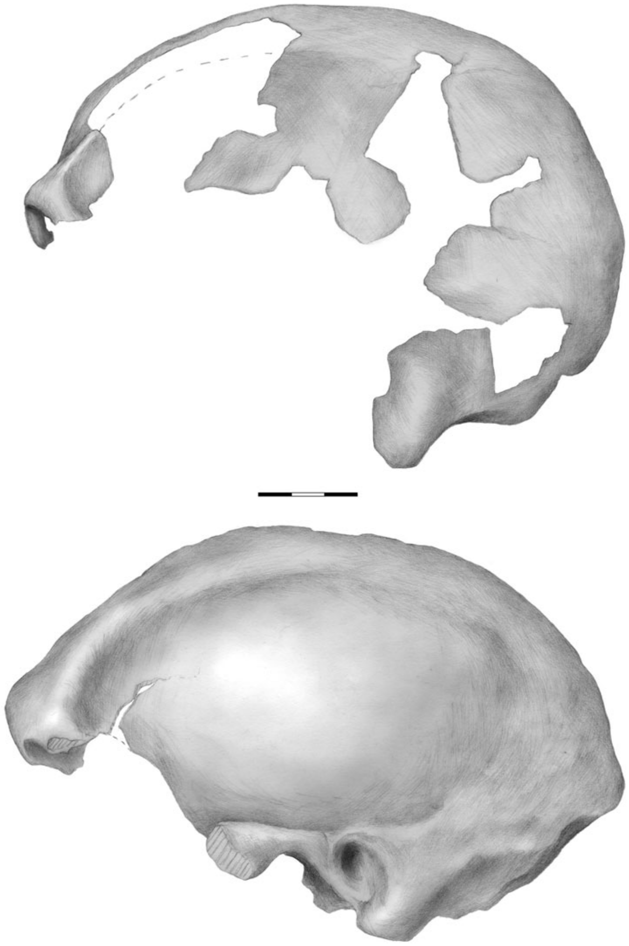

Fig. 17.7 Lateral views of the Omo I (*above*) and Omo II (*below*) calvaria from Member 1 of the Kibish Formation illustrating the differences in the frontal and occipital contours between these penecontemporaneous specimens. The image of Omo I is the right lateral view reversed. *Scale bar* in cms. Illustrations by Luci Betti-Nash from casts

scenarios. One sees this as reflecting the presence of (and possible admixture between) contemporaneous archaic and modern hominin populations, such as envisioned by Bräuer's (1992) "Hybridization and Replacement" hypothesis. A second interpretation, such as Smith's "Assimilation" hypothesis (Smith et al. 1989), holds that mosaic mixtures are to be expected in populations that represent part of an evolving lineage with roots in earlier, more archaic populations and descendants in later, more derived populations. Although the "Assimilation" hypothesis, as proposed, related to the assimilation of indigenous archaic Neandertal genes into the modern human populations expanding from Africa into Europe, this concept of genetic admixture could apply equally to archaic and modern populations in Africa. A third scenario might envision the presence of possibly contemporary archaic and more modern hominin populations with replacement of the former by the latter. This would be consistent with the strict "African Replacement" hypothesis of Stringer and Andrews (1988).

How does the late Quaternary African human fossil record accord with the results of studies of the modern human genome? An impressive array of evidence from mitochondrial DNA (mtDNA), the Y chromosome, non-coding autosomal microsatellites (short tandem repeats or STRs), and autosomal single nucleotide polymorphisms (SNPs) has been brought to bear on five germane questions. These relate to: (1) the geographic origin of the species *Homo sapiens*; (2) the age of the divergence of *H. sapiens* from the most recent common ancestor that we shared with our now-extinct sister species; (3) the possible assimilation of genes through introgression from contemporaneous archaic lineages into the *H. sapiens* genome, whether within or outside of Africa; (4) the phylogeographic structure of Africa populations and lineage divergence times; and (5) the timing of the most recent human migration out of Africa.

In the first instance, the late Quaternary African hominin fossil record, despite its manifestly incomplete nature, finds at least some consistency with an impressive array of genetic evidence that points to an African origin for our species (Cann et al. 1987; Ingman et al. 2000; Underhill et al. 2001; Salas et al. 2002; Frazer et al. 2007; Garrigan et al. 2007; Gonder et al. 2007; Behar et al. 2008; Li et al. 2008; Tishkoff et al. 2009). There is currently no question that the geochronologically oldest specimens attributable to *Homo sapiens* derive from sub-Saharan Africa (White et al. 2003; McDougall et al. 2008; Aubert et al. 2012; F. Brown et al. 2012).

In the second instance, most haploid mitochondrial DNA (mtDNA) and Y-chromosome genetic data indicate a coalescence of lineages to the most recent common ancestor of *Homo sapiens* at between 200 and 100 ka (Cann et al. 1987; Scozzari et al. 1999; Ingman et al. 2000; Underhill et al. 2000; Tang et al. 2002; Tishkoff and Verrelli 2003; Garrigan and Hammer 2006; Kivisild et al. 2006; Gonder et al. 2007; Behar et al. 2008). Previous estimates of the most recent female common ancestor have tended to fall closer to 200 ka, with a range of perhaps 240–150 ka (e.g., Cann et al. 1987; Ingman et al. 2000; Tang et al. 2002), while estimates of the most recent common male ancestor have been closer to 100 ka, with a range of some 50–142 ka (Pritchard et al. 1999; Thomson et al. 2000; Tang et al. 2002; Cruciani et al. 2011). Most recently, however, Poznik et al. (2013) analyzed new mtDNA and Y-chromosome genome data using comparable techniques, and found no statistically significant difference between the two loci. Both produce estimates for the most recent common ancestor (T_{MRCA}) dating to between 150 and 120 ka. However, as observed by Weaver (2012), these models need not be interpreted as being indicative of a severe population bottleneck at the time of coalescence. The same coalescence time could be achieved in a population of constant size with an effective population size equal to the harmonic mean effective population size of a severely bottlenecked population. For this reason, Weaver (2012) has noted that the coalescence time for human mtDNA and Y-chromosome need not be expected to correspond to the timing of the emergence of the species *Homo sapiens*.

However, these T_{MRCA} dates of 150–120 ka do place an upper bound on the time of population divergence among modern humans, such that prior to 120 ka there was a common ancestral population (early population divergence in Africa is discussed below). Inference of a bottleneck during MIS 4, MIS 5 or MIS 6 is eminently testable with genetic data, but current limited analyses have produced conflicting results (Henn et al. 2012). For example, employing the complete diploid genome sequences from an admittedly tiny sample of present day humans (N = 6), Li and Durbin (2011) found no evidence whatsoever for a bottleneck in human population size between 200 and 100 ka, although they did find strong evidence for both an African and non-African bottleneck occurring roughly 60–30 ka (see also Kidd et al. 2012).

In the third instance, the fossil record reveals the penecontemporaneous presence in the Late Pleistocene of individuals possessing more archaic morphologies and those with more derived attributes. While this is perhaps most reasonably (i.e., most parsimoniously) interpreted as simply attesting to the retention of some plesiomorphic traits (i.e., attesting to polymorphic allelic loci) in some populations and/or individuals, and a consequent enhanced degree of interindividual phenotypic variability, it also might be seen as being consistent with indirect evidence that suggests archaic admixture in the genomes of current Africans (e.g., Wall et al. 2009; Hammer et al. 2011; Lachance et al. 2012).

It should be noted, however, that the conclusions relating to "archaic" admixture in Africa by Hammer et al. (2011) derive from the analysis of sequence data from 61 regions of the genome in a sample of only three sub-Saharan populations. They suggested that these populations received a c. 2% contribution of genetic material from some extinct "archaic" population that would have split from the *Homo sapiens* lineage some 700 ka, and then interbred with a Central African population some 35 ka. Why it was deemed to have been Central African is unclear, and why it took nearly 665 kyr to accomplish this remains a mystery. Indeed, with reference to morphological studies that purport to show evidence in the terminal Pleistocene of Africa that is consistent with admixture of archaic lineages (e.g., Harvati et al. 2011), it is unclear how 2% archaic admixture in a few Central African hunter-gatherer populations manifest itself in the fossil record. While it is conceivable that discrete archaic features might be recorded in a fossil representative of the first filial (F_1) generation that resulted from such an introgessive cross, the presence of 2% archaic admixture inherited through tens of thousands of years would surely be morphologically indistinguishable from normal population variation.[4]

The scenario proposed by Hammer et al. (2011) might be seen to gain some support from the study by Mendez et al. (2013) of Y-chromosome composition in an African American who carries the apparent ancestral states for the single nucleotide polymorphisms (SNPs) that define the basal portion of the phylogenomic tree for this chromosome. Mendez et al. (2013) estimated the time to the most recent common ancestor for this Y-chromosome tree at a remarkably old age of between 581 and 237 ka. However, the ancient age estimated by Mendez et al. (2013) has been resoundingly criticized by Elhaik et al. (2014), who pointed out a number of statistical and methodological flaws with the study. Elhaik et al. (2014), in turn, estimated the Y-chromosome T_{MRCA} at c. 208 ka. Moreover, the studies by Hammer et al. (2011) and Mendez et al. (2013) – which emanate from the same lab – are heavily dependent upon the modeling of demographic population structure. Apart from the questions raised by Weaver (2012) with reference to some of these model assumptions, Eriksson and Manica (2011) have demonstrated that spatial population structure is expected to generate genetic patterns similar to those that might be attributed to ancient admixture through hybridization. Thus, they showed, with reference to the supposed admixture between Neandertals and modern Eurasians, their excess shared polymorphism is strongly linked to the structure of ancient populations, and is, in fact, compatible with scenarios in which no hybridization occurred. Currat and Excoffier (2011) also have presented strong statistical arguments in relation to paleodemography that question the degree of hybridization that has been inferred between archaic and modern populations.

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[4] There are some theoretical expectations and empirical observations to the effect that admixture may result in the expression of increased morphological anomalies, or of morphologies that may be intermediate in nature but with heightened levels or unusual modes of variation (Ackermann 2010). Still, we have very little expectation of how to recognize a hybrid individual (or sample) in the paleontological record. A number of specimens from sites in Europe that date to MIS 3 have been posited to represent hybrids, with most being viewed as evincing an overall modern aspect with some Neandertal features. These include the remains from Abrigo do Lagar Velho, Portugal (Duarte et al. 1999; Bayle et al. 2010), Peştera cu Oase, Romaina (Trinkaus et al. 2003; Rougier et al. 2007), Peştera Muierii, Romania (Soficaru et al. 2006), Mladeč, Czech Republic (Frayer et al. 2006; Wolpoff et al. 2006) and Cioclovina, Romania (Soficaru et al. 2007). These claims have not gone unchallenged (e.g., Tattersall and Schwartz 1999; Harvati et al. 2007). Perhaps one of the more interesting specimens in this regard is the 40–30 ka mandibular corpus from Riparo di Mezzena, Italy. This fragment has been interepreted as a Neandertal on the basis of its mtDNA, which shows "a classic Neandertal motif with the diagnostic transversion 16256 C/A" (Condemi et al. 2013: 6). However, it also displays an incipient mental trigone (chin), a feature that long has been held to be a distinction of *Homo sapiens* (Schwartz and Tattersall 2000).

Finally, Gokcumen et al. (2013) have shown that significant levels of (balancing) selection can mimic signatures of archaic admixture, bringing into question the notion that the ancient Denisovans from the Altai Mountains in southern Siberia somehow contributed some 5% of the genomes of the modern inhabitants of Papua New Guinea (Meyer et al. 2012; Wall et al. 2013). Thus, archaic admixture, while a distinct possibility, should only be regarded as a plausible scenario for modern genomic structure after more likely explanations relating to population/demographic history and natural selection have been discounted. Although beguiling, it is at best overambitious to interpret one or another feature of a single human specimen as suggesting anything at all about the depth or nature of population substructure in Africa.

With regard to the fourth set of questions enumerated above, there is considerable genetic evidence to indicate a relatively deep separation of human populations in Africa, with the ancestors of the southern African Khoe-San diverging early on from the population that gave rise to all other groups (Hammer et al. 2001; Ingman and Gyllensten 2001; Salas et al. 2002; Semino et al. 2002; Torroni et al. 2006; Gonder et al. 2007; Tishkoff et al. 2007, 2009; Behar et al. 2008; Schuster et al. 2010; Gronau et al. 2011; Henn et al. 2011; Pickerell et al. 2012; Schlebush et al. 2012, 2013; Veeramah et al. 2012). Within the mtDNA L0 lineage, the deeply divergent branches (L0d and L0k) are carried almost exclusively by the Khoe-San or their current near neighbors. Unfortunately, an estimate of population divergence has not been computed, although the coalescence time will be older than the population divergence.

Nevertheless, because L0 and the deepest clades within it have a southern African distribution, it seems very reasonable to conclude that it had a southern African origin. Three estimates of population divergence between the Khoe-San and other Africans have been performed recently on varying amounts of autosomal/genome-wide data (Gronau et al. 2011; Veeramah et al. 2012; Schlebusch et al. 2012). Schlebusch et al. (2012) estimated that six of seven sampled Khoe-San language/ethnic groups shared a common ancestor that had diverged from all other sub-Saharan African populations probably by 100 ka. Models based on sequence data support a divergence of Khoe-San from other African populations between 130 and 110 ka. A southern African origin is consistent not only with other human genomic data, but also with variation in strains of the gastric bacterium *Helicobacter pylori*. The latter indicate origin with an African human host (Salama et al. 2000; Linz et al. 2007), and coalescence of the two strains associated with southern African Khoe-San populations (hpAfrica 1 and hpAfrica 2) at some 116–88 ka (Moodley et al. 2012).

Some Late Pleistocene fossils have been interpreted at one time or another as sharing distinctive morphological similarities with, and therefore being in the ancestry of specific recent African populations – for example, the accentuated parietal bosses of the Singa calvaria suggested Khoe-San affinities to Woodward (1938) and Wells (1951) – but there is a rather noticeable lack of phenetic resemblance between the craniodental remains (and postcranial fragments) from the Late Pleistocene with those of these modern Holocene groups. Thus, for example, the Hofmeyr cranium from South Africa only dates to some 36 ka, and genetic evidence suggests the existence of a Khoe-San lineage in southern Africa dating back well beyond that (Henn et al. 2011; Schlebusch et al. 2013), but the analyses of the skull undertaken thus far reveal no specific morphometric affinity with Holocene Khoe-San crania (Grine et al. 2007). It is, of course, possible that more detailed analysis of the reconstructed specimen (Grine et al. 2010) may emphasize the tantalizing linear morphometric similarities hinted at earlier. Similarly, a number of the human dental samples from Late Pleistocene South African sites (e.g., Die Kelders) display morphological variants that characterize the teeth of the recent inhabitants of sub-Saharan Africa, but these similarities do not necessarily signify a close evolutionary relationship because these features appear to be plesiomorphic (Grine 2000).

The lack of morphologies in any of the Late Pleistocene fossils that can serve as ties to specific recent population groups in Africa is perhaps not unexpected. There is no reason to suppose that genetic variants associated with aspects of hard tissue development and growth (e.g., RUNX2, which codes for a key transcription factor for osteoblast and chondrocyte differentiation [Fujita et al. 2004; Komori 2010]), whose phenotypic effects might manifest as distinctive craniodental features, should be temporally associated with the changes implicated with the splitting of other genetic lineages. To date, only those crania from Holocene LSA contexts in South Africa display morphological patterns that can be identified as distinctly Khoe-San (Stynder et al. 2007a, b).

The absence of fossils from the Late Pleistocene with identifiable Khoe-San affinities led Morris (2002, 2003) to suggest that the Khoe-San morphotype arose relatively late in South Africa. He has hypothesized that the ancestors of recent Khoe-San populations underwent a population (and hence phenotypic) bottleneck associated with the Last Glacial Maximum of MIS 2 at c. 29–14 ka. Although this is an interesting suggestion, there is, unfortunately, no genetic evidence for it.

Given the sheer size of Africa (over 30,000,000 km^2) and its extensive modern climatic variation, it is perhaps understandable that the continent remains very much a black box with regard to environmental influences on Late Pleistocene human evolution. We think we know that our species emerged somewhere in sub-Saharan Africa close to 200 ka, and we know something about the people and their archaeological traditions in the Holocene, but the mechanisms and processes that were involved over the past two hundred millennia are frustratingly opaque. The period MIS 6-2 holds the key to understanding our evolution in the world's second largest continent. Despite three quarters of a century of research and exploration, we have only begun to glimpse our recent heritage, but what has been detected thus far is a clear enticement for further exploration and research.

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