CHAPTER TWENTY-FIVE

Hominini

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The late Miocene–Pliocene emergence of the Hominini coincides with considerable mammalian faunal turnover in Africa, including the endemic radiation of groups such as ruminants, suids, and cercopithecids; the first appearance through immigration of taxa such as *Equus* and *Giraffa*; the demise of previously successful groups such as anthracotheres; and, overall, an increased representation of taxa adapted to more open savanna-mosaic environments (e.g., Behrensmeyer, et al. 1992).

Most, if not all, of the major taxonomic events for the tribe occur in Africa, including the emergence of our own species. Only two hominin species (from one eurytopic genus) are found entirely outside Africa (*Homo neanderthalensis* and *Homo floresiensis*), and all hominins are restricted to the continent until just under 2 million years ago.

The principal adaptive changes of the tribe also occur in Africa. Early hominins are distinguished by a suite of postcranial features showing reliance on terrestrial bipedalism. By the late Pliocene (and possibly sooner), this form of locomotion places hominins among the most energetically efficient walkers of all mammals. The selective advantages that led to the evolution of terrestrial bipedalism (carrying? tool use? energetics?) are intensively discussed within paleoanthropology. Late Miocene–early Pliocene hominins are further characterized by an increase in the size of the postcanine dentition, a reduction in size of the anterior dentition, and a loss of the upper canine/lower premolar honing complex. Late Pliocene hominins then specialize in one of two ways: the australopiths (discussed later) become megadont, and *Homo* reduces postcanine tooth size. Like striding bipedalism, the selective factors responsible for these dental and masticatory changes are debated, as are the die tary implications.

It is only during the last one-third of the existing record for hominin evolution that brain size expands significantly and stone tools appear. As current evidence stands, the latter occurs prior to the former. These two innovations, likely reflecting complex biocultural feedback involving language, also coincide with a decrease in hominin diversity from the late Pliocene, when as many as five African species occur, to the mid-Pleistocene, after which only one evolving lineage dominates the continent.

Taxonomy in this chapter errs on the side of cutting up samples finely, as lumping may obscure potentially significant differentiation (Groves, 1989). We believe it is also generally easier to amalgamate taxa rather than subdivide, should variation later be shown to be less than, or exceed, that expected within a single species. However, there is also strong opinion against "diversity systematics" within paleoanthropology (e.g., Wolpoff, 1999), and an antidote against this approach has recently been offered by White (2009).

A taxon recognized by many in the paleoanthropological community as a valid species, *Homo ergaster*, is not considered separately here, because we are convinced by Spoor et al.'s (2007) argument that many of the cranial differences between it and *Homo erectus* are size related. Overall, we present a taxonomic scheme that we feel most accurately reflects current knowledge about hominin systematics and is widely used by paleoanthropologists. We are not wholly in agreement with this taxonomy and anticipate that taxonomic changes are imminent. For example, widespread recognition that *Australopithecus* is paraphyletic (e.g., Strait and Grine, 2004; Kimbel, 2007; Collard and Wood, 2007) will likely result in more genera for the australopith grade. Other taxa, currently conceived as potential chronospecies (*Australopithecus anamensis* and *Au. afarensis*; *Paranthropus aethiopicus*, and *P. boisei*) may be lumped; and the possibility exists that certain poorly known taxa may be subsumed within taxa with larger hypodigms, once evidence for more overlapping anatomical regions has been recovered and analyzed (e.g., *Orrorin* may be subsumed within *Ardipithecus, Au. bahrelgazeli* within *Au. afarensis*). We use the informal term *australopith* instead of the more traditional *australopithecine*, because the latter should only be used for taxa within *Australopithecus* and *Paranthropus* that are thought to belong in their own subfamily, the Australopithecinae. Likewise, we use the informal term *hominin* rather than *hominid* (the family-level colloquialism), since in cladistic taxonomies, which we support, Hominidae includes extant great apes as well as humans. Site abbreviations used throughout the text are defined in table 25.1.

Of previously published taxonomies, we follow Wood and Richmond (2000):

Superfamily Hominoidea
Family Hominidae
Subfamily Homininae
Tribe Hominini ("hominins")
Subtribe Incertae Sedis
Sahelanthropus
Orrorin
Ardipithecus

Subtribe Australopithecina (almost certainly a paraphyletic grouping)
Australopithecus
Paranthropus
Kenyanthropus
Subtribe Hominina ("hominans")
Homo

Systematic Paleontology

Family HOMINIDAE Gray, 1825
Subfamily HOMININAE Gray, 1825
Tribe HOMININI Gray, 1825
Subtribe INCERTAE SEDIS
Genus *SAHELANTHROPUS* Brunet et al., 2002*SAHELANTHROPUS TCHADENSIS* Brunet et al., 2002
Figure 25.1 and Table 25.2

Holotype The type specimen is TM 266-01-060-1 ("Toumai"), a nearly complete but distorted cranium (flattened dorsoventrally and depressed on the right side). A list of other specimens referred to *S. tchadensis*, including three mandibles from three localities, is provided by Brunet et al. (2002, 2005).

Age and Occurrence Late Miocene, Central Africa (table 25.2).

Diagnosis Based on Brunet et al. (2002). *Sahelanthropus tchadensis* differs from *Pan* and *Gorilla* in its short, more orthognathic subnasal region; smaller canines; short basioccipital and more anterior foramen magnum; flat, long, more horizontally oriented nuchal plane; and downward lipping of the nuchal crest. It further differs from *Gorilla* (which it has been claimed to resemble; Wolpoff et al., 2002) in its smaller-sized cranium, lack of supratoral sulcus, and lower crowned cheek teeth. It differs from the penecontemporaneous *Ardipithecus* in the well-developed crests and cingulum on the lingual aspect of I1, less incisiform upper canines with a low distal shoulder, BL-narrower lower canines with stronger distal tubercle and two-rooted p4. Lingual I1 topography also distinguishes *Sahelanthropus* from *Orrorin*, as do the short, apically worn upper canines.

Description A cranium with great ape-size brain case, U-shaped dental arcade, an orthognathic, anteroposteriorly short subnasal region and relatively vertical upper face, a wide interorbital pillar and large, continuous supraorbital torus, marked postorbital constriction and posteriorly located sagittal crest, a flat, long, approximately horizontally oriented nuchal plane with downward lipping of nuchal crest, anteriorly positioned foramen magnum, and short basioccipital. Dental remains show small, apically worn canines, no lower c/p3 diastema or upper I2/C diastema and the apparent absence of a functional honing C/p3 complex. The lower canine has a large distal tubercle and low shoulders. Mandibular premolars have two roots. Postcanine teeth are bunodont and slightly crenulated and enamel thickness (1.2–1.9 mm) is intermediate between *Pan* and *Australopithecus* (see Brunet et al., 2002, 2005; Zollikofer et al., 2005; Guy et al., 2005).

TABLE 25.1
Site abbreviations found throughout the text
Adapted from Wood and Richmond, 2000.

Abbreviation	*Site*
ALA-VP	Alaya—Vertebrate Paleontology
AL or A.L.	Afar Locality
AME-VP	Amba East—Vertebrate Paleontology
ARA-VP	Aramis—Vertebrate Paleontology
ASK-VP	Asa Koma—Vertebrate Paleontology
BAR	Baringo
BC	Border Cave
BOU-VP	Bouri—Vertebrate Paleontology
BSN	Busidima Formation
DNH	Drimolen
EP	Eyasi Plateau, Tanzania
ER	East Rudolf (Koobi Fora or East Turkana)
GAM-VP	Gamedah—Vertebrate Paleontology
GWM	Gona Western Margin
Is	Ishango
KGA	Konso Gardula
KNM	Kenya National Museum
KP	Kanapoi
KRM	Klasies River Mouth
KT	Koro Toro
LH or L.H.	Laetoli Hominin
LT	Lothagam
LU	Lukeino Formation
Ma	Mega annum
MLD	Makapansgat Limeworks Dump
OH or O.H.	Olduvai Hominin
OL	Olorgesailie
Omo (L)	Fossils recovered from Shungura Formation, Ethiopia
SAM-AP	South African Museum, Klasies River Cave
SE	Sterkfontein Extension site
SK, SKW	Swartkrans, or Swartkrans Wits hominin
SKX	Swartkrans Excavation
STD-VP	Saitune Dora—Vertebrate Paleontology
Sts	Sterkfontein type site
Stw, StW, Stw/H, or StW/H	Sterkfontein Wits hominin
TH	Taburin hominin
TM (in context of South African hominins)	Transvaal Museum
TM (in context of *Sahelanthropus*)	Toros-Menalla
UA	Uadi Aalad
UR	Uraha
WT	West Turkana (including Nariokotome)

Remarks The virtual reconstruction of the holotype cranium TM 266-01-60-1 (Zollikofer et al., 2005) is a crucial although potentially controversial anatomical reference, as the holotype is distorted by displacement of fragments around multiple fractures and by plastic deformation, most notably in the maxilla. Fortunately, there is good anatomical continuity along the sagittal and parasagittal planes of the skull, and no major regions are missing. The 3-D reconstruction of the cranium was

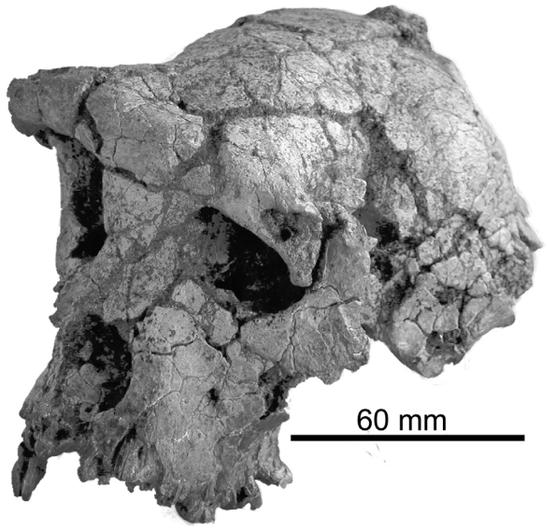


FIGURE 25.1 Holotype of *Sahelanthropus tchadensis*, cranium TM 266-01-60-1. Courtesy of Michel Brunet.

produced by disassembling a CT-generated digital representation along major cracks, removing matrix, and then reassembling the segments while ensuring that the face/neurocranium/basicranium fit together at multiple points (Zollikofer et al., 2005). Compared to the original, the reconstruction has a wider cranium, a sagitally rounder occipital contour, a more horizontally oriented nuchal plane, a taller face and larger, more rounded orbits (Zollikofer et al., 2005).

The cranium presents a mosaic of features that fall into three categories: primitive for African apes, derived relative to *Pan* and *Gorilla* (and some also derived relative to australopiths such as *Au. afarensis*), and autapomorphic features. Primitive features that clearly resemble the condition found in *Pan* and *Gorilla* are found primarily in the neurocranium: the superior contour is long and low, the brain size is small (360–370 cc), and there is pronounced postorbital constriction (Guy et al., 2005). The shape and shallowness of the palate also resemble the conditions found in *Pan* and *Gorilla* (Guy et al., 2005), and the mandibular premolars have two roots and three separate pulp canals (Brunet et al., 2005).

Derived features relative to *Pan* and *Gorilla* support the taxon's claim for hominin status and rest on two complexes of features. The first set of features is basicranial and may reflect habitual orthogrady and therefore bipedalism. The basioccipital is short and the foramen magnum is more anteriorly positioned than is typical of *Pan* and *Gorilla*. In addition, the angle formed between a line delimiting the rim of the foramen magnum in sagittal view and the orbital plane is about 90°, as in extant *Homo*. This angle is acute in *Pan* because although the orbital plane will always tend toward the vertical in lateral view, due to the superiorly sloping posterior aspect of the nuchal plane on which the foramen is situated, the plane of the foramen is oblique in *Pan*, not horizontal as in *Homo*. The condition in *Pan* is thought to reflect the latter's more frequent use of pronograde postures (Zollikofer et al., 2005). However, measurement of this angle is difficult unless specimens are complete, and Wolpoff et al. (2006) have claimed that there is overlap in the angle among *Pan* and early australopiths, potentially diminishing the utility of the character in diagnosing bipeds. TM 266-01-60-1 also has a flat nuchal plane and the nuchal crest exhibits downward lipping; both are similar to the condition in *Australopithecus* and *Homo* and unlike that seen in *Pan* (Zollikofer et al., 2005).

There is also a cluster of features related to the small canines. The subnasal region is short and flat. Both upper and lower canines show apical wear, there are no c/p3 or I2/C diastemae and a honing C/p3 complex is absent.

Autapomorphic features include the remarkably thick supraorbital region, outside the range of male *Gorilla* (Brunet et al., 2002).

If *Sahelanthropus* is not a hominin, it is closely related to them. While Wolpoff et al.'s (2006) argument that convergence may explain the reduced canines, *Ouranopithecus* being a salient example, basicranial features, which are plausibly linked to habitual orthogrady (or more recently to neural reorganization; see Suwa et al., 2009b) would seem less likely to be the result of convergence.

Three localities in the Toros-Menalla (TM) region of Chad (TM 266, 247, and 292) have yielded fossils of *Sahelanthropus*; their biochronological age, based on comparisons with the Lukeino fauna and fauna from the Nawata Fm., Lothagam, is 7.0–6.0 Ma (Vignaud et al., 2002; Brunet et al., 2005). The fauna is described as being more similar to Lothagam (7.4–5.2 Ma) than to Lukeino (ca. 6.0 Ma); for example, *Loxodonta* from Toros-Menalla is more primitive than the Lukeino species. This assessment is supported by recent cosmogenic nuclide dating that constrains the fossils between 7.2 and 6.8 Ma (Lebatard et al., 2008). Existing genetic evidence suggests a *Pan/Homo* split ca. 5–7 Ma (e.g., Steiper et al., 2004; Bradley, 2008) even allowing for subsequent gene flow (Patterson et al., 2006). Given the lack of a good fossil calibration, it is premature to claim *Sahelanthropus* is too old to be a hominin (*contra* Wolpoff et al., 2006); and if the Miocene hominoid *Chororapithecus*, dated at 10.5–10.0 Ma, is a member of the *Gorilla* clade as claimed (Suwa et al., 2007), this would also support a hominin divergence of at least 7.0 Ma.

TABLE 25.2
Major occurrences and ages of African hominins
? = attribution or occurrence uncertain; abbreviation: alt., alternatively.

Taxon	*Location*	*Formation*	*Age*	*References*
		TRIBE HOMININI, LATE MIOCENE–PRESENT		
		SUBTRIBE INCERTAE SEDIS, LATE MIOCENE–EARLY PLIOCENE		
Sahelanthropus tchadensis	Toros Menalla, Chad (type)	Anthracotheriid Unit	Late Miocene, ca. 7.0–6.0 Ma	Brunet et al., 2002, 2004, 2005; Vignaud et al., 2002; Zollikofer et al., 2005
			6.8–7.2	Lebatard et al., 2008
Orrorin tugenensis	Tugen Hills, Kenya (type)	Lukeino Fm.	6.2–5.6 Ma	Hill et al., 1985, 1986; Senut et al., 2001; Hill, 2002; Sawada et al., 2002; White, 2006
Ardipithecus kadabba	Saitune Dora, Alayla (type), Asa Koma, and Digiba Dora, Middle Awash; Ethiopia	Asa Kona Mb., Adu Asa Fm.	5.8–5.5 Ma	Haile-Selassie, 2001; Haile-Selassie et al., 2004b
	Amba East, Central Awash Complex, Ethiopia	Kuserale Mb., Sagantole Fm.	5.6–5.2 Ma	Haile-Selassie, 2001
	Gona, Ethiopia	Adu Asa Fm.	>5.4 Ma	Simpson et al., 2007; Levin et al., 2008
Ardipithecus ramidus	As Duma, Gona, Ethiopia	GWM-3 and 5 deposits	4.51–4.32 Ma	Semaw et al., 2005
	Aramis, Middle Awash, Ethiopia (type)	Above the Gàala Vitric Tuff Complex	ca. 4.4 Ma (4.48–4.29 Ma)	White et al., 1994, 1995; WoldeGabriel et al., 1994, 1995; Kappelman and Fleagle, 1995
			(alt. 4.39–3.89 Ma)	
	?Lothagam, Kenya		5.0–4.2 Ma	McDougall and Feibel, 1999
	?Tabarin, Baringo Basin, Kenya	Chemeron Fm.	4.48–4.41 Ma	Deino et al., 2002
		SUBTRIBE AUSTRALOPITHECINA, EARLY PLIOCENE–EARLY PLEISTOCENE		
Australopithecus anamensis	Kanapoi, Turkana Basin, Kenya		4.17 ± 0.03–4.07 ± 0.02 Ma and < 4.07	Leakey et al., 1998
	Allia Bay, Turkana Basin		3.95 Ma	Leakey et al., 1995
	Aramis, Middle Awash, Ethiopia	Adgantole Mb., Sagantole Fm.	4.2–4.1 Ma	White et al., 2006
	Asa Issie, Middle Awash, Ethiopia		4.2–4.1 Ma	White et al., 2006
	?Fejej, Ethiopia,	Harr Fm.	4.18–>4.0 Ma	Fleagle et al., 1991; Kappelman et al., 1996
	?Belohdelie, Middle Awash	Belohdelie Mb., Sagantole Fm.	3.89–3.86 Ma	Asfaw, 1987; White et al., 1993
Australopithecus afarensis	Laetoli, Tanzania	Upper Laetolil Beds	3.76–3.46 Ma	Drake and Curtis, 1987; Leakey, 1987
	Hadar, Ethiopia	Sidi Hakoma, Denan Dora and Kada Hadar Mbs., Hadar Fm.	3.4–2.95 Ma	Kimbel et al., 1994
	Dikika, Ethiopia	Basal Mb., Hadar Fm.	>3.4 Ma	Walter and Aronson, 1993; Alemseged et al., 2005
	Maka, Middle Awash, Ethiopia	Matabaietu Fm.,	3.4 Ma	White et al., 1993, 2000
	East Turkana, Kenya	Tulu Bor Mb., Koobi Fora Fm.	3.4 Ma	Kimbel and White, 1998; Brown, 1994
	West Turkana, Kenya	Lomekwi Mb., Nachukui Fm.	3.35–3.26 Ma	Feibel et al., 1989; Brown et al., 2001

Taxon	*Location*	*Formation*	*Age*	*References*
Australopithecus bahrelghazeli	Koro Toro, Tchad		3.5–3.0 Ma 3.6 Ma	Brunet et al., 1995, 1997 Lebatard et al., 2008
Australopithecus africanus	Sterkfontein, South Africa	?Mb. 2	?3.5–3.0 Ma (alt. 4.17 Ma; alt. 2.2 Ma)	Broom, 1936; Schwartz et al., 1994; Clarke and Tobias, 1995; Partridge et al., 1999, 2003; Kuman and Clarke, 2000; Partridge, 2000; Berger et al., 2002; Pickering et al., 2004a; Walker et al., 2006
		Mb. 4	2.8–2.6 Ma (alt. 2.5–1.5 Ma)	
	Makapansgat, South Africa	Mbs. 3, 4	ca. 3.2–2.9 Ma	Dart, 1948; McKee et al., 1995; Partridge, 2000; Herries, 2003; Latham et al., 2007
	Taung, South African (type)	Dart Deposits	ca. 2.8–2.6 Ma	Dart, 1925; McKee, 1993
	Gladysvale, South Africa	Eccles Fm.	ca. 2.5–1.7 Ma	Berger et al., 1993; Schmid, 2002; Pickering et al., 2007
Australopithecus garhi	Middle Awash, Ethiopia (type)	Hatayae Mb., Bouri Fm.	2.5 Ma	Asfaw et al, 1999; de Heinzelin et al., 1999
Paranthropus aethiopicus	Laetoli, Tanzania	Upper Ndolanya Beds	ca. 2.7–2.5 Ma	Drake and Curtis, 1987; Harrison, 2002
	Omo, Ethiopia (type)	Mbs. C–F, Shungura Fm.	2.6–2.33 Ma	Arambourg and Coppens, 1968; Suwa, 1988; Feibel et al., 1989; Rak and Kimbel, 1991; Wood and Constantino, 2007
	West Turkana, Kenya	Lokalalei Mb., Nachukui Fm.	ca. 2.5–2.4 Ma	Walker et al., 1986; Harris et al., 1988; Feibel et al., 1989; Grine et al., 1996
P. boisei	?Malema, Malawi	Unit 3A, Chiwondo Beds	ca. 2.5–2.3 Ma	Kullmer et al., 1999
	Omo, Ethiopia	Mbs. G, K, Shungura Fm.	ca. 2.33–1.39 Ma	Brown and Feibel, 1988; Suwa, 1988; Feibel et al., 1989; Wood et al., 1994
	Koobi Fora, Kenya	Upper Burgi Mb., KBS Mb., Okote Mb., Koobi Fora Fm.	2.0–1.39 Ma	Brown and Feibel, 1988; Wood et al., 1994
	West Turkana, Kenya	Kaitio Mb., Nachukui Fm.	1.87–1.65 Ma	Brown and Feibel, 1988; Harris et al., 1988; Wood et al., 1994
	Oludvai Gorge, Tanzania (type)	Beds I and II	ca. 1.85–?1.2 Ma (alt. 1.79–1.45 Ma)	Leakey, 1959; Hay, 1976; Wood et al., 1994; Tamrat et al., 1995; Wood and Constantino, 2007
	Peninj, Tanzania	Humbu Fm.	1.70–1.56 Ma (alt. 1.4 Ma)	Leakey and Leakey, 1964; Isaac, 1967; Wood et al., 1994
	Chesowanja, Kenya		>1.42 Ma	Carney et al., 1971; Bishop et al., 1978; Hooker and Miller, 1979; Gowlett et al., 1981
	Konso, Ethiopia	between Karat Tuff and Trail Bottom Tuff	1.43–1.41 Ma	Suwa et al., 1997; Silverman et al., 2001
P. robustus	Kromdraai B East, South Africa (type)	Mb. 3	ca. 2.0–1.7 Ma (alt. ca. 1.8–1.7 Ma)	Broom, 1938; McKee et al., 1995; Aiello and Andrews, 2000; Wood and Strait, 2004

TABLE 25.2
(CONTINUED)

Taxon	*Location*	*Formation*	*Age*	*References*
P. robustus continued	Sterkfontein, South Africa	Mb. 5	ca. 2.0–1.7 Ma	Clarke, 1994b; Kuman, 1994; Kuman and Clarke, 2000
	Drimolen, South Africa	Drimolen Main Quarry	ca. 2.0–1.5 Ma	Keyser, 2000; Keyser et al., 2000
	Coopers D, South Africa		ca. 1.9–1.6 Ma	Berger et al., 2003
	Gondolin, South Africa		slightly > 1.78 Ma (alt. ca. 1.9–1.5 Ma)	Kuykendall and Conroy, 1999; Menter et al., 1999; Herries et al., 2006
	Swartkrans, South Africa (type, *P. "crassidens"*)	Mbs. 1-3; ?Mb. 5	ca. 1.8–1.5 Ma (alt. ca. 1.8–0.7 Ma) (alt. ca. 1.7–1.0 Ma)	Broom, 1949; Vrba, 1985, 1995; Brain and Watson, 1992; McKee et al., 1995; Avery, 1998; Curnoe et al., 2001; de Ruiter, 2003
SUBTRIBE *INCERTAE SEDIS*				
Kenyanthropus platyops	Lomekwi, West Turkana, Kenya	Kataboi and Lomekwi Mbs., Nachukui Fm.	3.57–3.3 Ma	Leakey et al., 2001
SUBTRIBE HOMININA, LATE PLIOCENE–PRESENT				
Homo habilis	Olduvai, Tanzania	Bed I	1.87–1.75 Ma	Hay, 1976; Egeland et al., 2007;
		Lower Bed II	<1.75 Ma	Blumenschine et al., 2003; Walter et al., 1991
	East Turkana and Ileret, Kenya	Upper Burgi, KBS and Okote Mbs., Koobi Fora Fm.	1.9–1.44 Ma	Feibel et al., 1989; Gathogo and Brown, 2006; Spoor et al., 2007
	Omo, Ethiopia	Shunguru Fm.	2.4–2 Ma	Feibel et al., 1989; Suwa et al., 1996
	Hadar, Ethiopia	Kada Hadar Member, Hadar Fm.	2.33 Ma	Kimbel et al., 1996
	?West Turkana, Kenya	Kalochoro Member, Nachukui Fm.	>1.88 < 2.34 Ma	Harris et al., 1988; Feibel et al., 1989 Prat et al., 2005
	?Sterkfontein, South Africa	"StW infill" Mb.5 Mb, 4	<2.6–2 Ma ca 2–1.7 Ma 2.8–2.6 Ma (alt. 2.5–1.5 Ma)	Kuman and Clarke, 2000; Berger et al., 2002
	?Swartkrans, South Africa	Mbs. 1 and 2,	ca 1.8–1.5	Wood, 1992; Curnoe et al., 2001; de Ruiter, 2003
	?Baringo Basin, Kenya	Chemeron Fm.	2.4 Ma	Hill et al., 1985
Homo rudolfensis	East Turkana, Kenya	Upper Burgi Mb., Koobi Fora Fm.	1.88–1.9 Ma	Feibel et al., 1989; Gathogo and Brown, 2006
	?Omo, Ethiopia	Shunguru Fm.	2.4–2 Ma	Feibel et al., 1989; Suwa et al., 1996
	?Uraha, Malawi	?Chiwondo Beds,	2.5–2.3 Ma	Bromage et al., 1995a
Homo erectus	East Turkana and Ileret, Kenya	Upper Burgi, KBS and Okote Mbs., Koobi Fora Fm.	1.9–1.5 Ma	Leakey and Walker, 1976; Feibel et al., 1989; Antón, 2003; Gathogo and Brown, 2006; Spoor et al., 2007; Suwa et al., 2007
	Swartkrans, South Africa	Hanging Remnant Mb. 1, Lower Bank Mb. 1, Mb. 2, ?Mb. 3	ca. 1.8–1.0 Ma	Broom and Robinson, 1949; Clarke et al., 1970; Vrba, 1985; Delson, 1988; Curnoe et al., 2001
	Olduvai Gorge, Tanzania	Upper Bed II Bed III Bed IV, Olduvai Fm.	1.78–1.47 Ma ca. 1.47–1.2 Ma 1.2–0.78 Ma	Leakey, 1961; Hay, 1976; Walter et al., 1991; Manega, 1993; Tamrat et al., 1995

Taxon	*Location*	*Formation*	*Age*	*References*
H. erectus continued	Gona, Ethiopia	Busidime Fm.	ca. 1.7–1.5 Ma	Simpson et al., 2008
	Lincoln Cave, South Africa	Lincoln Cave South Deposits	ca. 1.7–1.4 Ma	Kuman and Clarke, 2000; Reynolds et al., 2007
	Sterkfontein, South Africa	Mb. 5 West	ca. 1.7–1.4 Ma	Robinson, 1962; Kuman and Clarke, 2000; Curnoe and Tobias, 2006
	Melka Kunturé, Ethiopia	Gomboré IB	ca. 1.7–1.6 Ma	Chavaillon et al., 1974, 1977; Westphal et al., 1979; Chavaillon and Coppens, 1986
		Garba IV, Level E	ca. 1.5 Ma	
		Gomboré II, Melka Kunturé Fm.	ca. 800–700,000 y	Condemi, 2004
	Nariokotome, West Turkana, Kenya	Natoo Mb., Nachukui Fm.	1.6–1.0 Ma	Brown et al., 1985; Feibel et al., 1989; Walker and Leakey, 1993; Brown et al., 2001
	Omo, Ethiopia	Mb. K, Shungura Fm.	1.5–1.4 Ma	Howell, 1976, 1978; Feibel et al., 1989
	Konso-Gardula, Ethiopia	Kayle Mb.	1.45–1.41 Ma	Asfaw et al., 1992; Nagaoka et al., 2005; Suwa et al., 2007
		Karat Mb., Konso Fm.	1.41–1.25 Ma	
	Laetoli, Tanzania	Lower Ngaloba Beds	ca. 1.2–0.12 Ma	Leakey and Harris, 1987
	Middle Awash, Ethiopia	Dakanihylo Mb., Bouri Fm.	1.0 Ma	de Heinzelin et al., 1999; Asfaw et al., 2002
	Uadi Aalad (Buia), Eritrea	Danakil Fm.	1.0 Ma	Abbate et al., 1998
	Olorgesailie, Kenya	Mb. 5 and 6/7 boundary, Olorgesailie Fm.	970–900,000 y	Potts et al., 2004
	Angamma-Yayo, Chad		?Early–?middle Pleistocene	Coppens, 1966; 1967
	Tighenif (Ternifine or Palikao), Algeria		ca. 700,000 y	Arambourg, 1954, 1955; Howell, 1960; Hublin, 1985; Geraads et al., 1986
Homo heidelbergensis	Olduvai Gorge, Tanzania	Masek Beds	ca. 780–490,000 y	Leakey, 1969; Hay, 1976; Walter et al., 1991; Manega, 1993; Tamrat et al., 1995
		Ndutu Beds, Olduvai Fm.	ca. 490–62,000 y	
	Kabwe, Broken Hill Cave, Zambia	No. 1 Kopje outcrop	ca. 700–400,000 y (alt. ca. 300–125,000 y) (alt. ca. 1.3–0.78 Ma)	Woodward, 1921; Vrba, 1982; Klein, 1994; Rightmire, 1998; McBrearty and Brooks, 2000; Barham et al., 2002
	Bodo, Ethiopia	Bodo Mb., Wehaietu Fm.	640–550,000 y	Conroy et al., 1978; Kalb et al., 1982; Clark et al., 1994
	Saldanha (Hopefield), South Africa	Elandsfontein Main, Elandsfontein Farm	ca. 600,000 y	Drennen, 1955; Singer, 1954; Klein et al., 2007
	Baringo Basin, Kenya	Middle Silts and Gravels Mb., Kapthurin Fm.	512–510,000 y	Leakey et al., 1969; Wood and Van Noten, 1986; Deino and McBrearty, 2002
	Cave of Hearths, Makapansgat, South Africa	Bed 3	ca. 500–200,000 y (alt. ca. 700,000 y)	Dart, 1948; Tobias, 1971; Mason, 1988; Latham and Herries, 2004; Beaumont and Vogel, 2006
	Lake Ndutu, Tanzania	?Masek Beds	ca. 500–300,000 y	Mturi, 1976; Clarke, 1976, 1990
	Littorina Cave, Sidi Abderrahman, Morocco		492–376,000 y	Arambourg and Biberson, 1956; Howell, 1960; Hublin, 1985; Rhodes et al., 2006
	Thomas Quarry, Morocco	Mb. 1, Oulad Hamida Fm.	470–360,000 y	Ennouchi, 1969; Hublin, 1985; Raynal et al., 2001; Rhodes et al., 2006

TABLE 25.2
(CONTINUED)

Taxon	*Location*	*Formation*	*Age*	*References*
H. heidelbergensis continued	Salé, Morocco		455–389,000 y	Hublin, 1985, 1991
	Lainyamok, Kenya	Skeleton Hill Patch	393–323,000 y	Shipman et al., 1983; Potts et al., 1988; Potts and Deino, 1995
	?Guomde, Kenya	Chari Mb., Koobi Fora Fm.	ca. 300–270,000 y (alt. minimum age 160,000 y)	Bräuer et al., 1992b, 1997
	Lake Eyasi, Tanzania	Eyasi Beds	ca. 300–200,000 y	Kohl-Larsen and Reck, 1936; Leakey, 1936; Mehlman, 1987; Bräuer and Mabulla, 1996; Trinkaus, 2004; Domínguez-Rodrigo et al., 2008
	Melka Kunturé, Ethiopia	Layer B, Garba III	ca. 300–200,000 y	Chavaillon et al., 1987
	Hoedjiespunt, South Africa	HOMS (Hominid Sands)	ca. 300–100,000 y	Churchill et al., 2000; Stynder et al., 2001
	Florisbad, South Africa	Peat I layer	ca. 260,000 y	Dreyer, 1935; Grün et al., 1996
	Wadi Dagadlé, Djibouti	>250,000 y		de Bonis et al., 1988
	Aïn Maarouf (El Hajeb), Morocco		?Early middle Pleistocene	Geraads et al., 1992; Hublin, 1992
	Rabat, Morocco	Khebibat (Mifsud-Giudice) Quarry	?Middle Pleistocene	Marçais, 1934; Howell, 1960; Saban, 1977
	Berg Aukas Mine, Namibia	Level 5, Berg Aukas Fm.	?Middle Pleistocene	Grine et al., 1995
	Loyangalani, Kenya		?Middle–early late Pleistocene	Twiesselmann, 1991
Homo sapiens	Omo, Ethiopia	KHS and PHS, Upper Mb. 1, Kibish Fm.	196,000 ± 2000 y (Middle Stone Age)	Day, 1969; Leakey, 1969; Rightmire, 1976; Stringer, 1978; Day and Stringer, 1982; McDougall et al., 2005; Brown and Fuller, 2008; Feibel, 2008; Fleagle et al., 2008
	Jebel Irhoud, Morocco		190–105,000 y (alt. 125–90,000 y) (Mousterian) (alt. 160–130,000 y)	Ennouchi, 1962. 1963, 1969; Biberson, 1964; Hublin and Tillier, 1981; Hublin et al., 1987; Grün and Stringer, 1991; Hublin, 1991
	Herto, Middle Awash, Ethiopia	Upper Herto Mb., Bouri Fm.	160–154,000 y (early Middle Stone Age or transition from Acheulean to MSA)	Clark et al., 2003; White et al., 2003
	Singa, Sudan	Limestone calcrete, exposed bed of Nile	>133,000 y (alt. 160-140,000 y, Oxygen isotope stage 6) (alt. 160,000 ± 27,000 y; 97,000 ± 15,000 y)	Woodward, 1938; Stringer, 1979; Stringer et al., 1985; Spoor et al., 1998; Grün and Stringer, 1991; McDermott et al., 1996
	Skhul, Israel	Layers B	135–130,000 y (alt. 119,000 ± 18,000 y) (Mousterian)	McCown, 1937; McCown and Keith, 1939; Grün and Stringer, 1991; Mercier et al., 1993; Grün et al., 2005
	Qafzeh, Israel		130–90,000 y (alt. 92,000 ± 5000 y) (Mousterian)	Schwarcz et al., 1988; Valladas et al., 1988; Grün and Stringer, 1991; Yokoyama et al., 1997
	Mumba Rock Shelter, Lake Eyasi, Tanzania	Bed VI	ca. 130,000 y (Middle Stone Age)	Mehlman, 1979, 1987, 1991; Bräuer and Mehlman, 1988

Taxon	*Location*	*Formation*	*Age*	*References*
H. sapiens continued	Laetoli, Tanzania	Ngaloba Beds	120,000 ± 30,000 y (Middle Stone Age) (alt. 130,000 y)	Day et al., 1980; Hay, 1987; Stringer, 1988; Cohen, 1996
	Aduma, Middle Awash, Ethiopia	Ardu Beds	Late Pleistocene; ?105–79,000 y (Middle Stone Age)	Haile-Selassie et al., 2004a
	Bouri, Middle Awash, Ethiopia	Beach deposit, cf. Ardu (B) Beds	Late Pleistocene, cf. Aduma (Middle Stone Age)	Haile-Selassie et al., 2004a
	Diré-Dawa (Porcupine Cave), Ethiopia		?Early late Pleistocene (Middle Stone Age)	Vallois, 1951; Briggs, 1968; Tobias, 1968
	Klasies River Mouth, South Africa		100–80,0000 y (Middle Stone Age I, II) (alt. 110,000 y) 60,000 y (MSA III)	Singer and Wymer, 1982; Deacon and Geleijnse, 1988; Grün et al., 1990; Rightmire and Deacon, 1991; Deacon, 1993; Grine et al, 1998; Grine, 2000; Vogel, 2001; Feathers, 2002
	Oranjemund, Namibia		ca. 100–50,000 y	Senut et al., 2000
	Die Kelders Cave, South Africa		80–60,000 y (Middle Stone Age)	Tankard and Schweitzer, 1974, 1976; Schweitzer, 1979; Grine et al., 1991; Avery et al., 1997; Grine, 2000
	Haua Fteah, Libya	Interface between layers XXXII and XXXIII	ca. 75,000 y (Mousterian) (alt. ca. 47,000 y)	McBurney et al., 1953a, 1953b; Tobias, 1967b; Trevor and Wells, 1967 (in McBurney et al., 1953b); Klein and Scott, 1986; Stringer and Brooks, 2000
	Mugharet el Aliya; Témara (Smugglers Cave); Dar-es-Soltane II cave; Zouhara Cave (El Harhoura), Morocco		60–35,000 y (Aterian Industry) (alt. Oxygen isotope stage 5 or 6, late middle Pleistocene or early late Pleistocene) (alt. >70,000 y)	Coon, 1939; Vallois and Roche, 1958; Ferembach 1976a, b; Debénath, 1975, 1980, 1991; Roche and Texier, 1976; Debénath et al., 1982, 1986; Hublin, 1992; Wrinn and Rink, 2003
	Taramsa Hill, Egypt		55,500 ± 3,700 y (late Middle Paleolithic)	Vermeersch et al., 1998
	Border Cave, South Africa		>48,700 y (final Middle Stone Age; Howieson's Poort, BC4) (alt. ca. 80–70,000 y; ca. 65–55,000 y, BC3 and BC5; 60-40,000 y, BC4)	Cooke et al., 1945; Wells, 1950; de Villiers, 1973, 1976; Beaumont, 1980; Grün and Stringer, 1991; Grün and Beaumont, 2001; Grün et al., 2003
	Nazlet Khater, Egypt		ca. 37,570 ± 350 y (alt. 33,000 y)	Thoma, 1984; Pinhasi and Semal, 2000; Crevecoeur and Trinkaus, 2004

TABLE 25.2
(CONTINUED)

Taxon	*Location*	*Formation*	*Age*	*References*
H. sapiens continued	Hofmeyr, Eastern Cape Province, South Africa	Dry channel bed, Vlekpoort River	36,200 ± 3,300 y	Grine et al., 2007
	Boskop, South Africa		Late Pleistocene (Middle Stone Age)	Haughton, 1917; Broom, 1918; Galloway, 1937a; Singer, 1961
	Eliye Springs, Kenya		?Late Pleistocene	Bräuer and Leakey, 1986a, b; Bräuer et al., 2004
	Mumbwa, Zambia		19,780 ± 130 y (Late Stone Age)	Jones, 1940; Gabel, 1963; Protsch, 1975a
	Wadi Kubbaniya, Egypt		19–17,000 y (Upper Paleolithic)	Stewart et al., 1986; Wendorf and Schild, 1986; Thorpe, 2003; Shackelford, 2007
	Esna, Egypt	Dune sand unit, Ballana Fm.	18,020 ± 330 y (Upper Paleolithic)	Wendorf et al., 1970; Butler in Lubell, 1974
	Olduvai Gorge, Tanzania	Naisiusiu Beds	16,920 ± 920y	Leakey et al., 1933; Protsch, 1974
	Taforalt, Morocco		16,750 y (alt. 21,000 y)	Ferembach, 1962, 1965
	Kalemba Rockshelter, Zambia		1: ca. 15,000 y; 2–4: 8–7,000 y; 5: 5–4,500 y (Late Stone Age)	Phillipson, 1976
	Wadi Halfa, Sudan		13,740 ± 600 y (Epipaleolithic)	Greene and Armelagos, 1972
	Kom Ombo, Egypt		ca. 13,000 BP	Reed, 1965; Smith, 1967, 1976; Churcher, 1972
	Afalou, Algeria		12,500–10,500 y (alt. 13,120 ± 370–11,450 ± 230 y)	Chamla, 1978
	Bushman Rockshelter, South Africa		12,500–10,000 y (Late Stone Age)	Vogel, 1969; Protsch and de Villiers, 1974
	Jebel Sahaba, Sudan		ca. 12,000 y (Epipaleolithic)	Anderson, 1968; Wendorf, 1968; Greene and Armelagos, 1972; Thorpe, 2003
	Fish Hoek (Skildergat), South Africa		?ca. 12,000 y (?Late Stone Age)	Keith, 1931; Protsch, 1975b; Deacon and Wilson, 1992
	Tushka, Egypt	Ballana Fm.	ca. 12–10,000 y	Wendorf et al., 1970
	Iwo Eleru, Nigeria		11,200 ± 200y (Late Stone Age)	Brothwell and Shaw, 1971
	Tuinplaas (Springbok Flats), South Africa		end of late Pleistocene (?Middle Stone Age) (alt. 5,570 y)	Broom, 1929; Galloway, 1937b; Schepers, 1941; Oakley et al., 1977; Hughes, 1990
	Afalou-Bou-Rhummel, Algeria		Late Pleistocene/ Holocene (Late Stone Age)	Arambourg, 1929; Vallois, 1952; Oakley et al., 1977
		Post-Pleistocene		
	Gamble's Cave II, Kenya		10–8,000 y (Kenya Capsian)	Leakey, 1931, 1935; Rightmire, 1975
	Naivasha Railway Site, Kenya		10,850 300 y (Kenya Capsian)	Leakey, 1942; Rightmire, 1975; Protsch, 1976
	Mechta-el-Arbi, Algeria		ca. 8,500 y (Epipaleolithic)	Arambourg et al., 1934; Briggs, 1950
	Bromhead's Site (Elmenteita), Kenya		7,410 ± 160 y (Elementeitan)	Leakey, 1927, 1935; Rightmire, 1975

Taxon	*Location*	*Formation*	*Age*	*References*
H. sapiens continued	Ishango, Democratic Republic of Congo	Zone Post-Emersion/ Katwe Ash	6,890 y (Bone harpoons)	Brooks and Smith, 1987; Boaz et al., 1990
		Niveau Fossilifere Principal	30–20,000 y (Bone harpoons)	
	Fayum, Egypt	Fayum Lake Beds	Ca. 6,000 y (Neolithic)	Oakley et al., 1977
	Gwisho Hotsprings, Zambia		5–3000 y (Late Stone Age)	Gabel, 1962; Fagan and Van Noten, 1971
	Otijiseva, South West Africa		4,440 ± 70y	Sydow, 1969; de Villiers, 1972
	Njoro River Cave, Kenya		3,000 y	Leakey and Leakey, 1950; Rightmire, 1975; Merrick and Monaghan, 1984
	Hyrax Hill, Willey's Kopje, Makalia Burial Site, Nakuru Burial Site, Kenya		1,000 B.C. ("Neolithic" [Gumban A, B] into 2nd millenium AD)	Leakey, 1931; Rightmire, 1975

At Toros-Menalla, the hominin-bearing part of the section for all three hominin localities consists of ~2 m thick sandstones, the Anthracothere Unit (AU), which represents a perilacustrine period of deposition. This middle unit is underlain by aeolian sandstones and capped by an upper unit sampling a true lacustrine environment. Within the AU at TM 266, bovids comprise 55% of all mammal remains and include high-crowned grazers, suggesting the presence of open grasslands. Giraffids and proboscideans point to wooded savanna, colobines to the probable presence of gallery forest, and numerous amphibious mammals (hippos, otters, anthracotheres) and shallow and deep-water fish indicate the presence of permanent water bodies. An isotopic study on the TM hippopotamids shows that they were mixed C_3 and C_4 plant eaters, similar to modern *Hippopotamus amphibius*, but with a greater proportion of C_3 plants in their diet (Boisserie et al., 2005). Whether this reflects a habitat difference, less hypsodonty, or a behavioral filter is unknown. Viewed as a whole, the fauna suggests the classic hominin "mosaic environment" reconstruction, in which both closed and open environments are in the vicinity; in this case, proximate habitats include a desert and a lake margin (Vignaud et al., 2002).

Sahelanthropus, like *Au. bahrelgazeli*, is of high biogeographic importance (discussed later) and points to the need for further work in locations outside the East African rift and the southern African cave sites.

Genus *ORRORIN* Senut et al., 2001*ORRORIN TUGENENSIS* Senut et al., 2001
Figure 25.2 and Table 25.2

Holotype The type specimen is BAR 1000'00, a fragmentary mandible (figure 25.2). A list of other specimens is provided in Senut et al. (2001).

Age and Occurrence Late Miocene, eastern Africa (table 25.2).

Diagnosis Based on Senut et al. (2001). The postcanine teeth are relatively small, with rectangular m2 and m3, triangular M3, and "thick" enamel. I1 large, C "short" with a shallow and narrow vertical mesial groove and no elevation of crown shoulders. The proximal femur has a large, anteriorly rotated, spherical head and a long neck (see Senut et al., 2001). *Orrorin tugenensis* differs from *Ardipithecus*, *Pan*, and *Gorilla* in its reportedly thicker enamel (3.1 mm at apex of paraconid of M3). It differs from *Australopithecus* in its smaller, mesiodistally shorter cheek teeth. It differs from *Australopithecus* and *Ardipithecus*, but resembles *Pan,* in the presence of a mesial groove on the upper canine.

Description The hypodigm includes dental and postcranial specimens from four localities. Unfortunately, none of the dental specimens are very complete and so comparisons are difficult. The "Lukeino molar" (KNM LU-335), a lower molar germ discovered in 1973 (Pickford, 1975), was reported to resemble chimpanzees in terms of cusp proportions (McHenry and Corruccini, 1980) and australopiths in terms of its buccal flare (Ungar et al., 1994), but interpretations were hampered by lack of knowledge about character polarity and lack of fossils of similar antiquity. The assignment of the specimen to *Orrorin* is reasonable given its location, but similarities between the lower molars in the holotype and the Lukeino molar were not explicitly made in the description of *Orrorin* by Senut et al. (2001). Singleton (2003) has posited that pronounced lower molar flare, a characteristic of KNM-LU 335, is a basal hominin synapomorphy, which would support its hominin status. However, she also notes that *Sahelanthropus* and *Ardipithecus* seem to lack any significant lower molar flare.

A broken m2 and an m3 are partially preserved in the holotype BAR 1000'00. Cusps are low, and enamel is described as "thick"; however, Haile-Selassie (2001) has criticized reports on enamel thickness based on unspecified natural breaks given the highly variable nature of this trait within and between teeth, a view with strong empirical support (Kono, 2004).

An upper central incisor originally allocated to *Orrorin* (BAR 1001'00) has since been reallocated to a nonhominin hominoid, as have two molars (from *"Orrorin"* sites Kapsomin and Cheboit) with purported similarities to *Gorilla* (Senut, 2007). The upper

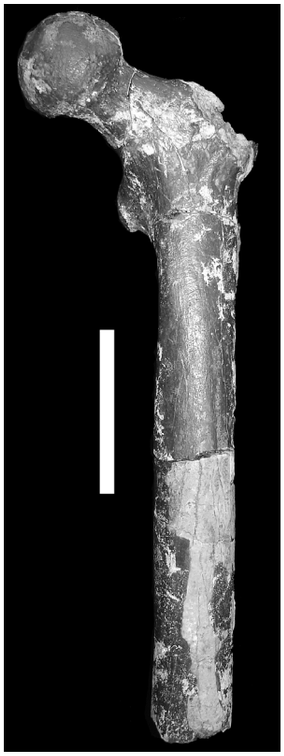


FIGURE 25.2 Anterior view of proximal femur of *Orrorin tugenensis*, BAR 1002'00. Courtesy of Martin Pickford.

canine (BAR 1425'00) resembles that of female *Pan* (i.e., is short with a pointed apex and a shallow mesial groove), and we are unaware of a published rationale for why this specimen is hominin (discussed later).

The most significant postcranial fossil is a relatively complete left proximal femur (BAR 1002'00) preserving the head, neck, lesser trochanter and about two-thirds of the shaft, but missing the greater trochanter and the distal end (Senut et al., 2001). The specimen is reported to have a long, anteroposteriorly flattened femoral neck (Pickford et al., 2002), and an obturator externus groove (OEG; Pickford et al., 2002). An OEG occurs on most but not all modern human femora, is rare or absent in other primates (Lovejoy et al., 2002; DeSilva et al., 2006), and its presence on this specimen is suggestive of the kind of full hip extension associated with bipedalism. The cortical bone of the femoral neck is reported to be thinner superiorly than inferiorly (Pickford et al., 2002; Galik et al., 2004); however, published computerized tomographic scans have had poor image quality so that the character state of this trait remains ambiguous (Ohman et al., 2005; Richmond and Jungers, 2008). The proximal shaft of the femur has been noted to be relatively wide mediolaterally, and Richmond and Jungers (2008) suggest that this reflects a response to high gluteal muscle bending moments engendered by the longer femoral neck and more widely flaring ilia in early hominin bipeds. In addition, published photographs of the *Orrorin* femur indicate that the articular surface distribution on the femoral head is more extensive anteriorly than posteriorly, whereas in *Pan*, the opposite is true. In modern humans, the more extensive articular surface on the anterior aspect of the head reflects a more ventrally and inferiorly oriented acetabulum, facilitates more medially oriented femoral positions and helps to maintain femoral-acetabular contact during adduction, while in *Pan*, the articular surface distribution reflects a more strictly laterally facing acetabulum and facilitates abduction (MacLatchy, 1996). Femoral head articular surface distribution thus tentatively suggests the same kind of femoral-acetabular relations as those found in hominin taxa that are almost certainly habitually bipedal.

Other postcranial specimens include a humeral shaft fragment BAR (1004'00), with a well-developed brachioradialis crest, similar to the condition found in *Pan* (Senut et al., 2001), and a proximal manual phalanx (BAR 349'00) with a degree of curvature similar to that of *Pan* phalanges (Richmond and Jungers, 2008).*Remarks* The Lukeino Formation, Tugen Hills, Baringo Basin, Kenya, has been independently dated by two teams. The dates concur, but those of Deino and colleagues using $^{40}Ar/^{39}Ar$ dating support a slightly older age (spanning 6.37 ± 0.05 to 5.73 ± 0.05 Ma; Deino et al., 2002; Kingston et al., 2002) than do those of Sawada et al. (2002) using K-Ar dating (6.17 ± 0.15 to 5.66 ± 0.14). Both teams agree that some relevant fossil sites are below a tuff dated at ~5.7 Ma and above a paleomagnetic reversal interval dated at 5.88 Ma (Deino et al., 2002; Sawada et al., 2002), bracketing most referred *Orrorin* fossils between 5.9 and 5.7 Ma, although doubts have been raised as to how well fossiliferous sediments can be traced laterally to dated beds within the Lukeino Formation (Kingston et al., 2002). In addition, two specimens, the Lukeino molar (KNM-LU 335) and a bone fragment attributed to a proximal femur (Senut et al., 2001) from lower in the section are constrained by the underlying trachyte lava that is older than 6.0 Ma.

Specimens are from four localities; Cheboit, Kapsomin, and Kapcheberek are up to 3 kilometers from one another, and Aragai is ~20 km to the south (based on coordinates in Pickford and Senut, 2001). Until more specific chronostratigraphic control is demonstrated for each of the localities or they are correlated laterally, the temporal range of uncertainty for the sites, as described, is on the order of several 100 ky. Thus, it is possible that the fragmentary *Orrorin* hypodigm represents more than one taxon, including nonhominin hominoids, as Senut (2007) has acknowledged. The preponderance of evidence supports bipedality as a significant component of the positional repertoire of the taxon represented by BAR 1002'00, however.

Comparatively little has been written about the teeth assigned to *Orrorin*. Molars are described as *Pan* sized with thick enamel, although the "thick" versus "thin" designation has been criticized as overly simplistic (Haile-Selassie, 2001; Haile-Selassie et al., 2004b). Senut et al. (2001) have suggested that *Orrorin* gave rise to *Homo* and that there was no megadont phase in this lineage prior to the emergence of *Homo*; that is, all australopiths are a side branch in human evolution, a view with little support (Haile-Selassie, 2001; Richmond and Jungers, 2008). The large canine with mesial groove resembles those of female *Pan* and lacks the elevated crown shoulders found in *Sahelanthropus, Ardipithecus*, and hominins from younger strata. Most of the Lukeino fossils (including *Orrorin*) are reported to be from shallow lake and floodplain deposits. Ruminants, especially impala, are common, suggesting open woodland, as are proboscideans, with five different species reported. The presence of *Colobus* suggests denser trees lining a lake margin (Pickford and Senut, 2001).

Genus *ARDIPITHECUS* White et al., 1995
Table 25.2

Synonymy *Australopithecus* (White et al., 1994).

Age and Occurrence Late Miocene–early Pliocene, eastern Africa (table 25.2).

Diagnosis A taxon with less postcanine megadontia, relatively larger upper and lower canines, small, narrow dm1 with minimal cuspule development, possibly thinner canine and molar enamel, and p3 and P3 more asymmetrical and with taller buccal cusps than *Australopithecus*. Temporomandibular joint lacks a definable articular eminence. Compared to *Pan*, the taxon has a smaller, more incisiform upper canine (especially *Ar. ramidus*) and smaller lower lateral incisors (White et al., 1994, 1995).

Referred Species *Ardipithecus kadabba* and *Ardipithecus ramidus*.

ARDIPITHECUS KADABBA Haile-Selassie et al., 2004
Figure 25.3 and Table 25.2

Synonymy *Ardipithecus ramidus kadabba*, Haile-Selassie, 2001.

Holotype The type specimen is ALA-VP-2/10, a right mandibular corpus with right m3, left i2, c, p4, m2, and an m3 root fragment. A list of other referred specimens is provided in Haile-Selassie (2001) and Haile-Selassie et al. (2004b, 2009).

Age and Occurrence Late Miocene, eastern Africa (table 25.2).

Diagnosis Sharp m3 lingual cusps; squared distal outline to M3 with four distinct cusps; shallow mesial fovea on P3; tendency for less relief on mesiolingual crown face of the lower canine; mesiolingually to distobuccally compressed lower canines; and clearly defined anterior fovea on p3. It differs from *Pan*, *Gorilla*, and other extant and Miocene hominoids, including *Orrorin*, in its tendency toward more incisiform lower canines with a developed distal tubercle and in its variable expression of mesial crown shoulder height and mesial marginal ridge development. It differs from *Ardipithecus ramidus* in its more basal termination of the mesial and distal apical crests on the upper canine, and by a more asymmetrical crown outline and relatively smaller anterior fovea on p3 (Haile-Selassie, 2001; Haile-Selassie et al., 2004b).

Description Eleven specimens collected between 1997 and 2001 from five middle Awash localities dated to between 5.8 and 5.2 Ma were initially allocated to a subspecies of *Ardipithecus ramidus, Ar. r. kadabba* (Haile-Selassie, 2001). In 2004, an enlarged hypodigm adding six more teeth from the Asa Koma locality (5.8–5.6 Ma) resulted in the elevation of all 17 specimens to a new species, *Ardipithecus kadabba* (Haile-Selassie et al., 2004b).

An upper canine and p3 recovered in 2002 were critical to the designation of the new species. Haile-Selassie et al. (2004b) have indicated that the upper canine has a more basal termination of the mesial apical crest and is higher crowned, and that the p3 crown outline of *Ar. kadabba* is more asymmetrical and retains a buccal wear facet, in contrast to *Ar. ramidus*. The right upper canine (ASK-VP-3/400) has little apical wear, and in this respect is more like *Pan* and unlike *Au. afarensis* and *Sahelanthropus*. The specimen also has low mesial shoulders. Upper and lower canines are projecting and interlocking. However, although not consistently expressed, lower canines are more incisiform, with better-developed distal tubercles and mesial marginal ridges, and elevated mesial crown shoulders compared to those of *Pan*. One lower canine (STD-VP-2/61) is taller with a narrow apex and has a lower mesial crown shoulder and less prominent distal tubercle than the lower canine in the holotype, which is shorter. The holotype canine has a distal tubercle, which has a posteriorly oriented wear facet, as in apes with a C/p3 honing complex; however, the facet is worn horizontally, not diagonally as in apes, suggesting that a fully functioning C/p3 honing complex was not operating (see Haile-Selassie et al., 2004b).

A left i2 is relatively small and has simple lingual morphology (Haile-Selassie et al., 2009). Lower third molar cusps are less rounded than in *Australopithecus*, and the m3 is smaller than those of *Au. anamensis* but larger than in *Pan* (Haile-Selassie, 2001). Maximum radial thicknesses of lateral enamel have recently been published for a number of molars and range between 1.0 and 2.0 mm (Haile-Selassie et al., 2009). Molars have more buccal than lingual wear, with scooped dentin exposure, unlike later hominins, and Haile-Selassie and colleagues (2009) have interpreted this to indicate "erosive" rather than "abrasive" wear. An M1 lacks the occlusal surface crenulation found in *Pan* molars (Haile-Selassie, 2001).

The mandible has been described as resembling those of *Sahelanthropus* and *Ar. ramidus* (including the Tabarin and Lothagam specimens, discussed later) in being smaller and thinner than is typical for early *Australopithecus* (Haile-Selassie et al., 2009).

Forelimb bones include the distal two-thirds of an intermediate hand phalanx (ALA-VP-2/11) that is larger than those of *Au. afarensis,* although it is similar to the latter taxon in terms of the deep fossae for the flexor digitorum superficialis muscle (Haile-Selassie, 2001). A distal humerus fragment (ASK-VP-3/78) has a deep olecranon fossa with steep walls (Haile-Selassie et al., 2009), and a clavicle (STD-VP-2/893) is robust with a strongly marked deltoid insertion (Haile-Selassie, 2001).

A left fourth proximal foot phalanx (AME-VP-1/71, from the chronologically youngest sediments) has a dorsally canted proximal articular surface (Haile-Selassie, 2001), suggesting force was transmitted during dorsiflexion rather than plantarflexion (like *Au. afarensis* and unlike *Pan*). This is provisional evidence for bipedality (Latimer and Lovejoy, 1990a, 1990b). Phalanx size and curvature correspond to known *Au. afarensis* specimens (Haile-Selassie, 2001) and are shorter and less curved than in *Pan* (Haile-Selassie et al., 2009).

Remarks As noted by Haile-Selassie et al. (2004b:1505): "No known *Ardipithecus ramidus, Australopithecus afarensis* or *Australopithecus anamensis* lower p3 exhibits any sign of a mesiobuccally oriented [honing] facet on its buccal crown face." The p3 of *Ar. kadabba* has a buccal wear facet; although this is distinguishable from that of extant apes, it suggests an intermediate stage of C/p3 anatomy not far removed from the presumed honing complex of the last common ancestor of *Pan* and *Homo*. The demonstration of this intermediate stage of C/p3 anatomy places *Ar. kadabba* in a possible basal hominin role.

Haile-Selassie et al. (2004b) have suggested that *Sahelanthropus*, *Orrorin*, and *Ardipithecus* may be congeneric (in which case the genus name would be *Ardipithecus*) and perhaps conspecific. Relatively little evidence contraindicates this for *Orrorin*; distinguishing dental features (e.g., molar flare and enamel thickness) are subtle and rest on small sample sizes. The canine has been distinguished from those of other homi-

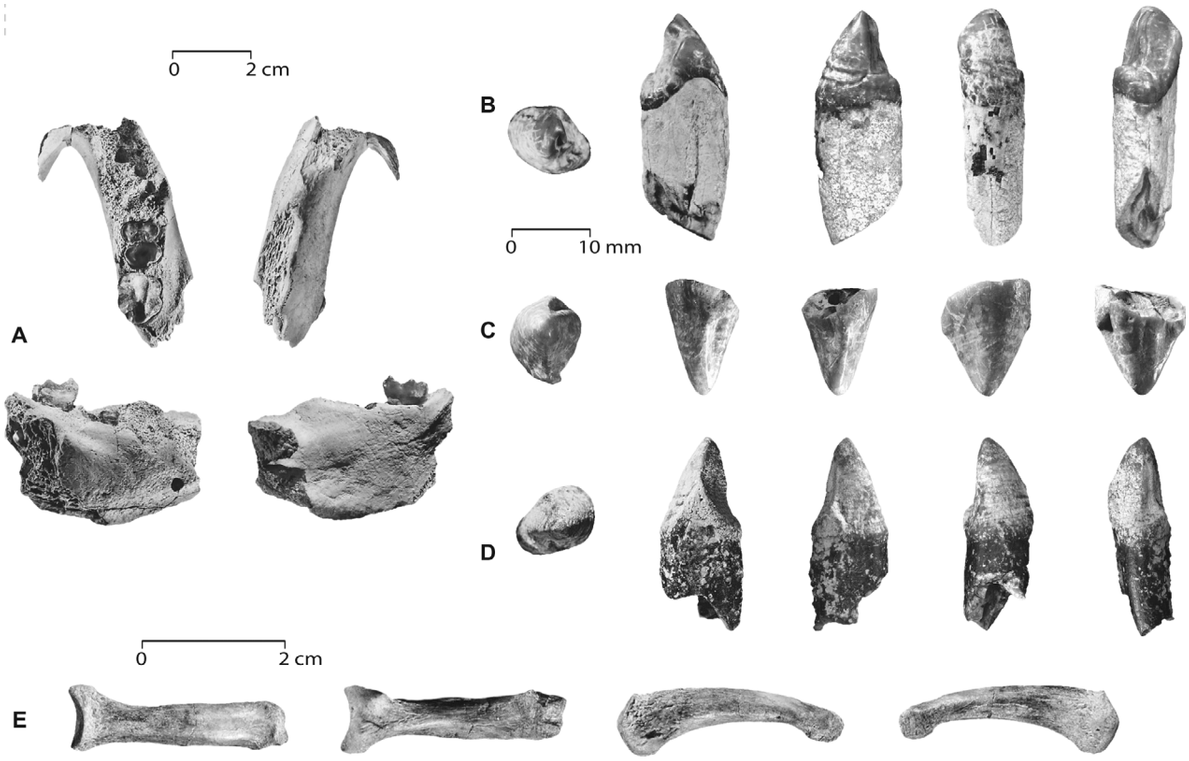


FIGURE 25.3 A) Holotype of *Ardipithecus kadabba*, mandible ALA-VP-1/10; B) holotype of *Ardipithecus kadabba*, canine ALA-VP-1/10; C) isolated right upper canine of *Ardipithecus kadabba* ASK-VP-3/400; D) isolated right lower canine of *Ardipithecus kadabba* STD-VP-2/61; E) proximal foot phalanx of *Ardipithecus kadabba* AME-VP-1/71. Courtesy of Tim White.

nins but not *Pan*, and as discussed, the *Orrorin* teeth may not represent the same taxon as the postcrania. Moreover, no femur is known for *Ardipithecus*. A greater number of features distinguish *Sahelanthropus* and *Ardipithecus* (e.g. in addition to features in the initial diagnosis, *Sahelanthropus* lacks a diastema between I2/C and has a much thicker browridge, even when sexual dimorphism is taken into account), but the two share derived aspects of basicranail morphology (Suwa et al., 2009b).

In a preliminary report on the environment, WoldeGabriel et al. (2001) note that the Adu-Asa Formation hominin sites (four of five hominin sites yielding 10 of 11 hominin fossils) are part of a vertebrate assemblage that includes reduncine bovids (suggesting open woodland or wooded grassland), *Tachyoryctes* (root rats, found today in upland grasslands), and *Thryonomys* (cane rats, found today at lake and river margins), but few hares (suggesting that open grassland is not well sampled). They contrast this with the slightly younger (5.2 Ma) Kuseralee Member of the Lower Sagantole Formation deposits that have yielded only one hominin fossil as part of an assemblage including unspecified bovids, carnivores, and cercopithecid monkeys. Pedogenic oxygen isotope values have been interpreted as evidence that the Adu-Asa sites are sampling higher-altitude and possibly wetter habitats than the Lower Sagantole sites, but sample size is small. Stable carbon isotopic $\delta^{13}C$ values from the paleosol carbonates do not distinguish between the two members (nine samples from the Adu-Asa Formation range between −7.5‰ and −4.1‰, with a mean of −6.4‰, while two samples for the Lower Sagantole are −5.2‰ and −6.3‰) and are compatible with woodland to grassy woodland habitats. These authors emphasize that the hominins are most common at the localities sampling higher elevation and possibly more closed habitats. However, the presence of pedogenic carbonates is itself a semiarid to arid indicator, and the carbon values are relatively enriched. This, along with limited published faunal data, suggests that additional evidence is needed to support this team's contention that hominins older than 4.4 Ma "may have been confined to woodland and forest habitats" (WoldeGabriel et al., 2001:177). An association with closed environments for *Ar. kadabba* has also been questioned by Levin et al. (2008), who find stable carbon isotopic data from fossil herbivore enamel from *Ar. kadabba*– (and *Ar. ramidus*–) bearing deposits at Gona (~ 90 km north of Middle Awash sites) to resemble the signatures found in extant herbivores living in bushland and eating both C_4 and C_3 plants.

ARDIPITHECUS RAMIDUS White et al., 1995
Figure 25.4 and Table 25.2

Synonymy *Australopithecus ramidus,* White et al., 1994; *Homo antiquus praegens,* Ferguson, 1989, in reference to the Tabarin mandible (see below).

Holotype The type specimen is ARA-VP-6/1, an associated set of teeth including left I1, C, P3, P4, and right I1, C, P4, and M2, and lower right p3–4 (White et al., 1994). A list of other specimens is provided by White et al., 1994, 1995, 2009a, and Semaw et al., 2005.

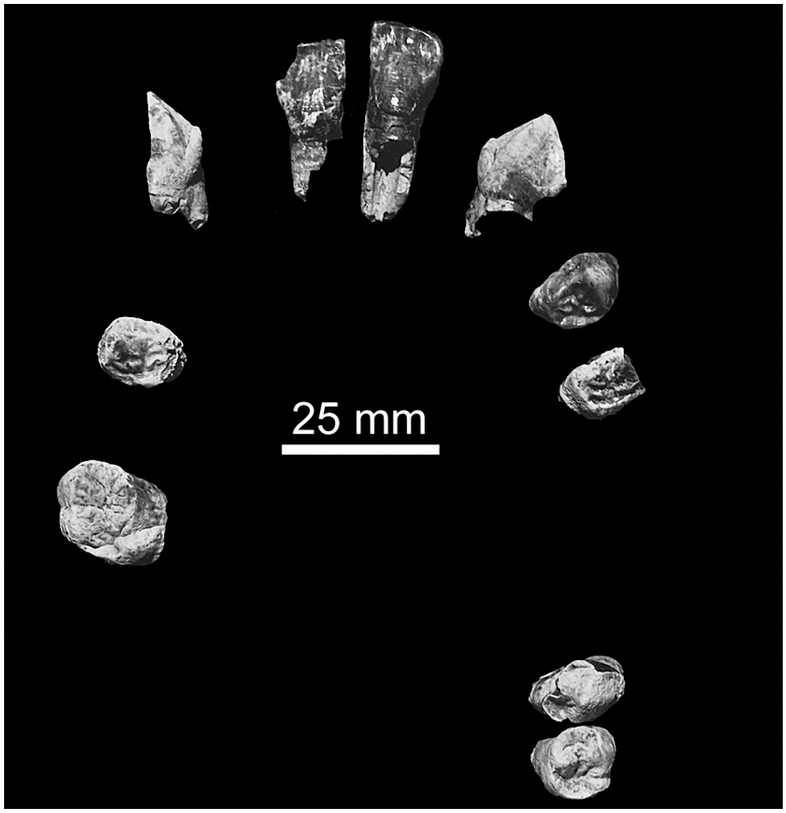


FIGURE 25.4 Holotype of *Ardipithecus ramidus*, associated teeth ARA-VP-6/1. Courtesy of Tim White.

Age and Occurrence Early Pliocene, eastern Africa (table 25.2).

Diagnosis Based on White et al. (1994). The features distinguishing this taxon from australopiths are listed in the generic diagnosis given earlier. *Ardipithecus ramidus* differs from extant apes in its more incisiform canine morphology and relatively higher canine crown shoulders; relatively small p3 without functional honing facet; relatively broader lower molars; and more anteriorly positioned foramen magnum. It is further distinguishable from *Pan* in its smaller I1, elongate and relatively larger m3, and less crenulated molars.

Description Key to assignment of *Ardipithecus* to Hominini is the upper canine and anterior lower premolar anatomy. The upper canine is less projecting and has more extensive mesial and distal apical crests that that of *Ar. kadabba*, while the p3 is reduced in size and lacks a honing facet. Several authors have noted that *Ar. kadabba–Ar. ramidus–Au. anamensis–Au. afarensis* form an increasingly derived continuum of canine/premolar anatomy (Leakey et al., 1995, 1998; Kimbel et al., 2006; White et al., 2006). Mean canine size in the Aramis sample is comparable to that of female *Pan*, and Suwa and colleagues (2009a) propose that the upper canine is relatively more reduced than the lower canine.

Canine dimorphism is low, with purported males having mean crown diameters only 10–15 % larger than assigned females (Suwa et al., 2009a). Incisors are smaller than those of *Pan* and *Pongo*, while postcanine teeth have been found to be less megadont than in *Australopithecus* or *Pongo*, but larger than in *Pan* (Suwa et al., 2009a). Molars from Aramis are not as broad buccolingually as are those attributed to *Au. afarensis* and they possess thinner enamel, though not as thin as in *Pan* (Suwa et al., 2009a) contra early assessments (White et al., 1994).

The morphology of the dm1 is also considered significant: it is narrow, lacks an anterior fovea, has a large protoconid, a small, distally placed metaconid, and a small, poorly differentiated talonid (White et al., 1994). In these features, it retains the presumed primitive morphology, resembling extant *Pan* and Miocene taxa such as *Dryopithecus*, and differs from the condition seen in australopiths (with the exception of *Au. anamensis*, which is intermediate in morphology between *Ar. ramidus* and *Au. afarensis* [Leakey et al., 1998]), which have buccolingually expanded crowns, larger metaconids, and larger talonids with distinct cusp relief (White et al., 1994).

A partial adult basicranium (ARA-VP-1/500) may also support the hominin status of *Ardipithecus*. The anterior border of the foramen magnum is almost at the level of the carotid foramina, and the skull is described as having a shorter basioccipital region of the cranial base than in extant apes (White et al., 1994; Suwa et al., 2009b), possibly reflecting more habitually erect postures (i.e., during bipedalism) than in these taxa or, alternatively, neural reorganization (Suwa et al., 2009b). This specimen and one other (ARA-VP-1/125) also preserve temporal bone anatomy: there is marked pneumatization of the temporal squama, the temporomandibular joint is flat and lacks an articular eminence, and the tympanic is tubular.

Discovery of a partial skeleton was reported by White et al. in 1995, but until 2009 the only published elements referred to *Ar. ramidus* remained restricted to some incomplete jaws, teeth,

cranial fragments, and a few postcranial fossils, mostly of the forelimb. The first additions to the *Ar. ramidus* hypodigm came from Gona (Semaw et al., 2005), but subsequently more fossils, including the ARA-VP-6/500 associated skeleton, have been recovered from the Aramis locality (White et al., 2009b), as well as from two other localities, Kuseralee Dora (KUS) and Sagantole (SAG), in the Central Awash Complex (White et al., 2009b). The fragmented skull of ARA-VP-6/500 includes portions of the vault, base, right face, and much of the left side of the mandibular corpus. The maxilla displays a diastema between I2 and C and has weak subnasal prognathism, which is reflected in a zygomatic root positioned above M1, more posterior than in *Australopithecus* but more anterior than in *Pan* (Suwa et al., 2009b). The frontal torus is at the low end of the range of vertical thickness found in *Pan troglodytes* (Suwa et al., 2009b) and is unlike the torus in *Sahelanthropus*, which exceeds that of *Gorilla* in size (Brunet et al., 2002). This character, along with the diastema, distinguish *Ardipithecus* from *Sahelanthropus*; otherwise the two genera share a similar cranial base morphology, a projecting midface, and a low endocranial capacity (Suwa and colleagues [2009b] estimate the endocranial volume of ARA-VP-6/500 to be in the range of 280–350 cc.)

Mandibular specimen ARA-VP-1/401 has a receding symphysis similar to that of *A. anamensis* but has a less inflated corpus (Suwa et al., 2009b). It also appears the canine was not incorporated into the incisor tooth row, unlike *Australopithecus* (Suwa et al., 2009b).

Although an associated left humerus, ulna, and radius (ARA-VP-7/2) were part of the original paratype of this taxon (White et al., 1994), ARA-VP-6/500, and other additions to the hypodigm reported in White et al. (2009a) greatly expand our knowledge of the postcranial skeleton of *Ar. ramidus*. The ARA-VP-6/500 individual, like the rest of the hypodigm from sites in the Central Awash Complex, is radiometrically dated at 4.4 Ma (WoldeGabriel et al., 2009). ARA-VP-6/500 has among the smallest canines for the entire Aramis sample, and probabilistic assessments using bootstrapping suggest it is unlikely that the canines could be attributable to a male, even assuming low–moderate dimorphism (Suwa et al., 2009a). The thin supraorbital torus has also been cited as evidence that the skeleton represents a female (Suwa et al., 2009b). However, body size estimates derived using geometric means of measures of the talus and capitate are in the range of 50 kg (Lovejoy et al., 2009b), larger than any female body weight estimates for sufficiently well-sampled australopiths, but similar to estimates of body weight derived from the limited *A. anamensis* remains. The latter lacks evidence for postcranial dimorphism (i.e., it has been assumed males have been sampled) but does evince canine dimorphism (Ward et al., 2001). Since the Aramis individual is at the high end of the postcranial size distribution, it could be suggestive of low–moderate body size sexual dimorphism, more comparable to that of genus *Pan* than *Gorilla* (Suwa et al., 2009a). Body size estimates from other remains, especially long bones, will be useful in evaluating this claim.

Hand bones of the individual are unusually complete and well preserved and have been interpreted by Lovejoy and colleagues (2009b) as lacking knuckle-walking features. For example, the dorsal surface of the proximal metacarpals do not possess ridges, and the heads are not expanded. Moreover, the hand is also interpreted as not having adaptations for suspensory behavior. The 5th metacarpal-hamate articulation is described as cylindrical/condyloid and therefore mobile, rather than planar and therefore rigid as in large-bodied suspensors (Lovejoy et al., 2009c). Likewise, the articular relations of metacarpals 2 and 3, and the capitate and trapezoid, lack the complexity that leads to rigidity in this region in great apes and that may be functionally related to stiffening the wrist for stable manual suspension. *Ardipithecus* is also reported to lack the elongation of the metacarpals that characterizes extant hominoids, though it does have moderately elongated phalanges. Proximal ulnar and distal humeral morphology are suggestive of full elbow extension with considerable loading in this position. For example, the olecranon process is short, and the zona conoidea of the humerus is deep, with a posteriorly extended lateral wall. However, it is proposed that a fully extended elbow joint was used during manipulative foraging rather than during suspension (Lovejoy et al., 2009c).

The pelvis of ARA-VP-6/500 is represented by an almost complete but crushed and distorted left innominate and a portion of the right ilium. If the published reconstruction accurately portrays the superior and lateral extent of the ilium, then the ilium was superoinferiorly shortened relative to all extant nonhuman hominoids, suggesting orthograde postural control in the sagittal plane, and laterally flaring, possibly resulting in enhanced abductor function during one-legged stance, an important adaptation for bipedality (Lovejoy et al., 2009d). The ischium, however, is African ape–like with a presumably large ischial tuberosity anchoring the important climbing muscles of the hamstrings (Lovejoy et al., 2009d). The pelvis also preserves an anterior inferior iliac spine. Lovejoy and colleagues' (2009d) reconstruction of the *Ardipithecus* pelvis also suggests that the lower lumbar vertebrae were not stabilized to the ilia with ligaments but instead were "free" and thus able to situationally produce lumbar lordosis during bipedal locomotion. However, this interpretation is likely erroneous, since the lower lumbar vertebrae of modern humans are both lordotic *and* powerfully fixed to the ilium by ligaments, and there is evidence that this was the case for australopiths, as well; furthermore, the lower lumbar vertebrae of all mammals have some degree of ligamentous connection to the pelvis (Sanders, 1998). The lower limb of *Ardipithecus* is represented by a fragmentary femoral shaft (ARA-VP-1/701), and parts of the femur, tibia, and fibula of ARA-VP-6/500. Both the fibula and the apparently nearly complete tibia remain essentially undescribed, though the tibia is reconstructed as roughly 262 mm in length. Both the femur and tibia of ARA-VP-6/500 are noted to have been quite damaged. The femur of *Ardipithecus* lacks a spiral pilaster, which delineates the attachment for the vastus lateralis and gluteus maximus muscles in African apes. Instead, this femur possesses a third trochanter and a rugosity similar that may be homologous to the hypotrochanteric fossa found in australopith femora. These morphologies are interpreted as primitive, with the spiral pilaster being derived in African apes (Lovejoy et al., 2009d).

As was the case with the hands, the foot bones of ARA-VP-6/500 are remarkably complete and well preserved, with 33 individual fossils and even 2 sesamoids represented (White et al., 2009b). Fifteen other foot fossils attributed to *Ardipithecus* have been found from sites within the Middle Awash study area (navicular, 7 metatarsals, and 7 phalanges; White et al., 2009b). The foot of *Ardipithecus* displays a unique combination of anatomies not seen in any extant or extinct hominoid. The following description of the foot is from Lovejoy et al. (2009a). The interpretation of this unique foot anatomy is that *Ardipithecus* was capable of both arboreal grasping and terrestrial propulsion. Most notably, the foot of *Ardipithecus* possesses a strongly abducted hallux, indicative of careful arboreal

climbing in this taxon. The abduction angle is 68°, similar to the mean in the African apes.

The tarsal region is represented by a talus, cuboid, and cuneiforms. The well-preserved talus (ARA-VP-6/500-023) is African ape–like, possessing a mediolaterally wide distal aspect of the talar trochlea, and a relatively high talar axis angle. This latter angle suggests that *Ardipithecus* lacked the strong bicondylar angle found in later *Australopithecus*. The talus also has a trapezoidal angle forming the groove for the flexor hallucis longus tendon, a feature found more often in African apes than in modern humans and australopiths. However, the talus does have a palpable tubercle for the anterior talofibular ligament, an important ligament for ankle stability found in modern humans but only rarely in the great apes.

The cuboid is a rarely preserved element in the hominin fossil record, yet both the right and a portion of the left are preserved in ARA-VP-6/500 (White et al., 2009b). Unlike modern humans and the OH 8 hominin, the *Ardipithecus* cuboid does not have an eccentrically positioned calcaneal process and therefore may have lacked the derived calcaneocuboid locking mechanism found in obligate bipeds. However, like modern humans, the cuboid is proximodistally elongated, which would increase the lever arm for the plantarflexors during toe-off. A proximodistally enlarged navicular (ARA-VP-6/503) also contributes to the elongated midtarsal region. The cuboid-metatarsal joint is flat, like that found in modern humans, and unlike the joint surface of nonhuman primates. This morphology suggests that *Ardipithecus* may have possessed a rigid midfoot, perhaps unable to produce midfoot flexion. This assertion is supported by the presence of a facet for the os peroneum on the lateral aspect of the cuboid. This sesamoid (perhaps represented by ARA-VP-6/500-093) repositions the peroneus longus tendon out of the cuboid groove to a position more obliquely oriented across the plantar aspect of the foot, helping to stiffen the midfoot. The os peroneum is normally not present in African ape, which has more midfoot mobility able to conform to arboreal substrates.

Further evidence for plantar rigidity can also be found in the relatively expanded bases of the lateral metatarsals, which are dorsoplantarly tall relative to the length of the metatarsals. The preserved lateral metatarsal head (ARA-VP-6/505-MT3) is domed and possesses a sulcus between the head and the shaft of the bone, consistent with the type of strong phalangeal dorsiflexion that occurs during the toe-off phase of bipedal locomotion. The second metatarsal (ARA-VP-6/1000) displays strong shaft torsion like that found in African apes, consistent with the presence of a grasping first ray. However, the third metatarsal does not possess African ape–like metatarsal torsion, and instead is more modern human–like, suggesting that any toe-off occurred along the oblique axis of the foot. The first metatarsal may have served a balance role during terrestrial travel, rather than a propulsive one, thus the shift to the transverse axis during the bipedal locomotion practiced by later hominins is a more recent adaptation. The pedal phalanges are curved, and are similar in relative length to that in the *Gorilla*, but unlike African ape phalanges, they have a dorsiflexion cant to them, a morphology found in modern human phalanges.

Ardipithecus ramidus specimens from Gona, Ethiopia, described by Semaw and colleagues (2005), include seven partial jaw and dental specimens, three manual phalanges, and a pedal phalanx. Both upper (GWM9n/P51) and lower (GWM9nP50) canines are represented. The upper canine is large and diamond shaped and, as in the Aramis sample, has distinct mesial and distal shoulders. The lower canine has an elevated mesial shoulder and a distinct distal marginal tubercle. An m1 is small, bunodont, and has enamel thickness (~1 mm) comparable to the Aramis specimens. Overall, wear rates seem low, suggesting a nonabrasive diet. Manual phalanges are reported to resemble those of *Au. afarensis,* except that the base of the proximal articular surface is transversely broad and long. A proximal pedal phalanx preserves the proximal articular surface, and has a dorsally oriented, transversely broad proximal facet, as reported for *Ar. kadabba* (Haile-Selassie et al., 2004b) and *Au. afarensis* (Latimer and Lovejoy, 1990b).

Remarks Two fragmentary hominoid specimens from Kenya (discussed later) are of the appropriate age and may belong to the *Ar. ramidus* hypodigm. White and colleagues were hesitant to refer them to *Ar. ramidus* when the latter taxon was erected because at the time (in 1994) they lacked diagnostic features.

- The Lothagam mandible (KNM-LT 329) is a fragment of the right side of the mandibular corpus preserving the m1 crown and roots of m2–3 (White, 1986a; Hill and Ward, 1988). It is from the Lothagam sequence in northern Kenya and is dated between 5.0–4.2 Ma (McDougall and Feibel, 1999).
- The Tabarin mandible (KNM-TH 13150), is a fragment of the right side of the mandibular corpus with worn m1–2 and portions of the alveoli of p4 and m3 (Ward and Hill, 1987). Although tentatively assigned to *Au. afarensis* (e.g., Ward and Hill, 1987), the publication of *Ar. ramidus* made apparent certain primitive features, including the narrower molars and thinner enamel, shared by the Tabarin specimen and *Ar. ramidus,* relative to *Au. afarensis* (Hill, 1999; Deino et al., 2002). The Tabarin mandible was recovered from the Chemeron Formation, Baringo Basin, Kenya, and is dated at 4.48–4.41 Ma (Deino et al., 2002).

Reported lack of suspensory adaptations in the hand of *Ardipithecus* has been used by Lovejoy and colleagues (2009a, 2009b, 2009c, 2009d; White et al., 2009b) to argue that these features, and therefore forelimb suspensory behavior in general, evolved independently in hylobatids and each great ape genus, rather than being lost in *Ardipithecus*. This perspective is echoed in this team's analysis of the entire postcranium, and shared features related not just to suspension, but vertical climbing and orthogrady, are considered hominoid homoplasies. Their assumption is that *Ardipithecus ramidus* preserves in many respects the attributes of the Last Common Ancestor (LCA) of *Pan* and *Homo*. Unfortunately, there is still considerable uncertainty as to the timing of the *Pan-Homo* split, with estimate ranging from 4–8 Ma (Bradley et al., 2008). Pinpointing this estimate is of importance, for if the younger estimates are true, then if *Ardipithecus* is a hominin, it may indeed preserve many features of the LCA. On the other hand, if the older estimates are true, then *Ardipithecus* may have experienced upward of 3 Ma of independent evolution since the split.

An alternative idea, that *Ardipithecus* is derived from a suspensory, orthograde ancestor, remains to be rigorously tested with more detailed comparative analyses and a more explicit consideration of the polarity of character states that also includes additional information about Miocene hominoids. It is also possible that *Ardipithecus* is not a hominin, in which case, features such as the foramen magnum, reduced canines, and bipedal features in the foot and pelvis would be homoplasies, or that *Ardipithecus* is a hominin but not ancestral to australopiths. For now, phylogenetic continuity among the

Ar. kadabba–Ar. ramidus–Au. anamensis–Au. afarensis series remains well supported biogeographically and by dental evidence, but the postcranial data, in light of the new partial skeleton, are ambiguous and controversial. If *Ar. ramidus* is a hominin, then the scale of homoplasy implied in closely related clades makes the hypothesis that it is a basal hominin a long way from the most parsimonious interpretation of this important new evidence for African higher primate evolution.

Despite the detailed functional reconstructions of the Aramis partial skeleton, the overall locomotor profile of ARA-VP-6/500 is enigmatic. It is suggested that this individual neither vertically climbed nor used forelimb suspension to any significant degree, was pronograde and palmigrade in the trees and orthograde and bipedal on the ground (Lovejoy et al., 2009a, 2009b, 2009c, 2009d). No modern or previously described fossil primate occupies such a niche. This functional interpretation raises the intriguing question of how a 50+ kg animal can be a successful arborealist, absent vertical climbing and suspension. Large-bodied extant pronograde monkeys are awkward in the trees (with the possible exception of *Nasalis*), and great apes rely critically on suspension to move arboreally. However, *Ardipithecus* is not reconstructed as a ripe fruit eater like *Pan* or *Pongo* (e.g., as evidenced by narrow incisors), but rather as a generalized frugivore/omnivore (Suwa et al., 2009a). Thus, if the locomotor limitations reconstructed are correct, then while foraging arboreally, it may have moved ponderously on large supports in the lower canopy rather than the upper canopy (Lovejoy et al., 2009b). The arboreal food resources available at this level, and which would have to have been incentive to maintain a grasping hallux, are not detailed, however.

If body size and canine dimorphism are low as suggested, then this may imply weak male-male competition, more comparable to *Pan paniscus* than *Pan troglodytes* (Suwa et al., 2009a). In addition, if *Ardipithecus* is the sister taxon to *Australopithecus*, and if canine reduction was initially a consequence of social change, then postcanine megadonty and thick enamel may have been enabled by a hypothetical decrease in selection to maintain long, interlocking canines. However, since *Ardipithecus* molars are relatively broad, and the enamel thicker than that of *Pan*, it is hard to resolve whether or not dietary selection was already at work. This is in part due the lack of relevant fossils of the African ape and modern human LCAs. Most middle and late Miocene taxa have thick enamel, so it is also possible that *Ardipithecus* had reduced enamel thickness relative to the LCA.

Seven localities at Gona have yielded fossils attributed to *Ar. ramidus*. The Gona Western Margin sequence is composed of small-scale fluvial, lacustrine, and volcaniclastic elements, and the environment of deposition is reconstructed as lakes, swamps, springs, and streams amid local volcanic centers (Semaw et al., 2005). Faunal remains support the presence of some open habitats; for example, papionines are more common than colobines and there are numerous grazing bovids. Stable carbon isotopic analyses of tooth enamel reveal a high proportion of grazing herbivores (Levin et al., 2008), while paleosol samples yielded mean $\delta^{13}C$ values of −7.5 ‰, indicating mixed habitat, with both C_3 and C_4 plants (Semaw et al., 2005). Semaw et al. (2005; Levin et al., 2008) note that although woodland, grassy woodland and C_4 grasslands were presumably present, habitat preferences within this mosaic are as yet unknown.

The Gona paleoenvironmental interpretation is somewhat at odds with the reading of the environment at Aramis, where hominins are localized as occupying "woodland with patches of forest" (White et al., 2009a:92). However, 28 paleosol carbonate values for the Lower Aramis Member (excluding those from the nonhominin-bearing sites to the east interpreted to be more open) have a mean of −4.1‰ (Woldegabriel et al., 2009), indicating a greater C_4 component and potentially more open habitats relative to Gona. Furthermore, $\delta^{13}C$ values from mammal tooth enamel at Aramis show evidence of herbivores with predominantly C_3, predominantly C_4 as well as mixed diets (White et al., 2009a), and include large-bodied grazers such as *Anancus,* which would require significant amounts of grass. Five *Ardipithecus* samples show little variation, with a mean $\delta^{13}C$ of −10.25‰, similar to values obtained for C_3 browsers (White et al., 2009a). Comparisons with published values for other hominoids suggest a diet enriched in ^{13}C plants relative to chimpanzees but less enriched than australopiths (Van Der Merwe et al., 2008; Smith et al., 2010; White et al., 2009a).

The Aramis fossils accumulated on a flat plain, and though tooth marks are common on the bone, carnivore activity is not thought to have resulted in bone concentration, and there is no evidence of fluviatile transport (WoldeGabriel et al., 1994; Louchart et al., 2009). Thus, taphonomic bias in terms of the ecomorphological implications of the faunal composition may be minimal, and the finding that woodland-adapted bovids (e.g. *Tragelaphus*) and arboreal cercopithecoids represent over 50 % of all macrovertebrate remains may be significant (White et al., 2009a). Nonetheless, overall, the local vegetative ecosystem appears to have been heterogeneous, like that at Gona, and where the specific ecological niche(s) of *Ardipithecus* fits within this mosaic is not obvious. It could be argued that *Ardipithecus*'s possession of a grasping hallux is one of the best indicators that the taxon may have preferentially used the woodland/forest over the grassy woodland savanna habitats.

Subtribe AUSTRALOPITHECINA Gregory and Hellman, 1939
Table 25.2

Partial Synonymy *Plesianthropus,* Broom, 1936; *Paranthropus*, Broom, 1938; *Homo,* Mayr, 1950; *Praeanthropus*, Senyurek, 1955

Age and Occurrence Early Pliocene–early Pleistocene, eastern, southern, and Central Africa (table 25.2).

Diagnosis Dart's (1925) initial description of the taxon was based on a juvenile cranium, the Taung child, and it referred to several features, such as an enlarged brain size relative to apes, and relatively slight facial prognathism, that would not be given emphasis now. However, the anteriorly positioned foramen magnum and robust mandible with small canines and no diastema remain key diagnostic characters.

Currently, the genus *Australopithecus* is recognized in the following gradistic terms, by a suite of both primitive and derived features, and is considered paraphyletic (see also Kimbel, 2007): extant ape-sized brain; small incisors and canines relative to body weight; lower anterior premolar does not hone the upper canine; postcanine teeth relatively large with thick enamel and bulbous cusps; premolars with more complex occlusal anatomy; robust maxilla, zygomatic bone and mandible; short, vertical midface; subnasal prognathism; anteriorly placed foramen magnum; and postcranial adaptations for bipedality.

Referred Species *Australopithecus africanus*, Dart, 1925; *Au. afarensis*, Johanson et al., 1978; *Au. anamensis,* Leakey et al., 1995; *Au. bahrelghazeli*, Brunet et al., 1995; *Au. garhi,* Asfaw et al., 1999.

Remarks See species' sections.

AUSTRALOPITHECUS ANAMENSIS Leakey et al., 1995
Figure 25.5 and Table 25.2

Holotype The type specimen is KNM-KP 29281, a mandible preserving all teeth but without rami. A partial left temporal bone is likely to be from the same individual and has the same accession number. More specimens are listed in Leakey et al., 1995, 1998 and White et al., 2006.

Age and Occurrence Early Pliocene, eastern Africa (table 25.2).

Diagnosis It differs from all other species of *Australopithecus* in its small, elliptically shaped external auditory meatus; long mandibular bodies; closely spaced, parallel tooth rows in both mandible and maxilla; mental region of mandible not strongly convex; symphysis steeply inclined posteriorly; canines with long, robust roots; trigons of upper molars wider than talons; smoothly continuous lateral nasal aperture; and small medullary cavity of humerus. It can be distinguished from *Ar. ramidus* by its thicker enamel; more buccolingually expanded molars; subequally sized m1 and m2; a tympanic tube that extends only to the medial edge of the glenoid process; somewhat larger dm1; and humerus with weakly developed lateral trochlear ridge (Leakey et al., 1995, 1998).

Description Relatively complete mandibular and maxillary remains referred to both male and female specimens have revealed a consistent suite of dental features that allow this taxon to be distinguished from the geologically more recent *Au. afarensis* (see Leakey et al., 1995, 1998). The canine in the holotype is smaller than two isolated canines and the canine socket in a large mandible (KNM-KP 29287); therefore, the type is presumed to be from a female and canine dimorphism is thought to be substantial; all canines have long, robust roots, and the upper canine has two basal tubercles and a large root. The long axis of the mandibular symphysis is posteriorly inclined, and the three mandibles have strongly receding but smoothly convex symphyseal contours, unlike many *Au. afarensis* specimens (especially those from Hadar). The tooth rows are closely spaced, and the cross-sectional profile of the corpora is unlike that of African apes, whose contours become flatter in section basally.

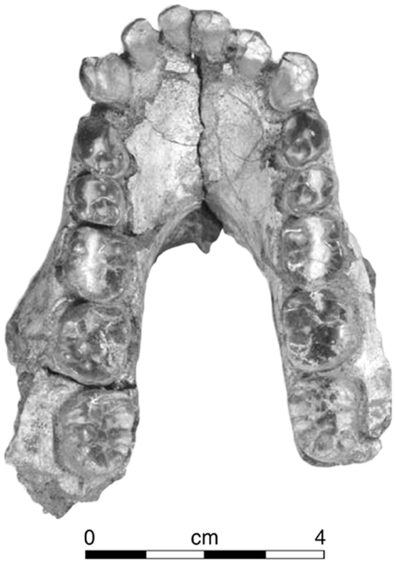


FIGURE 25.5 Holotype of *Australopithecus anamensis*, mandible KNM-KP 29281. Courtesy of National Museums of Kenya.

The i2 is larger, the p3 is more unicuspid and asymmetrical, and the C/p3 complex is more ape-like than in *Au. afarensis*. Molar enamel thickness is similar to that of *Au. afarensis* (1–2 mm), but thicker than in *Ardipithecus ramidus* and thinner than in *Paranthropus* taxa (Ward et al., 2001). Molars are more buccolingually expanded, and canine enamel thicker apically, than in *Ar. ramidus*. The lateral nasal aperture is smoothly continuous with the maxillary bone, as in apes, and unlike the condition in *Au. afarensis*, which has distinct lateral nasal crests.

Part of a left temporal bone is probably associated with the type mandible. The external auditory meatus is small and elliptical in outline, unlike the meatus of *Au. afarensis* but like those in *Pan* and *Ardipithecus*. The tympanic tube is shorter than in *Ardipithecus,* and the articular eminence is less well developed than in other australopiths and *Homo.*

Dental specimens from Asa Issie, Ethiopia (see White et al., 2006), all possess enamel thickness, molar size and canine shape that are similar to known *Au. anamensis* specimens from Kenya. The canines of a maxilla are as large or larger than those of *Au. afarensis* and *Au. anamensis,* and they are mesiodistally long as in *Au. anamensis* from Kenya.

Postcranial specimens attributed to *Au anamensis* have received considerable attention because of their large size and because the hindlimb is derived toward bipedality, while the forelimb retains numerous primitive features. A right tibia (KNM-KP 29285) preserving both epiphyses, but missing a connecting portion of the shaft, is larger than the largest Hadar tibia attributed to *Au. afarensis*. Using regression equations based on human data, the upper epiphyseal surface area yields a body mass estimate of 55 kg, while the lower epiphyseal surface area yields a body mass estimate of 47 kg (Leakey et al., 1995). Bipedal features of the tibia include rectangular proximal surface with anteroposterior lengthening of articular surfaces, concave condyles of equal area, vertically oriented, straight shaft, and an inferiorly facing, square-shaped distal articular surface (Leakey et al., 1995). Primitive features include a proximal metaphysis that is not expanded, and a strong insertion for the gracilis muscle next to the anterior border of the shaft.

Body mass regressions (using modern human data) for the Kanapoi left distal humerus (KNM-KP 271) first described in 1967 (Patterson and Howells, 1967) suggest an even greater body mass of 58 kg (McHenry, 1992a). In anatomy it closely resembles specimens attributed to *Au. afarensis*. It lacks the lateral extension of the trochlear joint surface found in apes (which is thought to resist loads during hyperextension of the elbow during knuckle walking) and lacks the prominent lateral epicondyle found in *Ar. ramidus* (Ward et al., 2001). It possesses very thick cortical bone, near the maximum of the observed range in African apes and modern humans and more like that found in *Pongo*.

The Kanapoi capitate (KNM-KP 31724) is more primitive than known specimens of *Au. afarensis* in that the articular facet for metacarpal II faces strictly laterally as in apes, suggesting little rotational capacity at the carpometacarpal II joint (Leakey et al., 1998). It has a large, globular head and is larger than two *Au. afarensis* capitates from Hadar. The facet for the lunate is greater than that for the scaphoid, as in other *Australopithecus* specimens.

The Allia Bay radius (KNM-ER 20419) is also large; if proportioned like *Homo*, then stature calculated for this individual ranges between 176 and 183 cm (Ward et al., 2001). Ward et al. (2001) consider it more likely that *Au. anamensis* had

relatively long arms. Richmond and Strait (2000) claim the radius retains evidence of knuckle walking, but Ward et al. (2001) dispute this because the former authors did not correct for the missing styloid process in a cast. The contact facet for the lunate is larger than the scaphoid, as in other *Australopithecus* radii.

There is also an *Au. afarensis*–like proximal manual phalanx from Kanapoi (KNM-KP 30503) attributed to *Au. anamensis* (see Ward et al., 2001), as well as a right femoral shaft fragment from Asa Issie (White et al., 2006). The latter does not retain either articular end but has thick cortical bone, a rugose attachment for gluteus maximus, and no linea aspera.

Remarks All but one of the specimens from Kanapoi, Turkana Basin, Kenya, are constrained between 4.17 ± 0.03 and 4.07 ± 0.02 Ma; the exception is a mandible that is slightly younger than 4.07 Ma (Leakey et al., 1998). The Allia Bay, Turkana Basin, Kenya sample is ~3.95 Ma in age (Leakey et al., 1995). The Asa Issie, Aramis, Middle Awash locality in Ethiopia is 4.2–4.1 Ma in age (White et al., 2006).

The history of finds for this taxon is a long one. Brian Patterson found the distal humerus during an expedition to Kanapoi in 1965. Many of the Allia Bay isolated teeth were found in the 1980s, including one hemimaxilla. The type specimen and tibia were found in 1994/95, and additional fossils (dm1, capitate) were found between 1995 and 1997. Finds from Aramis, Ethiopia were published in 2006. Temporally, however, all the specimens are from a tightly constrained window between 4.2 and 3.9 Ma in the Eastern Rift, and all evince an anatomy widely deemed intermediate between *Ar. ramidus* and *Au. afarensis* (Kimbel et al., 2006; White et al., 2006; Kimbel, 2007).

There are also six worn mandibular teeth and one unworn p4 from Fejej, Ethiopia (4.18–4.0 Ma [Kappelman et al., 1996]) that are contemporaneous with *Au. anamensis,* but the severity of the wear and fragmentary nature of the specimens make it difficult to assign them to *Au. anamensis* versus *Au. afarensis* (Ward et al., 2001). Ward et al. (2001) have also noted that the Belohdelie frontal (3.89–3.86 Ma [White et al., 1993]) may represent *Au. anamensis,* but appropriate comparisons cannot be made because a frontal bone is not yet represented in the *Au. anamensis* sample.

The dietary and adaptive implications of the dental and masticatory features are significant; the increase in masticatory robusticity over *Ar. ramidus* is dramatic and may represent a punctuated event in anatomical adaptation (White et al., 2006). The molar expansion, thicker enamel, reduced anterior tooth wear, somewhat reduced canines, and robust mandible may all reflect the beginning stage of an emphasis on processing harder, tougher, more abrasive food items than were processed by the earlier purported hominins (Ward et al., 2001). Microwear comparisons among *Ar. ramidus*, *Au. Anamensis*, and *Au. afarensis* will be useful in evaluating this hypothesis.

Postcranial implications are of considerable importance, as the tibia is, *Orrorin* apart, presently the oldest uncontested evidence of well-adapted bipedality (Leakey et al., 1995, 1998; Ward et al., 2001). The ankle and knee joints were clearly reorganized relative to those of all extant apes, to facilitate stable movement of flexion and extension, but constrain dorsiflexion and inversion at the ankle, and axial rotation at knee. Primitive features of the upper limb may reflect tree-climbing abilities and perhaps compensated for a hindlimb with restricted joint mobility; alternatively, features such as long arms may have been selectively neutral. It has been argued that the adaptive significance of primitive retentions is not easily testable unless the features have a strong epigenetic component (see Ward et al., 2001; Ward, 2002).

Thus far, recovered postcrania are large, and canine dental dimorphism is high, suggesting attribution of existing postcrania to males. Ward et al. (2001) have posited that large male body size may have conferred reproductive advantages resulting from male-male combat.

Available published evidence indicates that *Ar. ramidus* has no derived features that would preclude it from being ancestral to *Au. anamensis*; likewise, the latter cannot be excluded from ancestry of *Au. afarensis*, and there is evidence (discussed later) that they may be time-successive species. *Australopithecus anamensis* is more similar to (older) Laetoli *Au. afarensis* specimens than to Hadar specimens, and the Allia Bay sample, which is younger than the Kanapoi sample, is most similar to Laetoli. For example, the first lower deciduous molar is larger than the very small, narrow dm1 of *Ar. ramidus,* but smaller than that of *Au. afarensis*. The dm1 also lacks buccal and lingual grooves and basin differentiation found in *Au. afarensis*. Thus, *Au. anamensis* and *Au. afarensis* may have been an evolving chronospecies (Kimbel et al., 2006; White et al., 2006; Kimbel, 2007). In the case of the *anamensis-afarensis* transition, Kimbel and colleagues currently favor retaining the taxonomic status quo because it "helps localize and communicate about the clustering of morphology in time and space." (2007:145) In the case of the *ramidus-anamensis* transition, White et al. (2006) claim that the record is still too sparse to determine whether branching may have occurred between 4.4 and 4.2 Ma.

Faunal reconstructions for Kanapoi are based on over 30 mammalian taxa (Leakey et al., 1995). Cercopithecids outnumber colobines and several bovid species are represented, including *Tragelaphus*, impala and kudu. The most common carnivore is *Parahyaena* (Leakey et al., 1995), and tooth marks on bones are common (Ward et al., 2001). Stable carbon isotopic analysis of paleosols has shown soils that are associated with semiarid vegetational mosaics and a mixed ecosystem including edaphic grasslands, bush/woodland and gallery woodland (Wynn, 2000). Ward et al. (2001) have cautioned that transport of fossils by carnivores is a possibility, and so it is difficult to know if *Au. anamensis* was actually living in the dry environments sampled isotopically. Faunal and isotopic analyses for Allia Bay indicate a mosaic of environments ranging from woodland with extensive canopy to open grasslands (Coffing et al., 1994; Schoeninger et al., 2003). White et al. (2006) have undertaken preliminary analyses of the two Asa Issie localities. (Note, at the Aramis locality, the single *Au. anamensis* specimen [maxilla VP-14] was unaccompanied by significant associated faunal remains and paleoecological reconstructions have not been attempted.) At ASI-VP-2 and ASI-VP-5, hominins are associated with more than 500 other vertebrate fossils, with primates being most common, followed by bovids. Colobines outnumber cercopithecines 57:9 and among bovids, *Tragelaphus* is the most abundant. Stable carbon isotopic analysis of paleosols from these sites have been interpreted as indicative of humid woodland/savannah environments, with ca. 25%–35% C_4 grass. Overall, paleoecological reconstructions for Kanapoi, Allia Bay, and Asa Issie indicate that *Au. anamensis*, like *Au. afarensis*, was associated with habitat heterogeneity. Specific environmental preferences within this variability are unknown and taphonomic factors have yet to be fully accounted for. Currently, we are limited to inferring that early members of the *Au. anamensis–Au. afarensis* lineage utilized and/or tolerated a wide range of habitats.

AUSTRALOPITHECUS AFARENSIS Johanson et al., 1978
Figure 25.6 and Table 25.2

Partial Synonymy *Meganthropus africanus*, Weinert, 1950; *Praeanthropus africanus*, Senyurek, 1955; *Praeanthropus afarensis*, Strait and Grine, 2004.

The Garusi I maxilla from Laetoli was named *Praeanthropus* by Hennig (1948), but no type was designated. Later, Weinert (1950) proposed the specimen should be placed in *Meganthropus africanus* because of similarities to an Indonesian taxon (now *H. erectus*). Johanson et al. (1978) did not recognize either of these taxa and instead placed relevant Laetoli and Hadar material in *Australopithecus afarensis,* but Strait et al. (1997) suggested that *Praeanthropus africanus* be resurrected. In 1999, the International Commission for Zoological Nomenclature ruled *africanus* be suppressed but left *Praeanthropus afarensis* available. Currently, some authors (e.g., Strait and Grine, 2004; Grine et al., 2006) use *Praeanthropus afarensis*, but this usage has not been widely accepted.

Holotype The type specimen is L.H. 4, a mandibular corpus with right broken c, p3–4, m1–3, and left p4, m1–2. For additional specimens, see Johanson et al., 1978 and *American Journal of Physical Anthropology* 57(4), 1982 (Hadar); Leakey and Harris, 1987 (Laetoli); White et al., 2000 (Maka); and Alemseged et al., 2005 (Dikika). An overview of the hypodigm is provided in Kimbel, 2007.

Age and Occurrence Early to mid-Pliocene, East Africa (table 25.2).

Diagnosis Compared to *Au. anamensis*, *Au. afarensis* has a larger external auditory meatus; a less inclined anterior corpus profile of mandible; an asymmetric upper canine with more apically placed mesial crown shoulder; more symmetric, molarized p3 crown with frequent development of the metaconid (second cusp); more molarized dm1; and sharper lateral margins and a more distinct inferior margin to the nasal aperture. Compared to later australopiths, it has relatively large upper central incisors; absolutely smaller postcanine dentition; a strongly protruding, convex subnasal plane that projects beyond the bicanine line; a less vertical anterior corpus profile of mandible; shallower mandibular fossa and less well developed articular eminence; and a horizontally inclined, tubular tympanic. The canines are asymmetrical with considerable size variation and mandibular tooth rows vary from subrectangular to U shaped. Diastemata often occur between I2/C and c/p3, and although there are sometimes vertical wear striae on the buccal face of p3, the C/p3 complex is considered functionally nonhoning. The mandibular corpus is relatively deep anteriorly in large specimens; the ramus of the mandible is broad and relatively low; and there is strong alveolar prognathism. Compared to *Kenyanthropus*, it has larger upper molars (Leakey et al., 2001). See Johanson et al. (1978) for initial diagnosisand Kimbel (2007) for an updated summary. Diagnostic postcranial features are numerous, compatible with bipedality in the hindlimb (see Ward, 2002) and described later.

Description *Australopithecus afarensis* is perhaps the most thoroughly known australopith. Some 400 specimens are attributed to the taxon, about 90% of which are from Hadar in the Afar depression of Ethiopia (Kimbel et al., 2004). The Hadar remains include the famous "Lucy" skeleton (A.L. 288-1 [3.18 Ma]), a collection of fossils from A.L. 333 (3.2 Ma) known as the "First Family" that likely represents members of a single population, as well as the most complete cranium and mandible of a single adult *Au. afarensis* individual (A.L. 444-2 [3.0 Ma]).

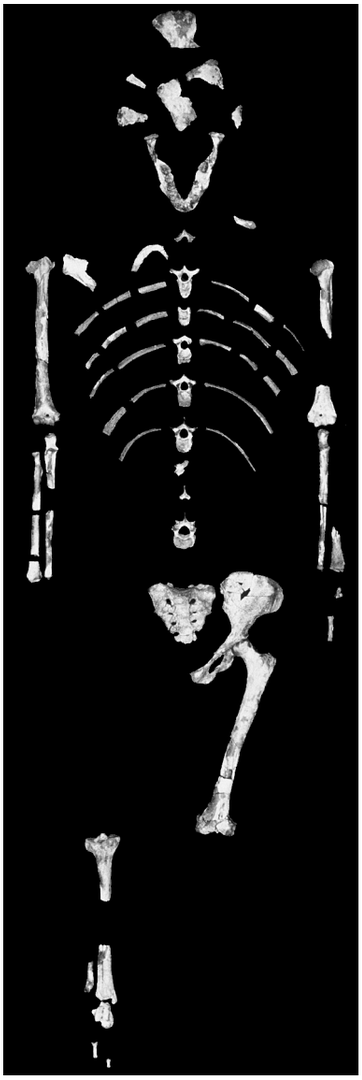


FIGURE 25.6 Partial skeleton of *Australopithecus afarensis*, AL 288-1 "Lucy." Courtesy of the Cleveland Museum of Natural History.

As the most intact adult hominin skeleton prior to 1.5 Ma, A.L. 288-1 is of unparalleled significance (Johanson et al., 1982). It is small (~27 kg; McHenry, 1991b) and for various reasons (overall size, morphology) is presumed to be female (Johanson and White, 1979; Tague and Lovejoy, 1986). Additional postcranial fossils from Hadar have augmented the information obtained from the Lucy skeleton, and they suggest a taxon with an amalgam of primitive and derived features, along with distinctive features that are challenging to interpret functionally as they have no analog among extant hominoids. Primitive features include manual and pedal phalanges that are more curved than those of *Homo* (Stern and Susman, 1983); a cranially oriented glenoid fossa (Stern and Susman, 1983); a funnel-shaped thorax (McHenry, 1991a); a relatively long foot (Jungers and Stern, 1983); lower limbs that are short relative to upper limbs (Jungers, 1982); small vertebral centra including small sacral body (Sanders, 1990); and lesser cranial expansion of the acetabular articular surface (MacLatchy, 1996). Derived features that resemble the

condition found in *Homo* include lumbar lordosis and sacral retroflexion (Lovejoy, 2004); expansion of the retroauricular region of the ilium, superoinferiorly short, mediolaterally expanded iliac blades and short ischium (McHenry, 1991a); flattened inferior contour of the lateral femoral condyle, deep patellar groove with high lateral lip and high femoral bicondylar angle (Johanson and Coppens, 1976; Tardieu, 1981); perpendicular orientation of the distal tibial articular surface (Latimer et al., 1987); anteriorly unexpanded distal tibial articular surface (DeSilva, 2008); large calcaneum with well-developed structures to dissipate stress at heel strike (Latimer and Lovejoy 1989); convergent hallux (Latimer and Lovejoy, 1990b); proximal pedal phalanges with dorsally oriented proximal articular surfaces, suggesting dorsi- rather than plantar flexion (Latimer and Lovejoy, 1990a); and relatively short pedal phalanges (White, 1994).

Novel features are particularly evident in the pelvis of A.L. 288-1. The iliac blades are laterally flared but lack the sagittal alignment found in *Homo* pelves. The flaring iliac blades, which are found in other australopiths, have been interpreted to provide sufficient spatial displacement (in conjunction with a long femoral neck) to increase the lever arm length for the lesser gluteals to effect abduction and control body torque during single leg stance on an extended lower limb (e.g., Lovejoy, 2004). However, Stern and colleagues propose that without iliac blades that are oriented in the sagittal plane, the lesser gluteals would not act as abductors but rather as medial rotators, stabilizing the trunk on a flexed thigh (e.g., Stern and Susman, 1981, 1983, 1991). Other disagreements about the best way to reconstruct *Au. afarensis*'s positional behavior (i.e., especially in relation to other novel features, such as limb proportions) are considered here.

The craniodental anatomy is well represented, and the hypodigm includes over 60 mandibles and mandible fragments (Kimbel et al., 2004). The mandible is characterized by a deep mandibular corpus that is rounded and bulbous anteriorly, and hollowed laterally; a low, rounded inferior transverse torus; a weak to moderate superior transverse torus; integration of the canine crown into the pre- rather than postcanine dental arch (Kimbel et al., 2004)(though this is less true of L.H. 4; Kimbel et al., 2006); and a vertical, anteriorly positioned ramus. Like other australopiths, the mandibular corpus is transversely thick, even when considered relative to molar size (Teaford and Ungar, 2000).

The large sample size reveals variation in some characters. Mandibular corpus size increases over time (Lockwood et al., 2000), the slope of the symphyseal axis is highly variable (Kimbel et al., 2004), and the symphyses of some Laetoli mandibles have a convex external surface and recede inferiorly, similar to the condition in *Au. anamensis*, and unlike the straight external contour found in Hadar mandibles (Kimbel et al., 2006). Dental features show stasis overall, but lower canine dimensions vary with regard to degree of mesiodistal compression; and p3 mesiodistal length decreases, and M3 dimensions increase, from the Laetoli to the Hadar sample (Lockwood et al., 2000). Laetoli upper canines also appear to resemble those of *Au. anamensis* and are mesiodistally longer than those from Hadar (Kimbel et al., 1996). As with other australopiths, premolars and molars are large compared to incisors and canines; molars have low, bunodont cusps and thick enamel; and the postcanine tooth area is large (Teaford and Ungar, 2000).

Cranially, *Au. afarensis* shares a number of derived features with later hominins, including reduced upper facial prognathism; anteriorly positioned foramen magnum; short anterior cranial base; distinct lateral margins in the nasal aperture; and a larger auditory meatus (Kimbel et al., 2004; Kimbel, 2007). Plesiomorphic features include compound temporonuchal crests, shallow mandibular fossae with weakly developed articular eminences, somewhat flat, low frontal squama, no frontal trigon, vertical midface and convex subnasal plane, distinct subnasal and intranasal parts of clivus, narrow interorbital and nasal aperture breadths, flat, wide, robust zygomatic region, and weakly flexed cranial base and tubular tympanic (Walker et al., 1986; Kimbel, 2007). Endocranial capacities are known for three adult and one subadult specimen, and fall in the range of extant great apes: A.L. 444-2, ca. 550 cm^3; A.L. 333-45, ca. 500 cm^3; A.L. 162-28, ca. 400 cm^3; A.L. 333-105 (juvenile), ca. 320 cm^3 (Falk, 1985; Kimbel, 2004).

A second important partial *Au. afarensis* skeleton from Ethiopia is the Dikika juvenile dated to 3.35–3.31 Ma (Wynn et al., 2006) and described by Alemseged et al. (2006). The M1 crown is fully formed but unerupted; using ape models of development, the individual may have been about 3 years old at time of death. Several features are worthy of note. The hyoid bone was African ape–like; since this bone is highly modified by the time of Neanderthals (Arensburg, 1989), its primitive form in *Au. afarensis* suggests that selection for vocal anatomy reorganization had not begun. The manual phalanges of the Dikika child are already curved; if this is an epigenetic trait, then it suggests some climbing was being undertaken. The scapula is also ape-like, with a cranially tilted glenoid fossa, but overall the anatomy is reported to be more like that of *Gorilla* than *Pan*, although with a reduced supraspinous fossa. Derived hindlimb features include a femoral bicondylar angle, robust calcaneum, and a transversely expanded proximal tibia.

Remarks High levels of variability in the *Au. afarensis* sample have been the subject of considerable study, with an emerging, complex picture of geographical separation, phyletic change over time (especially between the Laetoli and Hadar samples) and sexual dimorphism as contributing factors (Lockwood et al., 2000; Kimbel et al., 2004, 2006; Kimbel, 2007). Nonetheless, there is a "paleoanthropological consensus . . . that *Au. afarensis* is, indeed, both biologically and statistically speaking, a 'good' species" (Kimbel et al., 2004:4–8) and that variation can be attributed to intraspecific anagenesis (Grine et al., 2006).

Although it is now well accepted that Hadar is sampling a single species, the level of dimorphism within this comparatively well-sampled taxon is still debated. The conventional view that *Au. afarensis* had high body size dimorphism, with males (45 kg) estimated to be 50% larger than females (29 kg) (McHenry, 1992a), or even double the mass of females (e.g., Richmond and Jungers, 1995), has been challenged by Reno et al. (2003, 2005) using the A.L. 333 sample of individuals and A.L. 288-1. Using the proportional relationships among skeletal elements within Lucy, they estimated the femoral head size that would correspond to each postcranial element from the A.L. 333 sample. They concluded that the pattern of femoral head size variation is similar to that of modern *Homo*, and thus that intraspecific variation (including sexual dimorphism) is lower than previously thought. The implications of this pattern of sexual dimorphism are potentially far-reaching because certain behavioral characteristics are correlated with higher degrees of body size dimorphism, including polygynous social systems, male-male aggression, and male-driven predator aggression and territoriality (McHenry, 1994a; Ward, 2002). Closer similarity in body sizes is associated with lower reproductive variance in males, more similar operational sex

ratios and are compatible with earlier theories linking bipedality and pair bonding (Lovejoy, 1981). Although the view that *Au. afarensis* had low–moderate levels of sexual dimorphism has been vigorously challenged (Plavcan et al., 2005), an emphasis on skeletal over body size dimorphism may prove a useful paleontological approach overall.

The pointed disagreement over the functional interpretation of individual postcranial features, as discussed, has led to difference in opinion in how to synthesize the wealth of information that comes from the remarkable postcranial record, with some postulating that *Au. afarensis* was a committed and efficient terrestrial biped (e.g., Latimer et al., 1987; Latimer and Lovejoy, 1989, 1990a, 1990b; Lovejoy, 2004) and others that *Au. afarensis* was an inefficient biped still utilizing arboreal supports (e.g., Stern and Susman, 1983, 1991; Susman et al., 1984). Furthermore, both efficiency and performance style of *Au. afarensis*'s bipedality remain contested. For example, some researchers support a bent knee, bent hip (BKBH) gait on the grounds that it would have minimized oscillations in center of mass, lessened peak vertical reaction forces and increased stride length (Schmitt, 2003) while others suggest that BKBH gaits would be too energetically expensive and would have raised core body temperature to such a degree as to be unsustainable (Crompton et al., 1998; Carey and Crompton, 2005). Furthermore, the Lucy pelvis and other sufficiently well-preserved australopith pelves all show evidence of a ventral pelvic tilt, which places hip extensor muscles in a more favorable position so that they can retract the lower limb when legs are straight. Chimpanzees lack this tilt and must walk with a BKBH gait when bipedal in order to place the extensor insertions anterior to the pelvic origins so that they can retract the leg.

However, as Ward (2002) has summarized, researchers have been approaching the reconstruction of posture and locomotion from different philosophical vantages and with different goals in mind. Stern and Susman advocate the examination of all anatomical features and contend that the current, inferred utility of features is of paramount importance in reconstructing what australopiths were *capable* of doing (e.g., Stern and Susman, 1991). For example, since long fingers are good for grasping arboreal supports and a cranially oriented glenoid fossa would facilitate elevating the forelimb above the head, *Au. afarensis* was likely climbing trees. Latimer and Lovejoy weight characters more explicitly and give primitive characters less consideration if there is some evidence of directional selection. They reason that if fingers are less curved than the condition inferred for the LCA of *Pan* and *Homo* (itself difficult to determine), then climbing ability is being compromised and either selected against or having a neutral effect on fitness.

One of the most evocative lines of evidence of the bipedalism of *Au. afarensis* comes from the trail of hominin footprints in Tuff 7 of the Laetolil beds, discovered by Andrew Hill in 1976 (Leakey and Harris, 1987) and dated to 3.66 Ma (Deino, in press). White and Suwa (1987) have made a strong case that these prints were made by *Au. afarensis* on the basis of foot anatomy, rather than on the basis of age and location alone. The tuff preserves three sets of footprints, with one individual stepping "pace for pace" in the footprints of an individual moving ahead, and a third individual walking alongside creating a parallel trackway (Leakey, 1987; Robbins, 1987). The footprints preserve several modern human–like attributes, including heel strike, hallucal toeing off, a lateral to medial shift in weight bearing on the sole of the foot, an adducted hallux, and a longitudinal arch (Tuttle, 1987), but Bennett et al. (2009) take the view that there are significant differences between the Laetoli prints and those of habitually unshod modern humans.

The diet of *Au. afarensis* has also been the subject of much research, but a lack of isotopic sampling leaves a large lacuna in our knowledge. The postcanine tooth crowns of *Au. afarensis* are larger than those of *Au. anamensis*, and the enamel is thicker. Flat teeth with planar surfaces would presumably be inefficient at processing pliant foods such as meat, leaves or tough fruit, but efficient at crushing hard, brittle foods, as well as weak foods (Teaford and Ungar, 2000). Thickly enameled teeth would also resist abrasion and, depending on microstructure, be less likely to fracture under stress when hard objects are being consumed (Lucas et al., 2008).

A relatively small anterior dentition implies that *Au. afarensis* probably did not regularly eat fruit with thick husks, or fruits with flesh adhering to seeds (Teaford and Ungar, 2000). Microwear on anterior teeth include scratches and pits, suggesting incisors may have been used to strip gritty plant parts (Ryan and Johanson, 1989). Recent analysis of molar microwear (Grine et al., 2006) from Hadar and Laetoli shows little variation over time. Teeth possess scratches reminiscent of mountain gorilla teeth and compatible with an abrasive and possibly tough diet, but none of the pitting associated with hard object feeding in extant primates (Grine et al., 2006). This characterization is more similar to microwear results for *Australopithecus africanus* than for *Paranthropus robustus* (Grine and Kay, 1988; Scott et al, 2005). Similarity in microwear between *Gorilla* and *Au. afarensis* contrasts with observed differences in molar topology, the shearing crests of the former contrasting with the relatively flat teeth of the latter. However, Grine et al. (2006) explore the idea that the robust masticatory system of *Au. afarensis* may have evolved to process seasonal hard foods (i.e., the hard foods were critical, fall-back foods, rather than staple foods). Overall, the gross dental anatomy, if not the microwear, suggests that *Au. afarensis* was puncturing, grinding and chewing abrasive, hard, and/or tough food, while the robusticity of the mandible would have provided a high resistance to mechanical failure (Teaford and Ungar, 2000).

There has been considerable interest in reconstructing the paleoecology of *Au. afarensis* sites, in large part as they may bear on the selective forces at work in the maintenance of the signature adaptations of the genus: bipedality and megadonty. A consensus is growing that *Au. afarensis* tolerated a wide range of environmental conditions and was broadly distributed across a heterogeneous landscape (e.g., White et al., 1993; Bonnefille et al., 2004; Reed, 2008).

The faunal composition of the Laetolil beds, Laetoli (including invertebrates, chelonians, galagids, cercopithecids, rodents, carnivores, perissodactyls, suids, giraffids, and bovids) was initially reconstructed as indicating dry wooded or bush savanna ecosystems with well-defined wet and dry seasons (see references in Leakey and Harris, 1987, especially Harris, 1987). Its proximity to an active volcano would have produced a soil/vegetation gradient with grassland grading into woodland at increasing distance from the volcano (Andrews, 1989). Harris (1987) noted that because the depositional environment was volcanic, and not fluviatile or lacustrine like most Ethiopian and Kenyan sites, it actually may be more representative of much of East Africa, and the Serengeti has been invoked as a likely modern analog (e.g., Andrews, 1989). Recently, additional research has complicated this picture. Some faunal analyses indicate there was a high proportion of arboreal and frugivorous mammals (Walker, 1987;

Andrews, 1989; Reed, 1997) and isotopic work on Laetoli herbivores indicates dietary guilds dominated by mixed browsing/grazing or browsing foraging strategies, suggesting woodland as a more important component of the environment than previously recognized (Kingston and Harrison, 2007). Andrews and Bamford's (2008) topographic reconstructions, and the inferred soils, drainage, and vegetation that would accompany their topography, also support a significant woodland component. Su and Harrison (2008:678) support a "predominantly open woodland" environment at Laetoli, and reason that the low density of hominin remains relative to Hadar implies less optimal habitats, which they attribute to the less densely wooded, drier mosaicism of Laetoli compared to Hadar. Recent syntheses of Hadar paleoecology (Bonnefille et al., 2004; Reed, 2008) do not support a significant difference between these two localities, however, and the resolution needed to address ecological and taphonomic sources of differences in species' fossil densities is not readily available (Cote, 2008). Although there appears to be a trend toward increasingly open environments in the Hadar sequence associated with *Au. afarensis* (Reed, 1997, 2008), detailed pollen analyses suggest a variety of habitats were present over its stratigraphic range (Bonnefille et al., 2004), and faunal analyses of over 4,000 mammalian specimens also support heterogenity, with bushland, open woodland, shrubland, and edaphic grassland as habitat components (Reed, 2008). Other *Au. afarensis* sites have yet to be subjected to such detailed paleoenvironmental analyses. White et al. (1993) have described the Maka fauna as broadly comparable to that from the Denen Dora Member, which Reed (2008) has reconstructed as bushland or woodland/floodplain grassland. The Tulu Bor Member of Koobi Fora has a depositional environment and faunal list compatible with floodplains (Feibel et al., 1991; Reed, 1997), and shrubland/wetland/grasslands/woodlands have also been invoked (Harris, 1991; Reed, 2008). At Dikika, *Au. afarensis* occurs in the oldest or Basal Member of the Hadar Formation, and the younger Sidi Hakoma Member (Alemseged et al., 2005, 2006). Reed (2008) has looked at faunal composition of these members in deposits from the other side of the Awash River at the Hadar site and reconstructs the Basal Member as a woodland/shrubland mosaic, and Sidi Hakoma as similar, but trending toward drier and more open conditions. However, Wynn et al. (2006) have noted that the Sidi Hakoma Member at Dikika preserves a relatively high proportion of grazing bovids, and so was perhaps a more open habitat than the more wooded regions represented at Hadar

It is apparent that *Au. afarensis* is no longer the most primitive member of *Australopithecus*, and as additional *Ar. kadabba*, *Ar. ramidus* and *Au. anamensis* fossils have been recovered, the evidence for ancestor-descendant relationships among the four taxa has strengthened (White et al., 2006; Kimbel et al., 2006). Bipedalism and moderate megadontia remain hallmarks of *Au. Afarensis*, and it continues to serve as a key basis of comparison for all other late Miocene through Pliocene taxa. This is because of the relative richness of its fossil record as well as a general lack of autapomorphies that would preclude it from an ancestral relationship to later taxa (Kimbel et al., 2004; but see Rak et al., 2007, regarding the gorilla-like ramal anatomy of Hadar specimen A.L. 822-1).

AUSTRALOPITHECUS BAHRELGHAZELI Brunet et al., 1996
Figure 25.7 and Table 25.2

Synonymy *Australopithecus afarensis,* Brunet et al., 1995.

Holotype The type specimen KT12/H1 is an anterior mandibular corpus with right i1 alveolus and i2–p4 and left i1 alveolus, i2 root and c-p4 (Brunet et al., 1995). An isolated P3 is the only other published specimen (Brunet et al., 1996) although the presence of *Australopithecus* sp. was reported from nearby locality KT13 (Brunet et al., 1997).

Age and Occurrence Mid-Pliocene, Central Africa (table 25.2).

Diagnosis Long axis of mandibular symphysis oriented subvertically; lower canines and incisors large and canines with high crowns and cingulum; lower premolars have three roots, and are buccolingually broad with buccal cingula; p3 is bicuspid with a strong metaconid; p4 is molarized with a small talonid; P3 has three roots and an asymmetrical crown. The taxon differs from *Ar. ramidus* in its thicker enamel, three-rooted premolars and less asymmetrica; p3; from *Au. anamensis* in its more vertical symphyseal region, short planum alveolare, reduced inferior transverse torus and bicuspid p3 with strong metaconid; from *Au. afarensis* by its subvertical, relatively flat symphyseal region and three-rooted lower premolars; from *Au. africanus* by its less vertical posterior symphysis, less robust corpus, larger anterior dentition and three-rooted lower premolars (see Brunet et al., 1995, 1996).

Description Brunet and colleagues (1995, 1996) cite the flat, more vertical orientation of the symphyseal region as distinguishing it from *Au. afarensis*, but metrics supporting this view have yet to be published. If additional finds support the characterization of a less prognathic taxon, it would be interesting in light of the fact the anterior teeth are *Au. afarensis* sized. The canine is asymmetrical with a long distal cuspule and strong lingual crest. The upper third premolar has three roots, like most robust australopiths but unlike most *Au. afarensis* and *Au. africanus*, which have two roots; the lower premolars have three distinct roots.

Remarks The referral of the two published fossils to a new species has been disputed on the grounds that there is insufficient material (White, 2002), and that the diagnostic features are represented in the Laetoli, Hadar and Maka *Au. afarensis* collections (Kimbel, 2007). For example, L.H. 24 has a three-rooted premolar (White et al., 2000) and A.L. 444-2 has a vertical symphyseal cross section (Kimbel et al., 2004).

The biogeographic importance of the Chadian finds is nonetheless undiminished, regardless of whether additional fossils eventually bolster the case for a distinct species, or confirm the occurrence as a variant of East African *Au. afarensis*. The former sets up a scenario of increasing cladogenesis in the mid-Pliocene; if *Kenyanthropus platyops* is ultimately shown to be another, separate taxon from this interval (discussed later; Leakey et al., 2001) then hominins may have up to three lineages between 3.5 and 3 Ma.

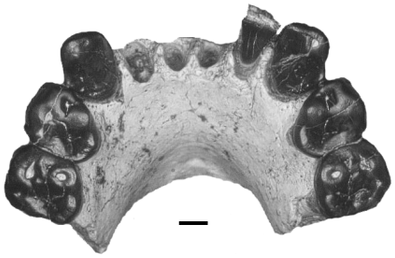


FIGURE 25.7 Holotype of *Australopithecus bahrelghazeli*, mandible KT12/H1. Courtesy of Michel Brunet.

The alternate, single-taxon scenario extends the range of *Au. afarensis* so that it is no longer confined to a 1,500-km swath along a north-south gradient of the East African rift and extends it 2,500 km to the northwest. Although *Au. afarensis* might not have been present over this broad a geographic area at any point in time, it would have been sufficiently mobile to thrive at least for intervals across a heterogeneous landscape. This does not necessarily imply a taxon of more generalized niche, however. Many of the KT taxa, both woodland (e.g., *Kolpochoerus afarensis*) and grassland (e.g., *Hipparion* sp. aff. *afarense/hasumense*) "specialists" are the same species as those found at Hadar and Laetoli, indicating that these taxa were also are widely distributed latitudinally in sub-Saharan Africa. At the least, this suggests that dispersal of taxa with either woodland or grassland affinities was not limited by profound habitat homogeneity; rather, habitats were potentially varied enough over a small scale, but over a wide enough geographic area and time depth to permit habitat specialists to attain a wide geographic distribution. Brunet et al. (1995) have characterized sub-Saharan Africa, from the Atlantic to the Indian Ocean, southward to Cape of Good Hope, as a woodland savannah belt. The heterogeneous nature of such a belt, and associated variation in factors such as seasonality, rainfall, and altitude has played a major role in theories of hominin diversification (e.g., Potts, 1998; Kingston, 2007).

The nonhominin fauna at KT 12 include silurid fish, suggesting a lakeside environment, as well as taxa indicating the presence of forest or woodland (e.g., reduncine bovids, *Kolpochoerus afarensis*) and more open habitats (e.g., *Ceratotherium* and *Hipparion*)(Brunet et al., 1995). Locality KT 13 has a similar biochronological age and environmental reconstruction (Brunet et al., 1997).

AUSTRALOPITHECUS AFRICANUS Dart, 1925
Figure 25.8 and Table 25.2

Partial Synonymy *Australopithecus transvaalensis*, Broom, 1936; *Plesianthropus transvaalensis,* Broom, 1937; *Australopithecus prometheus,* Dart, 1948; *Homo transvaalensis*, Mayr, 1950; *Australopithecus africanus africanus*, Robinson, 1954; *Australopithecus africanus transvaalensis,* Robinson, 1954; *Homo africanus,* Robinson, 1972; Olson, 1978.

Holotype The type specimen is Taung 1, a juvenile skull with endocast.

Age and Occurrence Mid- to late Pliocene, southern Africa (table 25.2).

Diagnosis Dart's (1925) original description of *Australopithecus africanus* differentiates this taxon from modern apes by a slightly enlarged brain, with a posteriorly positioned lunate sulcus caused by enlarged parietal lobes, and an anteriorly positioned foramen magnum suggestive of upright walking. In addition, the Taung mandible is robust, though equipped with small canines, and no diastema. Further diagnosis has been aided by additional discoveries of *Au. africanus* (Lockwood and Tobias, 1999, 2002; Moggi-Cecchi et al., 2006) and by the analyses of White et al. (1981). Relative to *Au. afarensis*, *Au. africanus* has a slightly less prognathic face with a flat nasoalveolar clivus, a deeper palate, a more robust mandibular corpus and increased buttressing of the anterior corpus, larger postcanine dentition, and a deciduous lower molar crown with a twinned medial basin. Pneumatization is restricted to the mastoid region, unlike in *Au. afarensis*, where it extends to the temporal squama. *Australopithecus africanus* crania do not possess the compound temporal nuchal crest present in *Au. afarensis* fossils and have a maxillary furrow lateral to the nasal opening rather than the canine fossa found in *Au. afarensis*. Though variation exists for all of these features in *Au. afarensis*, *Au. africanus* specimens uniformly have a bicuspid third premolar, canines with apical wear pattern, and no diastema between the maxillary canine and lateral incisors. In *Au. afarensis* and *Paranthropus robustus*, the third molar is typically the largest tooth, whereas in *Au. africanus* the second molar tends to be the largest. Unlike *Paranthropus*, *Au. africanus* fossils have an enlarged anterior dentition, distinct supraorbital morphology often consisting of a supraciliary eminence and strongly pronounced glabellar region, the absence of temporal lines merging with the supraorbital torus, moderate postorbital constriction, only weakly developed sagittal cresting on male crania, an expanded cranial base, and lower fourth premolars with three rather than two cusps. Relative to specimens assigned to *Homo*, *Au. africanus* possesses a shallower temporomandibular fossa and a small cranial capacity.

FIGURE 25.8 *Australopithecus africanus* cranium STS 5 "Mrs. Ples." Courtesy of the Transvaal Museum, (Northern Flagship Institution).

Description Besides the juvenile Taung skull, *Au. africanus* is craniodentally represented by Sts 5 ("Mrs. Ples"), an almost complete female cranium lacking the maxillary dentition, StW 505, a presumed male, which preserves an almost complete right side of the cranium and parts of the left frontal and maxilla (Lockwood and Tobias, 1999), and Sts 71, which preserves most of the left part of a skull and the right maxilla (note, Sts 71 may be associated with the mandible Sts 36; Wallace, 1972). MLD 37/38 preserves most of the calvaria, though the face has been sheared off. Other relatively complete specimens include the partial cranium StW 252, a distorted partial cranium StW 13, a basicranium Sts 19, and the associated maxilla StW 52a and mandible StW 52b, and perhaps StW 53 (Kuman and Clarke, 2000; though see Curnoe and Tobias, 2006, who consider StW 53 to be early *Homo*).

Lockwood and Tobias (1999) have commented that *Au. africanus* has very few autapomorphies and instead possesses an amalgama of plesiomorphic features found in *Au. afarensis* and derived features found in later *Homo* and *Paranthropus* specimens. Present on most *Au. africanus* craniofacial fossils are prominent columns of bone along the nasal-maxillary junctions, termed the anterior pillars (Rak, 1985). This morphology has been suggested to be an adaptation that resisted bending forces in the facial skeletal skeleton in *Au. africanus* associated with dietary changes and molarization of the premolars (Rak, 1985). The presence of anterior pillars in *Au. africanus* and *P. robustus* may be a shared-derived feature suggestive of an ancestor-descendant relationship (Rak, 1985).

This feature is particularly robust in specimens such as StW 13, though only weakly developed on others like TM 1512, and perhaps absent altogether in StW 391 (Lockwood and Tobias, 2002). *Australopithecus africanus* crania also have flaring zygomatics with strong zygomatic prominences. Though there is usually not a sagittal crest present (but see Sts 17), the temporal lines are positioned high on the cranium. Furthermore, *Au. africanus* dentitions combine the large anterior teeth found in earlier *Au. afarensis* remains with the large postcanine dentition found in later robust australopiths and in some early *Homo*. In this respect, some *Au. africanus* fossils, including StW 252, are similar to the type specimen of *Au. garhi*.

Average cranial capacity in *Au. africanus* is 463.9 $cm^3 \pm 51.9$ cm^3 (range 400 cm^3–560 cm^3) based on data from eight crania and endocasts (Conroy et al., 1990, 1998, 2000a; Holloway et al., 2004). This is slightly greater than the mean cranial capacity (383.4 cm^3) of the similar-sized chimpanzee (Tobias, 1971). In addition to brain size, brain organization has been studied in detail for *Au. africanus*. Based on CT scans of MLD 37/38, it has been suggested that *Au. africanus* shares with *Homo* expanded anastomotic channels efficient for cooling cranial blood (Falk and Conroy, 1983; Conroy et al., 1990). This is in contrast to *Au. afarensis* and the paranthropines, which typically have an enlarged occipital-marginal sinus (Conroy et al., 1990). However, there is variation in this feature, as the type cranium from Taung has an enlarged occipital-marginal sinus, despite having other endocranial features clearly linking this specimen to *Au. africanus* and not to *Paranthropus*. These include squared-off frontal lobes (Falk and Clarke, 2007), features found in the endocasts of *Au. africanus* and early *Homo*, but not in *Paranthropus* taxa (Falk et al., 2000).

Examples of almost all of the skeletal elements (minus a few tarsal, carpal, and phalangeal elements) of *Au. africanus* have been recovered from the Sterkfontein cave (for an inventory of the 1936–1999 discoveries, see the appendix in Pickering et al., 2004b). Even a fossilized stapes is known for *Au. africanus*, and suggests that this hominin could hear higher frequencies than modern humans (Moggi-Cecchi and Collard, 2002). More complete postcranial remains include the partial skeletons Sts 14 and StW 431, and potentially the StW 573 "Little Foot" remains, though Clarke (2008) suggests that StW 573 may belong to a different *Australopithecus* species. The morphology of the vertebral column, pelvis, and lower limb has clearly demonstrated that *Au. africanus* was an habitual biped (Robinson, 1972; Lovejoy, 1974). In fact, the southern African *Au. africanus* remains led Washburn and Patterson (1951) to propose that instead of encephalization, it was adaptations for upright walking that differentiated the earliest hominins from the apes. Based on postcranial remains, *Au. africanus* males were approximately 1.38 m tall and 41 kg, whereas the females were roughly 1.15 m tall and 30 kg (McHenry, 1992a; McHenry and Coffing, 2000). The level of sexual dimorphism is presumed to have been like that of the common chimpanzee (Lockwood, 1999).

The StW 431 pelvis has modern human–like attachments for the gluteals and latissimus dorsi (Häusler, 2002) and to judge from the rugosity of their attachments the sacrotuberous, dorsal iliac and interosseous ligaments were well developed, powerful, and would have helped maintain the tilt of the sacrum in upright posture (Sanders, 1998). Pelvic remains from StW 441/465 are also reconstructed as well adapted for bipedality (Häusler and Berger, 2001). As in *Au. afarensis*, the ilia flare laterally in Sts 14 and StW 431 (Kibii and Clarke, 2003). Macchiarelli et al. (1999) found that the trabecular patterns in the ilia Sts 14, Sts 65, StW 431, MLD 7, and MLD 25 differed slightly from the modern human condition and may reflect differences in the magnitude and direction of stress incurred on the ilium during locomotion.

The morphology of the lumbar region of the vertebral columns of StW 14, StW 431, and StW H8/H41 is generally consistent with adaptations for bipedality, though *Au. africanus* had very small centra (Shapiro, 1993; Sanders, 1998; Toussaint et al., 2003). Based on the morphology of the vertebrae, in conjunction with other postcranial features, it has been suggested that *Au. africanus* may have been more versatile in its locomotor capacities and perhaps engaged in both bipedalism and climbing activities (Shapiro, 1993; Sanders, 1998). However, because a short lumbar region (usually three vertebrae) is thought to be an adaptation for orthograde climbing in the hominoids, climbing would have been kinematically different from that practiced by modern apes, as *Au. africanus* had either five or six lumbar vertebrae (Sanders, 1998; Touissant et al., 2003). Whitcome et al. (2007) recently found that the lordosis angle in Sts 14 and StW 431 fits the pattern distinguishing modern male and female lumbar vertebrae, suggesting full bipedality and concomitant adaptations for pregnancy in the presumed female Sts 14.

The femora StW 99, StW 598, and MLD 46 possess a long femoral neck, which would help to increase the mechanical advantage of the lesser gluteals during the single-legged, stance phase of the walking cycle (Reed et al., 1993; Partridge et al., 2003). StW 99 also has a mediolaterally expanded subtrochanteric region, which may have helped to resist bending loads during bipedalism (Richmond and Jungers, 2008). The fragmentary proximal femur StW 522 has a strikingly deep obturator externus groove, which suggests hyperextension at the hip, though this specimen also has a short femoral neck and an ape-like margin around the rim of the femoral head. Distal femora TM 1513 and Sts 34 both possess a strong bicondylar angle, suggesting that the knee of *Au. africanus* was positioned directly under the center of mass. The proximal tibia StW 514 has a curved lateral condyle and a single attachment for the lateral meniscus, leading Berger and Tobias (1996) to suggest that *Au. africanus* may have had chimpanzee-like locomotor capacities. However, Organ and Ward (2006) found that the convexity of the lateral condyle does not discriminate between modern humans and extant African apes. A single point of attachment for the lateral meniscus of StW 514 is similar to what is found in *Au. afarensis*. To judge by the horizontally oriented distal tibial articular surface relative to the long axis of the shaft in StW 358, StW 389, and StW 514b, in these specimens the ankle was also aligned under the knee and thus under the center of mass (DeSilva, 2008). These tibiae and the tali StW 88, StW 102, StW 347, StW 363, and StW 486 also lack adaptations that would allow *Au. africanus* to put its foot in positions of dorsiflexion and inversion, which are important during vertical climbing (DeSilva, 2008). However, the tali of *Au. africanus* are also ape-like in possessing a deep trochlear groove (Harcourt-Smith, 2002; Deloison, 2003). The calcaneum of *Au. africanus* StW 352 is similar to *Au. afarensis* calcanei in having a cross-sectional area in the range of modern humans and larger than that found in African apes (Latimer and Lovejoy, 1989). The large peroneal tubercle of the StW 352 calcaneus resembles the condition seen in *Au. afarensis*.

The morphology of the StW 573 foot has been interpreted as being consistent with a grasping hallux (Clarke and Tobias, 1995), but this hypothesis has been refuted by more detailed studies, including a morphometric analysis of the medial

cuneiform and first metatarsal (Harcourt-Smith, 2002; Harcourt-Smith and Aiello, 2004; Kidd and Oxnard, 2005; McHenry and Jones, 2006).

Many *Au. africanus* metatarsals and phalanges await description and functional analysis. An analysis of the fourth metatarsal StW 485 and complete fifth metatarsal StW 114/115 suggests a stable lateral column of the foot in *Au. africanus* (DeSilva and MacLatchy, 2008; DeSilva, 2009; Zipfel et al., 2009).

Despite the many adaptations of the lower limb for habitual bipedality, the morphology of the *Au. africanus* upper limb is suggestive of some degree of arboreality. The associated humerus, radius, and ulna of StW 431 are robust (Toussaint et al., 2003) and exhibit relatively larger upper than lower limb joint surfaces (McHenry and Berger, 1998). A study of upper to lower limb size in multiple *Au. africanus* fossil specimens using a resampling approach found that *Au. africanus* had more ape-like proportions than did *Au. afarensis* (Green et al., 2007). This surprising result suggests that *Au. africanus* may have engaged in more activities that loaded the upper limb, such as arboreality, than *Au. afarensis* (Green et al., 2007). Interestingly, though, preliminary examination of StW 573 suggests that the arms of this *Au. africanus* individual are not long relative to its associated legs (Clarke, 2002).

The metacarpals of *Au. africanus* are modern human–like in their length, which would allow modern human–like manual dexterity, though they lack the robusticity useful for tool-making grips (Green and Gordon, 2008). The distal thumb phalanx (StW 294) of *Au. africanus* is more robust than that found in apes and may be evidence for power gripping in *Au. africanus*. This is consistent with the robust thumb of StW 573 currently being excavated. These morphologies may be evidence for climbing or tool making in *Au. africanus* (Ricklan, 1987; Clarke, 1999, 2002). The hand of StW 573 appears to have modern human–like proportions with short fingers and a long thumb (Clarke, 2002). If *Au. africanus* was still engaged in arboreal locomotion, reduced finger length would indicate that it climbed in a manner different from and perhaps less efficient than modern apes (Ricklan, 1990).

Remarks Pollen data collected from *Au. africanus*–bearing deposits at Makapansgat suggest that this hominin lived along a forest margin. In a synthesis of data from the faunal fossil record, pollen, and geomorphology of the Makapansgat Valley, Rayner et al. (1993) reconstruct the *Au. africanus* habitat as consisting of patches of subtropical forest. These data are consistent with analyses of fossilized wood from Sterkfontein Member 4 identified as *Dichapetalum* cf. *mombuttense*, which grows as a liana in closed forests (Bamford, 1999). Reduced pitting on the molars (Grine, 1986) and microwear patterns on the incisors (Ungar and Grine, 1991) are consistent with a diet rich in soft fruit and leaves. But the diet of *Au. africanus* may have included resources from a drier open woodland or grassland environment. Faunal analysis of Sterkfontein Member 4 reconstructs the paleoenvironment as an open woodland (Reed, 1997). Isotope analysis found that four teeth of *Au. africanus* recovered from Makapansgat have relatively high $-^{13}C$ values of -5.6 to -11.3 ‰, suggesting that this species exploited not only leaves and fruits, but also C_4 plant resources from an open woodland or grassland environment (Sponheimer and Lee-Thorp, 1999). Additional isotopic work on 10 teeth from Sterkfontein Member 4 deposits yielded similar results ($\delta^{13}C$ range of –4.4 to –8.8 ‰), suggesting that *Au. africanus* ate a varied diet perhaps consisting of grasses, seeds, underground storage organs, invertebrates, and grazing mammals in addition to the occasional leafy vegetable and soft fruit (van der Merwe et al., 2003). Elevated Sr/Ca ratios in *Au. africanus* are also consistent with a diet consisting of insects and underground storage organs (Sponheimer et al., 2005). These data suggest that *Au. africanus* was capable of exploiting a range of environments.

Close to 600 individual fossils, including 495 teeth, have been recovered from Member 4 deposits at Sterkfontein. There is enough morphological diversity in the Sterkfontein Member 4 hominin assemblage, however, for some to suggest that two hominin species are represented. This hypothesis has been promoted primarily by Clarke (1988, 1994) who argues that a "pre-*Paranthropus*" hominin, possibly represented by the StW 252 cranium and the StW 573 skeleton, is a distinct species from *Au. africanus* as represented by the Taung skull and crania such as Sts 5 and Sts 17. Clarke (1988) notes in particular the similarity in postcanine tooth size between StW 252 and the *P. robustus* maxilla SK 13/14 (though StW 252 has much larger anterior teeth than any *Paranthropus*). In a thorough description of the craniodental remains from Member 4, Lockwood and Tobias (2002) argued that specimens StW 183, StW 255, and the partial cranium StW 252 are morphologically similar to one another, but distinct from the *Au. africanus* hypodigm, and may be members of a different species, and the similarity of StW 255 to *P. aethiopicus* KNM-WT 17000 has also been noted (Spoor, 1993). Other specimens from Member 4 that have received attention include Sts 19, which was thought not to be *Au. africanus* by some (Kimbel and Rak, 1993) but believed to be part of the normal variation within a species in another study (Ahern, 1998). The juvenile specimen StW 151 has been regarded as *Homo*-like and potentially distinct from *Au. africanus* (Moggi-Cecchi et al., 1998). Partridge et al. (2003) have argued that the variation found in the cranial remains and femora of Member 4 hominins and fossils recovered from the older Jacovec Cave deposits cannot be accommodated within a single species, and Schwartz and Tattersall (2005) recognize two distinct morphs in the Sterkfontein Member 4 assemblage.

Despite these suggestions for a second species besides *Au. africanus* in Member 4, none has yet been named or described. Furthermore, in a recent study of the Sterkfontein Member 4 dental remains, the morphological variation in the sample was less than that known in *P. boisei* or *H. habilis sensu stricto* (Moggi-Cecchi et al., 2006). The troublesome fossil StW 252 has enlarged postcanine dentition like *Paranthropus*, but like other members of *Au. Africanus*, it retains the enlarged anterior dentition as well. It is possible that the variation seen in *Au. africanus* can be accounted for by variation within a single species, perhaps being sampled across different time periods.

Phylogenetically, *Au. africanus* has been proposed as a sister taxon to *Homo* (e.g., Strait et al., 1997) or a sister taxon to *Paranthropus* (e.g., Johanson and White, 1979; Rak, 1983). Either hypothesis has been regarded as possible in recent work (Asfaw et al., 1999; Kimbel et al., 2004).

AUSTRALOPITHECUS GARHI Asfaw et al., 1999
Figure 25.9 and Table 25.2

Holotype The type specimen is BOU-VP-12/130, an adult male cranium consisting of frontal, parietals, lower face, palate, and upper dentition.

Age and Occurrence Late Pliocene, East Africa (table 25.2).

Diagnosis Based on Asfaw et al. (1999). *Australopithecus garhi* differs from *Au. afarensis* in having absolutely larger anterior and postcanine dentition, and in having a more derived upper third premolar morphology consisting of a more oval, symmetrical

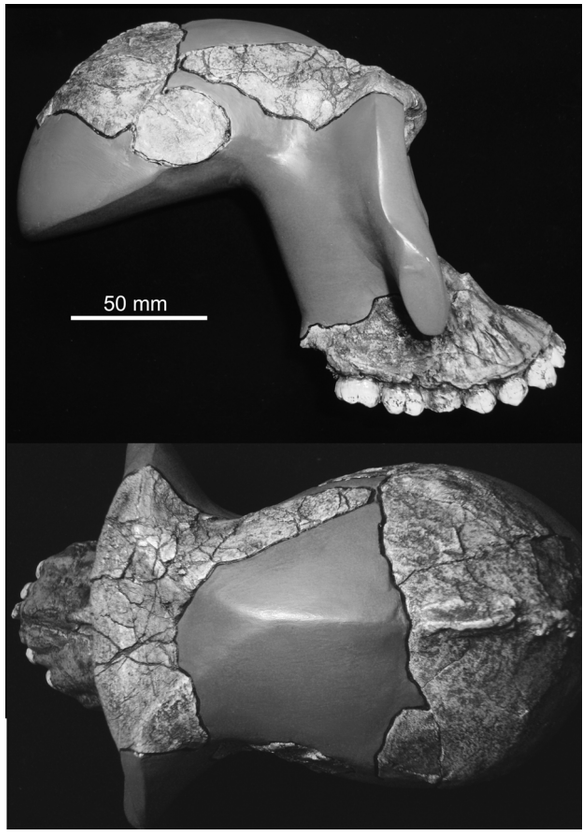


FIGURE 25.9 Holotype of *Australopithecus garhi*, cranium BOU-VP-12/130. Courtesy of Tim White.

occlusal outline and a weaker projection of the mesiobuccal enamel line. *Australopithecus garhi* differs from *Au. africanus* in having a more primitive subnasal region with a convex clivus contour and lacking anterior pillars; and in aspects of its frontal anatomy, such as the presence of a frontal trigon, frontal convergence of the temporal lines, and a strong sagittal crest. *Australopithecus garhi* lacks the derived facial anatomy of *Paranthropus* and also differs from *Paranthropus* in having a relatively larger anterior dentition and thinner tooth enamel. The canine to molar ratio is *Homo*-like, though the prognathic lower face is reminiscent of more primitive hominins like *Au. afarensis*.

Description Based on Asfaw et al. (1999). The type cranium shows a combination of primitive and derived anatomies. BOU-VP-12/130 has a small brain of approximately 450 cm^3. The frontal bone shows evidence of a frontal trigon and has strong temporal lines and a marked postorbital constriction. The parietals are complete enough to demonstrate the presence of a strong sagittal crest. The facial anatomy of BOU-VP-12/130 is *Au. afarensis*–like, with a prognathic subnasal region that possesses a convex clivus contour, and canine and lateral incisor roots that are in line with or lateral to the nasal aperture. Unlike *Paranthropus robustus* and most *Au. africanus* specimens, the maxilla is not reinforced with anterior pillars. The dental arch is U shaped, and a small diastema is present between the upper canine and lateral incisor. Perhaps the most striking feature of the BOU-VP-12/130 cranium is the absolute size of the teeth. The postcanine dentition, and in particular the premolars, are as large and in some cases larger than *Paranthropus* teeth. However, unlike *Paranthropus*, BOU-VP-12/130 has large canines and incisors as well. Therefore, the relative proportions of the teeth are *Au. africanus* and *Homo*-like, though the absolute sizes of the teeth are some of the largest yet discovered in the hominin fossil record. The large dentition and the presence of strong ectocranial markings, such as a sagittal crest, are evidence for this cranium belonging to a male individual.

For now, only the holotype cranium BOU-VP-12/130 is assigned to *Australopithecus garhi*. However, other specimens found nearby in stratigraphic horizons of similar age to that yielding the type (Asfaw et al., 1999; White et al., 2005), and megadont specimens from Omo and sites in Kenya may be included in the hypodigm in the future. Between 2.7 and 2.3 million years ago, the fossil remains currently known from East Africa can be broadly grouped into those that were moving toward the *Paranthropus* condition, and nonrobust specimens that share morphology found in early *Homo* (Suwa et al., 1996). Craniodental remains primarily from the Omo do not support the hypothesis of multiple nonrobust species between 2.7–2.3 Ma (Suwa et al., 1996). For this interval, the only two named East African hominins are *P. aethiopicus* and *Au. garhi*. Fossils from 2.7–2.3 million years ago not assignable to *Paranthropus* may ultimately be united under the hypodigm of *Au. garhi*. These include BOU-VP-17/1, a 2.5 Ma mandible with dentition, GAM-VP-1/1, an edentulous left mandibular corpus, and GAM-VP-1/2, a parietal fragment, from 3.0–2.0 Ma deposits at the site of Gamedah. White et al. (2005) concluded that nothing about the morphology of the Gamedah fossils would preclude them from being assigned to *Au. garhi* but stopped short of doing so. The two mandibles, based on similar morphologies to the BOU-VP-12/130 type, may represent *Au. garhi* females (Asfaw et al., 1999). The BOU-VP-12/130 *Au. garhi* cranium has postcanine dental arcade length and proportions that are quite similar to the 2.7 Ma associated teeth from Turkana, KNM-ER 5431 (White et al., 2005). The BOU-VP-17/1 and GAM-VP-1/2 mandibles share derived premolar and molar morphology with 2.7–2.5 Ma nonrobust Omo specimens L824-5, L362-14, and L45-2 (Asfaw et al., 1999; White et al., 2005).

There are currently no postcrania assigned to *Au. garhi*. However, in the description of *Au. garhi*, Asfaw et al. (1999) reported the discovery of a femur and associated humerus, ulna, and radius, partial fibula, and foot phalanx (BOU-VP-12/1A-G) in the Bouri Hata sediments. These were described by DeGusta (2004). This partial skeleton was found in the same 2.5 Ma horizon, 278 m away from the BOU-VP-12/130 cranium. The femur, humerus, and radius are complete enough to estimate limb proportions in BOU-VP-12/1, and Asfaw et al. (1999) suggest that this skeleton represents the earliest evidence for modern human–like limb proportions, with a relatively elongated femur. The forearm is still quite long in BOU-VP-12/1, similar to the condition found in the A.L. 288-1 *Au. afarensis* skeleton. These data suggest that femur elongation preceded forearm shortening in the taxon represented by this individual.

One of the few comparable postcranial elements from this time period in East Africa is the KNM-WT 16002 femur from 2.7-million-year-old deposits in the Lomekwi Member in West Turkana, Kenya. The morphology of this femur, however, is reportedly distinct from the femur from the BOU-VP-12/1 skeleton (Lovejoy, pers. comm. in Brown, et al., 2001). Brown et al. (2001) tentatively suggest that the KNM-WT 16002 femur may belong to *P. aethiopicus*.

Remarks There are few fossil hominin remains from East Africa between 3.0 and 2.0 Ma. Although this time period is well represented in the southern African fossil record, the discovery of *Au. garhi* provides important insights into the

evolutionary trajectory of hominins in East Africa during this part of the late Pliocene. Soon after 2.5 million years ago, the earliest members of the genus *Homo* appeared. Until the description of *Au. garhi* in 1999, *P. aethiopicus* was the only named East African hominin between 2.7 and 2.3 million years ago, and it was evidently more closely related to *P. boisei* than to early members of the genus *Homo*. Although Asfaw et al. (1999) are cautious in assigning phylogenetic significance to BOU-VP-12/130, they regard *Au. garhi* as a "candidate ancestor" for the genus *Homo*. The authors note, for instance, that the length and proportions of the dental arcade in the type cranium are "equivalent" to the 2.15 Ma early *Homo* mandible from the Shunguru Formation Omo 75–14 (Asfaw et al., 1999).

Important in this discussion of craniodental anatomy is a comparison of *Au. garhi* with the temporally contemporaneous southern African hominin *Au. africanus*. Asfaw et al. (1999) list nine features found primarily in the maxillary and frontal regions that differentiate *Au. garhi* and *Au. africanus*. However, many of the distinguishing characters are variably present in the collection of *Au. africanus* specimens from the Member 4 deposits in Sterkfontein Cave. For example, an I2/C diastema is present in the partial cranium StW 252, which also has tooth proportions and overall tooth dimensions that are quite similar to BOU-VP-12/130. A frontal trigon and frontal convergence of the temporal line is present in Sts 17, and anterior pillars are absent in TM 1512 and StW 498, though StW 498 is from an immature individual (Lockwood and Tobias, 1999). StW 391 also lacks strong anterior pillars and has a convex clivus contour, though this specimen may also be from an adolescent (Lockwood and Tobias, 1999, 2002). The apparent close similarities between BOU-VP-12/130 and certain specimens currently assigned to *Au. africanus*, such as StW 252, are worthy of further investigation.

Faunal analysis suggests that the Hata hominins were living along a lake margin rich with grazing bovids, and zooarchaeological remains found in the same horizon as the BOU-VP-12/130 type cranium and the BOU-VP-12/1 skeleton suggest that hominins were utilizing these bovids as a food supply (de Heinzelin et al., 1999). The Hata material, in the form of percussion and cut marks on bovid mandible and tibia, and an equid femur provides the earliest direct evidence for meat and marrow acquisition in the hominin fossil record (de Heinzelin et al., 1999), and the earliest stone tools have been recovered from 2.6-million-year-old sediments at Gona, roughly 100 km north of the Bouri formation (Semaw, 2000).

With this circumstantial evidence that at least one Bouri hominin species was beginning to modify stone to acquire meat and marrow, and evidence that a species of hominin had evolved elongated lower limbs, the fossils of the Hata deposits preserve evidence of two of the major evolutionary transitions in the hominin lineage (the incorporation of significant amounts of meat and marrow into the diet, and a shift to a more efficient form of bipedal locomotion). Whether these transitions occurred in the species *Au. garhi*, or in another taxon, remains to be established.

Genus *KENYANTHROPUS* Leakey et al., 2001
KENYANTHROPUS PLATYOPS Leakey et al., 2001
Figure 25.10 and Table 25.2

Synonymy *Australopithecus afarensis*, White, 2003.

Holotype The type is KNM-WT 40000, a nearly complete but distorted cranium, and the paratype is KNM-WT 38350, a left partial maxilla (Leakey et al., 2001).

Age and Occurrence Mid-Pliocene, eastern Africa (table 25.2).

Diagnosis Based on Leakey et al. (2001). Cranium with ape-size brain. Facial contour is flat in the transverse plane at a level just below the nasal bones; zygomaticoalveolar crest low and curved; tall malar region; vertically oriented maxillary zygomatic process positioned above P3–P4; nasoalveolar clivus long and transversely and sagittally flat; moderate subnasal prognathism; incisors in line with canine; thin palate; M1 and M2 small with thick enamel; upper incisor roots of similar size, small external auditory meatus (as in *Au. anamensis* and *Ar. ramidus*, and unlike more derived australopiths); and mediolaterally long tympanic element lacking a petrous crest.

Kenyanthropus platyops differs from *Ar. ramidus* in its buccolingually narrow M2, thicker molar enamel, a more cylindrical articular eminence and deeper mandibular fossa; from *Australopithecus* in its reduced subnasal prognathism, more anteriorly positioned maxillary zygomatic process; transversely and sagittally flat nasoalveolar clivus, low and curved zygomaticoalveolar crest, similarly sized upper incisors, and small M1–2 crowns. It differs from *Paranthropus* in its tall malar region, flat midface, thinner palate, stepped entrance to the nasal cavity, small M1–2 crowns, and thinner enamel.

Description Based on Leakey et al. (2001). The holotype cranium KNM-WT 40000 is relatively complete but is considerably distorted and lacks most of the basicranium and the anterior and premolar tooth crowns.

One of the most striking features of the holotype is the flat transverse facial contour below the nasal bones. The incisor alveoli are situated almost on the bicanine line, contributing to an orthognathic subnasal region. However, unlike *Paranthropus*, the midface is flat, not dished.

The M2 in KNM-WT 40000 is the only tooth whose width and length can be measured, and it falls below the range of known early hominins. The M1 of KNM-WT 38350 is also small, but comparable to the smallest known specimens of *Au. anamensis*, *Au. afarensis* and *H. habilis*. Molar enamel is thick, comparable to that found in *Australopithecus*, but not as thick as in *Paranthropus*.

Remarks There are several interesting evolutionary implications associated with this genus, should its taxonomic validity be substantiated. White (2003, 2009) has disputed its validity because he contends the type has been so altered

FIGURE 25.10 Holotype of *Kenyanthropus platyops*, cranium KNM-WT 40000. Courtesy of National Museums of Kenya.

by expanding matrix distortion (EMD) that its true anatomy cannot be accurately gauged. EMD, a type of postmortem deformation, results when matrix becomes interspersed between adjacent fragments of fossil bone, displacing the fragments relative to one another and altering anatomy in an unpredictable way. White's caution may be warranted in terms of whether the facial part of the diagnosis can differentiate *Kenyanthropus* from *Au. afarensis*. However, the relatively diminutive molar size is unaffected by distortion and remains evidence for consideration of a new taxon given that postcanine megadontia is a defining characteristic of *Australopithecus*.

The implications of the taxon, as currently described, are as follows. First, it suggests modest hominin diversification between 4.0 and 3.0 million years ago, since, as currently interpreted, this interval is occupied by the *Au. anamensis*-*Au. afarensis* lineage. However, as White (2003) argues, two to three (if *Au. bahrelghazeli* is included) taxa between 4.0 and 3.0 Ma may not qualify as the components of an adaptive radiation per se.

A second implication is that it provides a plausible backstory to the enigmatic cranium KNM-ER 1470 attributed to *Homo rudolfensis*, and dated at 1.9 Ma. This taxon has long been troubling to anthropologists because of its large, flat face and big brain, contemporaneous with smaller-brained specimens with relatively delicate faces that are difficult to reconcile as belonging to a single taxon. If *Kenyanthropus* gave rise to *Homo rudolfensis*, but not *Homo habilis*, and later *Homo erectus*, then a possible corollary is that big brains may have evolved more than once.

A third implication concerns the unique combination of a *Paranthropus*-like facial morphology combined with small molars. The zygomatic arch is anteriorly positioned, a configuration typically associated with a more anterior line of action for the masseter and hence more chewing power. An anterior zygomatic and large molars have been thought to be functionally and developmentally linked, but it appears that they can be independent (i.e., an anterior zygomatic is not just the result of large masticatory musculature, driven by large tooth/jaw size; Leakey et al., 2001). Leakey et al. (2001:439) suggest that *Kenyanthropus* occupied a "distinct dietary adaptive zone," but the nature of its dietary niche was not elaborated. One possibility is that the combination of strong masseters and thick enamel with unexpanded molars would enable the jaws to exert higher bite forces per unit area, as would be useful in hard object feeding. It is also tempting to look to the paleoenvironment for clues. Although Leakey et al. (2001) conclude that the Lomekwi paleoenvironment may have been more vegetated and wetter than at Hadar, paleoecological resolution remains too coarse to identify specific ecological factors that might be associated with such a novel dietary niche.

Genus *PARANTHROPUS* Broom, 1938
Table 25.2

Partial Synonymy *Zinjanthropus*, Leakey, 1959; *Australopithecus*, Tobias 1967.

Age and Occurrence Late Pliocene to early Pleistocene, eastern and southern Africa (table 25.2).

Diagnosis Same as for *P. robustus*.

Referred Species *Paranthropus aethiopicus* Arambourg and Coppens, 1968; *P. boisei* Leakey, 1959, *P. robustus* Broom, 1938.

Remarks The hominins in this genus are often called "robust," but this is a misleading term that should only refer to their heavy jaws, megadont to hypermegadont cheek teeth, and inferred massive masticatory musculature (Grine, 1988; McHenry, 1991b; McCollum, 1999), as body size estimates based on regression analysis of postcranial dimensions to body mass and stature show that they were not heavier or taller than so-called gracile hominin taxa in the genus *Australopithecus* (Jungers, 1988; McHenry, 1988, 1991a, 1991b, 1992a, 1992b). Grine (1988) has recommended that these misleading terms be abandoned. There is some disagreement about the proper genus allocation of *P. aethiopicus*, *P. boisei*, and *P. robustus*, with many authorities preferring to place them in *Australopithecus*. Nonetheless, their derived craniofacial architecture, associated novel alignment of powerful chewing muscles, the disproportion of their small anterior teeth to their large (immense in the case of *P. boisei*) cheek teeth, and analyses of tooth wear and dental isotopic composition suggest that they had substantial trophic differences from *Au. afarensis* and *Au. africanus*, and thus separation at the genus level appears justified (Clarke, 1996). Whether the genus is truly monophyletic remains more uncertain, and depends on the phylogenetic position of *P. robustus* vis-à-vis the East African *Paranthropus* taxa and *Au. africanus* (Aiello and Andrews, 2000; Wood and Constantino, 2007). The reason for their disappearance is also not well understood and may be due less to competition with sympatric early species of *Homo* than to other factors, such as the effect of turnover of carnivore guilds during the early Pleistocene (Walker, 1984; Klein, 1988). Considerable work remains to be done on the dietary and postural and locomotor adaptations of this most unusual group of hominins.

PARANTHROPUS AETHIOPICUS (Arambourg and Coppens, 1968)
Figure 25.11 and Table 25.2

Partial Synonymy *Paraustralopithecus aethiopicus*, Arambourg and Coppens, 1967, 1968; *Australopithecus africanus* (in part), Howell, 1978; *Australopithecus boisei*, Walker et al., 1986; *Paranthropus aethiopicus*, Chamberlain and Wood, 1987; *Au. aethiopicus*, Kimbel and White, 1988; *Au. aethiopicus*, Kimbel et al., 1988; *Au. walkeri*, Ferguson, 1989; *Paranthropus aethiopicus*, Clarke, 1996; *Au. boisei*, Curnoe, 2001; *Paranthropus aethiopicus*, Wood and Constantino, 2007.

Holotype Omo 18-1967-18, mandible lacking rami and tooth crowns except for a partial left canine (figure 25.11), Mb. C, Shungura Fm., Omo, Ethiopia (Arambourg and Coppens, 1967), dated to 2.6 Ma (Feibel et al., 1989). A list of other specimens referred to *P. aethiopicus* is provided by Wood and Constantino (2007).

Age and Occurrence Late Pliocene, East Africa (table 25.2).

Diagnosis The species was provisionally recognized by Arambourg and Coppens in 1967, and formally named by these authors in 1968, based on a nearly toothless mandible from Mb. C, Unit C8 of the Shungura Fm., Omo, Ethiopia. The original diagnosis purported to differentiate the specimen from other early hominin jaws by its overall morphology, including the general massivity of the specimen, very thick corpora, deep genioglossal fossa, inferred macrodonty of cheek teeth, short, parabolic aspect of the alveolar rows, very reduced size of the canine and incisor region, and a deep, receding symphysis (Arambourg and Coppens, 1968). The referral of cranium KNM-WT 17000 to the species permits the diagnosis to be more meaningfully emended to include, in comparison with other species of *Paranthropus* (and *P. boisei* in particular), more

prognathic face; palate less retracted; weaker flexion of the cranial base; longer distance between M1 and the temporomandibular joint; higher inclination of the nuchal plane; shorter postcanine tooth row; shallower mandibular fossa; lower articular eminence; flatter, shallower palate; smaller cranial capacity; parietals low and sloping; maxillary process directed backward; nasomaxillary basin more pronounced; possibly larger incisors; and inferred greater I1–C length relative to buccolingual width of P4 (Walker et al., 1986; Ferguson, 1989; Suwa, 1989; Wood and Richmond, 2000; Wood and Constantino, 2007).

Description Despite initial claims for uniqueness (Arambourg and Coppens, 1967, 1968), the type specimen closely resembles mandibles of *P. boisei* in the robustness of its corpora, inferred massiveness of its postcanine teeth, and small size and transversely straight alignment of its canine-incisor row. It also exhibits wide extramolar sulci, and prominent superior and inferior transverse tori (Howell and Coppens, 1976). The V-shaped configuration of its alveolar profile and relatively modest height (33.0 mm) and width (26.0 mm) of the corpora at m2 contrast with the condition seen in many *P. boisei* mandibles (Wood et al., 1994); however, the robusticity index of corpus dimensions (W × 100/H at m2 = 79) fall within the range of indices for *P. boisei* (65–87), and the shape of the jaw and absolute dimensions are close to those of presumed female mandibles of that species (Sanders, 1987; Leakey and Walker, 1988; Walker and Leakey, 1988).

A slightly geologically younger (ca. 2.45 Ma) partial mandible from West Turkana, Kenya, KNM-WT 16005, is larger than Omo 18-1967-18 and presumably from a male individual (Walker et al., 1986; Leakey and Walker, 1988; Walker and Leakey, 1988). It also had relatively small incisors and canines, immense cheek teeth, and massive corpora. The size of the incisors and canines is inferred from their mesiodistally compressed roots (Leakey and Walker, 1988). Only the crowns or partial crowns of left p3–m2 and right p3–m1 are preserved. The mesiodistal and buccolingual dimensions of the left tooth crowns are p3 = 10.7 × 13.8 mm, p4 = est. 12.0 × est. 15.0 mm, m1 = 15.7 × 14.3 mm, and m2 = est. 17.0 × 16.7 mm, respectively (Walker et al., 1986; Leakey and Walker, 1988). The p3s are asymmetrical in occlusal outline, while the p4s are more molarized (Leakey and Walker, 1988). Anteriorly, the symphysis has a mild central keel, with slight concavities between the keel and the canine juga (Leakey and Walker, 1988). The closest similarity in dimensions of this specimen is with the *P. boisei* mandible from Peninj, Tanzania (Walker et al., 1986; Walker and Leakey, 1988).

Undoubtedly the most distinctive specimen documenting *P. aethiopicus* as a valid species (Kimbel et al., 1988; but see Curnoe, 2001) is KNM-WT 17000, the so-called Black Skull (e.g., Bower, 1987; Wilford, 1987), an adult cranium lacking the portion of the frontal posterior to the frontal trigon, the midsections of the zygomatic arches, large sections of the parietals, particularly anteriorly, and fragments from the occipital, pterygoid processes, and maxillae, as well as all of the teeth except for a premolar and half a molar (figure 25.11; Walker et al., 1986; Leakey and Walker, 1988). This specimen is close in geological age (ca. 2.5 Ma) to Omo 18-1967-18, and is remarkable for having the largest sagittal crest and one of the smallest fossil hominin cranial capacities (and most diminutive brain size among "robust" australopiths, 410 cm^3; Walker et al., 1986; Falk, 1987; Falk et al., 2000). It also would have accommodated an immense mandible, similar in size to the largest known for *P. boisei* (Walker et al., 1986; Leakey and Walker, 1988). Morphology of the specimen was described in detail by Walker et al. (1986) and Leakey and Walker (1988). Only its most salient features are listed here: cranium massively built, with a large, prognathic face; neurocranium relatively very small; incisor and canine roots disproportionately small relative to size of cheek tooth roots; P4 = 16.2 mm long × 11.5 mm wide; palate very large, broad (45.0 mm wide between P3 and 4), and flat; nasal opening pear shaped with slightly everted superolateral margins; low infraorbital foramina; visorlike flare of the zygomatics; triangular nasomaxillary basins bordered laterally by more anteriorly set zygomatic "visors"; root of zygomatic above P3; temporal foramen very large; bar-like supraorbital tori joined by a modestly inflated glabella; strong frontal trigon; sagittal crest most pronounced posteriorly, implying hypertrophy of the posterior fibers of the temporalis mm.; foramen magnum heart shaped; and cerebellar lobes of the endocast not tucked under occipital poles of the cerebrum (Walker et al., 1986; Leakey and Walker, 1988).

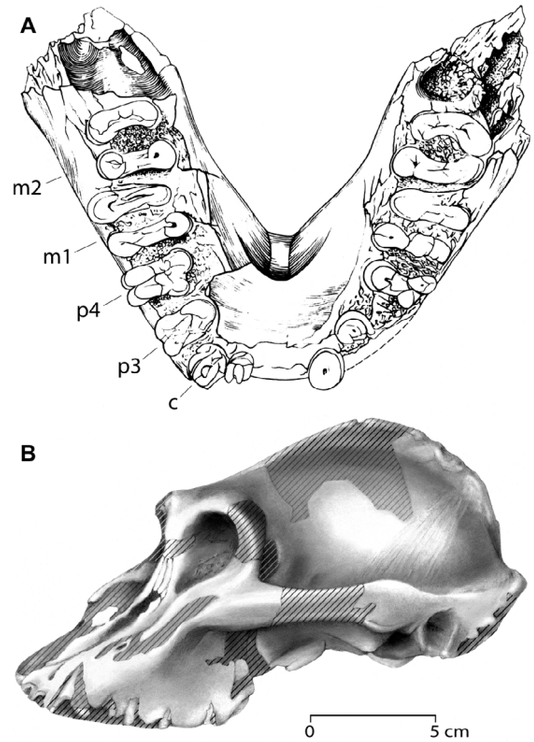


FIGURE 25.11 A) Holotype of *Paranthropus aethiopicus*, mandible Omo 18-1967-18; B) *Paranthropus aethiopicus* cranium KNM WT 17000.

Another cranial specimen assigned by some (e.g., Wood and Constantino, 2007) to *P. aethiopicus* is the posterior portion of a juvenile calotte from Mb. E, Shungura Fm., Omo, Ethiopia, L338y-6 (Howell, 1976). This specimen was described in detail by Rak and Howell (1978), who placed it in *Australopithecus boisei*. It is close in age to KNM-WT 16005. The calotte is comprised of the occipital squama, most of the parietals, and a small portion of the frontal and is associated with a basioccipital fragment. A hole in the anterior part of the right parietal bone may be a tooth puncture mark from a large carnivore (Rak and Howell, 1978); a carnivore tooth mark is also present in KNM-WT 17000, just posterior to the right temporal line at the point of the middle of the orbit (Leakey and Walker, 1988). Cranial capacity is low, estimated

at 427 cm^3 (Holloway, 1983). Age is estimated by the openness of its sutures, and the prominence of its muscle markings suggests that it is from a male individual (Rak and Howell, 1978). Due to the young age of the individual, postorbital constriction is inferred to still have been moderate at death, the sagittal contour of the calotte is rounded, and the temporal lines, though prominent, had not yet approximated a sagittal crest. The nuchal planum is roughened, and there is a pronounced external occipital protuberance. Paired salient depressions about the midline of the basilar part of the occipital are inferred to have been insertions sites for longus capitis muscles, a condition found in apes and other australopiths, but not humans (Rak and Howell, 1978). The foramen magnum was apparently heart shaped. Ridges on the temporal margins of the parietals indicate substantial overlap between the temporals and parietals, typical of *Paranthropus* (Rak and Kimbel, 1991). The superomedial position of these striae especially resemble their distribution in *P. boisei* crania, where they are located evenly along the arc of the parietotemporal suture, and contrast with their inferred arrangement in KNM-WT 17000, where the area of most substantial striae and overlap between the temporal and parietal is narrowly oriented posteromedially, in alignment with the most rugose segment of the sagittal crest (Rak and Kimbel, 1991; 1993; but see Walker et al., 1993). Variation in this feature between KNM-WT 17000 and L338y-6 could be ontogenetic. Based on cranial capacity, pattern of meningeal branching, cerebellar morphology, and perceived absence of an enlarged occipital-marginal venous sinus, Holloway (1981) concluded that the closest similarity of the endocast of L338y-6 is with either *Au. afarensis* or *Au. africanus*. These features were subsequently shown to be incorrectly interpreted or taxonomically uninformative, and other aspects of the endocast of L338y-6 link it with *Paranthropus* (White and Falk, 1999).

Possibly the oldest specimens of *P. aethiopicus* derive from the Upper Ndolanya Beds at Laetoli, Tanzania (table 25.2; Harrison, 2002). They include a portion of the lower face and palate (EP 1500/01), and left proximal tibia (EP 1000/98) that await comprehensive description. Morphometrically, the tibia resembles that of *Au. afarensis* individual A.L. 288-1, and the cranial fragment is similar to KNM-WT 17000 in the shallowness of its palate and position of the infraorbital foramen.

Remarks Although *Australopithecus* and *Paranthropus* have been used interchangeably in the literature to refer to *P. aethiopicus*, Groves (1999) has pointed out that the first usage of *Au. aethiopicus* was in reference to *Au. afarensis* from Hadar (Tobias, 1980), and that application of this nomen to a species typified by Omo 18–1967–18 would constitute a taxonomic homonym and be invalid. If *Paranthropus* is not deemed monophyletic, the available name for the species would be *Australopithecus walkeri* (Ferguson, 1989).

Specimens of *P. aethiopicus* represent the oldest occurrences of the genus, succeeded closely in time in East Africa by *P. boisei* (table 25.2). Little attention was paid initially to the type mandible from the Omo, but interest in the specimen was rekindled two decades later by the finding of the similar-aged cranium KNM-WT 17000. Although WT 17000 was characterized as an early member of the *"Australopithecus boisei"* lineage by its describers, they cautiously noted that its combination of primitive similarities to *Au. afarensis* and *Paranthropus* "robust" australopith features might warrant assignment to a different species, which because of temporal and geographical connections to the Omo mandible they suggested should be named *"Australopithecus aethiopicus"* (Walker et al., 1986). In addition, Suwa (1988) showed that *P. aethiopicus* lacked the extreme expansion of p4 talonids, diagnostic of *P. boisei*. This combination of features, dominated as it is by traits held in common with *Au. afarensis*, contrasts with the small number of synapomorphies shared with *P. boisei*, and is evidence supporting the validity of *"Au. aethiopicus"* (Kimbel et al., 1988; Ward, 1991).

More importantly, recognition of *P. aethiopicus* as an early stage of *Paranthropus* served to dramatically reconfigure early hominin systematics. While Rak (1983) had envisioned an evolutionary progression of *Au. Africanus* > *P. robustus* > *P. boisei*, temporal and morphological considerations suggest that *P. aethiopicus* was intermediate between *Au. afarensis* and *P. boisei/P. robustus*, with *Au. africanus* essentially left as a side branch (Kimbel et al., 1988) or perhaps antecedent only to *P. robustus* (Walker and Leakey, 1988). Wood and Constantino (2007) felt that *P. aethiopicus* and *P. boisei* could be viewed as chronospecies within an evolving lineage; indeed, the oldest known cranium attributed to *P. boisei*, Omo-323, from the 2.1 Ma–aged Mb. unit G8 of the Shungura Fm., retains traits of *P. aethiopicus* in the morphology of its glabellar region, supraorbital tori, and articular eminence, but otherwise has *P. boisei*-type features (Alemseged et al., 2002). This is just the sort of mosaic change one would expect in a lineage evolving anagenetically (Alemseged et al., 2002). Acceptance of a close phylogenetic relationship between these two species has not been universal, however, and others have posited *P. aethiopicus* as part of a polyphyletic group, separate from a *P. boisei*+*P. robustus* clade (Skelton and McHenry, 1992).

Almost nothing is known of the postcranial skeleton of this species (Wood and Richmond, 2000), making it difficult to reconstruct its paleobiology. However, it has been suggested that *P. aethiopicus* inhabited more closed environments than *P. boisei* (Reed, 1997).

PARANTHROPUS BOISEI (Leakey, 1959)
Figure 25.12 and Table 25.2

Partial Synonymy *Zinjanthropus boisei*, Leakey, 1959; *Paranthropus boisei*, Robinson, 1960; *Australopithecus* (*Zinjanthropus*) *boisei*, Tobias, 1967.

Holotype OH 5, subadult male cranium, Olduvai Gorge, Tanzania (Leakey, 1959; figure 25.12).

Age and Occurrence Late Pliocene–early Pleistocene, East Africa (table 25.2).

Diagnosis The type cranium was discovered by Mary Leakey in July, 1959 at locality FLK 1 in Olduvai Gorge, near the bottom of Bed I. The original diagnosis of the type cranium placed it in a new genus, *"Zinjanthropus,"* which was distinguished from other australopiths (including southern African *Paranthropus*) by greater reduction of the canines; extent of muscular attachment area on the malars; a deeper palate; coincidence of nasion with the most anterior aspect of the glabellar region; thinness of the parietals; development of the nuchal crest as a continuous ridge across the occipital in males; high vaulted posterior region of the cranium; less elongate foramen magnum; occurrence of a massive horizontal torus above the mastoids; extensive pneumatization of the mastoid region of the temporals; development of keeled anterior margins of the sagittal crest for attachment of anterior temporalis muscle fibers; great interorbital width; shape and position of the external orbital angle elements of the frontal bone; m2 > m3; and greater overall massiveness of the cranium, especially the face (Leakey, 1959).

Later detailed description of *P. boisei* crania shows that they can be further discriminated from those of *P. robustus* by presumed merging (and consequent loss) of anterior pillars into the maxillary infraorbital surface; absence of maxillary fossula; expansion of the lateral infraorbital region into broad "visors" (in some cases); development of a nasomaxillary basin; blunt lateral margins of the pyriform aperture; extent of palatal retraction and extreme forward extension of the masseter muscle attachments; very wide flare of the zygomatic arches; and extreme postorbital constriction and very capacious extent of the temporal foramen (Rak, 1983). Also distinctive of *Paranthropus boisei* is the robustness of its mandibles and its hypermegadont posterior dentition, with premolars more "molarized" and cheek tooth crown areas larger than those of other hominins (Kimbel and White, 1988; Suwa, 1988).

Description Based in part on Leakey (1959); Tobias (1967a); Howell (1978); Rak (1983); Leakey and Walker (1988); Walker and Leakey (1988); Brown et al. (1993); Suwa et al. (1997); McCollum (1999); Alemseged et al. (2002). The history of recovery of fossils attributed to *Paranthropus boisei* is summarized in Wood and Constantino (2007). Crania, mandibles, and teeth, particularly of male individuals, are relatively abundant in the fossil sample of this species, due in part to their heavy construction. The crania recovered of *P. boisei* include the type OH 5, from Olduvai, Omo 323-1976-896, the oldest of the species, KNM-ER 23000, KNM-ER 406, KNM-ER 13750, and the presumed female crania KNM-ER 407 and KNM-ER 732 from East Turkana, KNM-WT 17400, from West Turkana, and the geologically relatively young KGA10-525 specimen from Konso, Ethiopia (table 25.2). Although Rak (1983) depicted an idealized cranial morphology for *P. boisei* that was starkly contrasted with the cranial anatomy of *P. robustus*, more recent work, especially by Brown et al. (1993), Suwa et al. (1997), and Alemseged et al. (2002), reveals a great degree of polymorphism beyond that expressed via strong sexual dimorphism in the *P. boisei* sample, and shows that morphological distinctions between the two species are not always clear-cut.

Nonetheless, in general, the facial mask of *P. boisei* is less complicated than that of *P. robustus*, with no anterior pillars or maxillary fossulae. The face of *P. boisei* is broader and longer than in *Australopithecus* (Bilsborough and Wood, 1988), and the lateral infraorbital region sweeps out into the shape of a "visor," but this is less pronounced in some specimens (Brown et al., 1993). Other features exhibiting variability in presumed male crania are the position of the greatest projection of the sagittal crest, the shape of the supraorbital tori, the degree of massiveness of the glabella, the size and projection of the lower face, and the size of the temporal foramen. The midface comprises a sunken, nasomaxillary basin, or "dished" face. The nasal aperture has blunt lateral margins, and the nasoalveolar "gutter" and clivus resemble those of *P. robustus* (discussed later). Nasion is coincident with the glabella. Nasal bones are tucked well under the glabella and are narrow inferiorly. Supraorbital tori vary widely in thickness. Postorbital constriction is strong, and the temporal lines bound a small, concave frontal trigon. The forehead is flattened. Zygomatic arches are high, strongly constructed (Corruccini and Gill, 1993), and flare widely. The mastoids are large in males, with a strong crest above, and the cranium

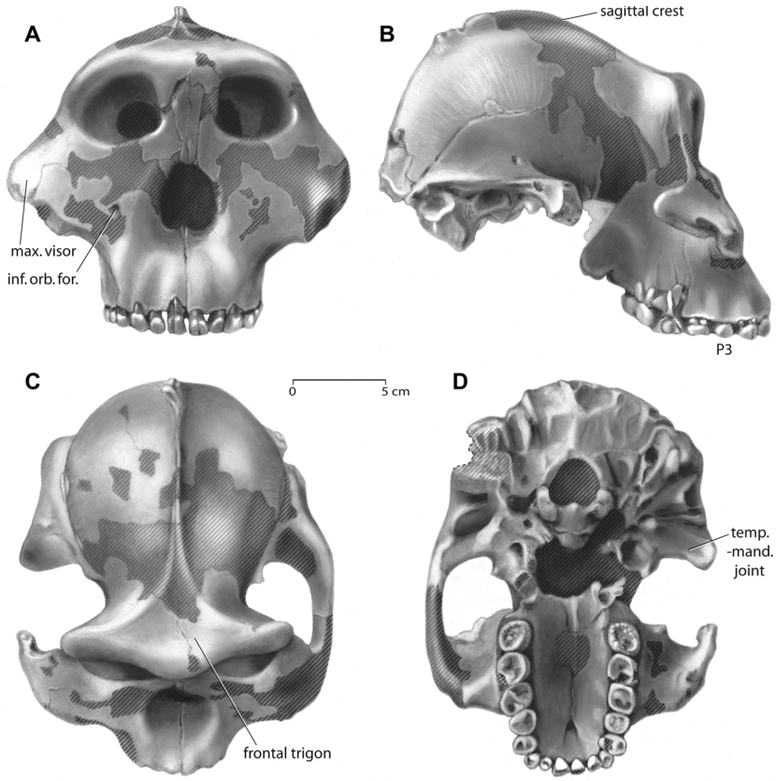


FIGURE 25.12 Holotype of *Paranthropus boisei*, cranium OH 5.

is pneumatized in this region. The palate is very retracted and the massester muscle attachment sites are extended forward to a greater degree than in any other australopith. The palate may be very deep and is bounded by a dentition in a parabolic arcade that has disproportionately large premolars and molars, compared with the very reduced canines and incisors (which are crowded in a transverse line at the anterior end of the tooth row). Temporomandibular joints tend to be large. There may be a compound temporal-nuchal crest. The foramen magnum is heart shaped and situated well forward of the bitympanic line (Dean and Wood, 1982). Occipital condyles are diminutive. Venous drainage of the cranium in *P. boisei* occurred primarily through an enlarged occipital-marginal sinus system (Falk, 1986, 1988); however, in KNM-ER 23000, drainage on the left side of the cranium occurred via a transverse-sigmoid sinus system (Brown et al., 1993). Cranial capacity ranges slightly higher than in other australopiths; Falk et al. (2000) estimated 500 cm^3 for OH 5, and 438 cm^3 and 466 cm^3 for the presumed female specimens KNM-ER 407 and KNM-ER 732, respectively. In addition, Brown et al. (1993) estimated endocranial volumes of 490 cm^3 for Omo 323-1976-896, 491 cm^3 for KNM-ER 23000, and 500 cm^3 for KNM-WT 17400. The greatest cranial capacity estimated for a specimen of *P. boisei* is that of KGA10-525 from Konso, 545 cm^3 (Suwa et al., 1997). These estimates are substantially lower than those for sympatric early *Homo*.

Examples of polymorphism in male crania of *P. boisei* include greater prognathism in KNM-ER 406 than in OH 5 (Rak, 1983), which is not an expression of regional intraspecific differences, since KNM-WT 17400 is more like OH 5 in this regard (Leakey and Walker, 1988). The zygomatic processes of OH 5 and KNM-ER 23000 are less visorlike than those of KNM-ER 406 and KNM-ER 13750, and their sides parallel the cranium reminiscent of the manner in *P. robustus* (Brown et al., 1993). KGA10–525 departs the most from the "ideal" cranial morphology envisioned for *P. boisei* by Rak (1983). Its zygomatic processes are configured similarly to those of *P. robustus*; it has a short lower face like that of KNM-ER 406, but more orthognathic than that of OH 5; its sagittal crest is more posteriorly developed, as in the *P. aethiopicus* cranium KNM-WT 17000; it has a high placement of the infraorbital foramen; and its palate is autapomorphically broad, shallow, and anteroposteriorly short, with a *Homo*-like shape (Suwa et al., 1997). Suwa et al. (1997) felt that the shape of the zygomatic processes and several other features in this individual strengthened the case for monophyly of *Paranthropus*. The morphological uniqueness of KGA 10–525, however, occurs primarily in features that have low heritability and are strongly liable to mechanical strains from mastication (Wood and Lieberman, 2001), which suggests that cranial polymorphism in *P. boisei* may be associated with a wide range of dietary habits.

Gorilla-like levels of sexual dimorphism in cranial morphology are also observed in *P. boisei*: female crania (e.g., KNM-ER 732, KNM-ER 407) are much smaller than those of males and lack ectocranial cresting, though they do exhibit features consistent with their placement in the species, such as depressed nasal bones, advanced placement of the malar region, and coronally oriented petrous temporal bones (Dean and Wood, 1982; Bilsborough and Wood, 1988). Despite its geographic range and temporal extent, in nearly all aspects of its skull anatomy, *P. boisei* does not exceed the degree of variation observed in extant hominoids (Silverman et al., 2001; Wood and Lieberman, 2001), although the very derived morphology of *P. boisei* means that detailed comparisons cannot be carried out.

There is a relative abundance of mandibles in the species sample, particularly from East Turkana, where some 20 specimens representing both sexes have been recovered. In contrast to their crania, other than the less robust corpora and smaller postcanine dentition in females (Walker and Leakey, 1988), mandibles of *P. boisei* exhibit only a small degree of variability (Wood and Lieberman, 2001). In addition, there appears to have been little mandibular or dental morphological change over geological time in *P. boisei* (Wood et al., 1994). Mandibles of this species have corpora that are absolutely and relatively very broad and high (almost rounded in cross section in some individuals), with tall, thick symphyses, wide extramolar sulci, and tall rami that are rooted as anterior as m2 and that have extensive muscle attachment areas, particularly for mm. masseter and the medial pterygoid muscles. The symphysis is posteriorly inclined, and has prominent superior and inferior transverse tori; the superior torus may continue as far posterior as the premolars, and bounds a deep median fossa. As with the upper dentition, the lower dentition exhibits a gross imbalance between diminutive anterior teeth and massive cheek teeth, including strongly molarized premolars. Deciduous premolars are very large and molarized. The p4 of *P. boisei* exceeds that of all other hominins in expansion of the talonid (Suwa, 1988), and in size and occlusal area of its cheek teeth the species is unmatched (Kimbel and White, 1988; Suwa et al., 1994). While M3 may be smaller or equal in size to M2, m3 is usually larger than m2.

Studies of tooth development and emergence indicate that in *Paranthropus*, permanent incisors and first molars formed their crowns at about the same time (similar to modern humans), but that they came into occlusion earlier in the life of an individual than in humans (Bromage and Dean, 1985; Smith, 1986; Dean, 1987a, 1988). However, there is some disagreement about the timing and speed of crown formation in *P. boisei*, with competing claims of rapid development (Benyon and Wood, 1987; Dean, 1987b, based on samples from East Turkana and Olduvai) versus rapid enamel differentiation and secretion, but longer overall crown formation time than in modern humans, associated with hyperthick enamel (Ramirez-Rozzi, 1993, based on samples from Omo).

For the most part, postcranial remains are only tentatively attributed to *P. boisei* (Wood and Richmond, 2000). Most of these are limb bones (Howell, 1978; McHenry, 1994b; McHenry et al., 2007), which yield mean body mass and height estimates of 49 kg and 137 cm for males and 34 kg and 124 cm for females (McHenry, 1991a, 1991b, 1992a, 1992b), with body mass ranging from 33.0 kg to 88.6 kg, depending on the regression used (Jungers, 1988). Feldesman and Lundy's (1988) estimates of stature for *P. boisei* are slightly greater than McHenry's (1991a) calculations; nonetheless, it is clear that this species was very similar in stature and body mass to other australopith species, and that sexual dimorphism in body size was likely considerable. A partial skeleton associated with a mandibular fragment, KNM-ER 1500, has been assigned to *P. boisei* (Grausz et al., 1988; but see Wood, 2005). This specimen, presumably of a female, has relatively large forelimbs and small hindlimbs, in comparison with modern humans, and similar to the condition in *Au. afarensis* (McHenry, 1994b). Many of the forelimb bones attributed to *P. boisei* males are relatively even larger, which could be due to sexual selection (McHenry, 1994b) or retained adaptation

to climbing. Distal tibial morphology is consistent with bipedality (McHenry, 1994b; DeSilva, 2009), but astragalar morphology indicates that the distal tibiofibular articulation with the ankle differed from the arrangement in modern humans (Grausz et al., 1988).

Remarks Given the extraordinary morphology of its masticatory system and its broad sympatry with early *Homo*, the most important questions about *P. boisei* involve diet and parameters of its ecological niche. The relative and absolute massiveness of the mandibular corpora and molar hypermegadonty of *P. boisei* are unmatched among primates, and have been referred to as "super-simian" by Wood and Aiello (1998). Biomechanical analysis of cross-sectional dimensions of the corpus in *P. boisei* indicates adaptation to resist transverse bending ("wishboning") and torsion during the power stroke of mastication (Daegling, 1989), possibly caused in part by the lateral position of the masseter muscles, relative to the occlusal plane, and large horizontal movements of the cheek teeth during chewing (Hylander, 1988). This is consistent with a need to powerfully crush and grind food, probably plant materials that required prolonged and extensive chewing (Hylander, 1988). Although it has been estimated that *P. boisei* could have generated much greater bite force across its cheek teeth than apes and modern humans, this force scales to the size of the occlusal platform in a manner similar to that in other hominids (Demes and Creel, 1988). Along with light construction of its facial skeleton (Ward, 1991), this evidence indicates its masticatory adaptations may not have been particularly suitable to break down hard, gritty food items, but could have processed tough or fibrous vegetation.

It has been argued, from an analysis of many factors of its lifeways and morphology, that *P. boisei* was a dietary eurytope, capable of eating a wide range of foods while maintaining the ability to access tough or hard specialized, seasonal fallback plant parts (Wood and Strait, 2004). It is also possible that *P. boisei* was capable of exploiting a wide range of habitats. The study of Shipman and Harris (1988) on faunal association of *P. boisei* concluded that it occupied primarily closed, wet habitats, while other studies (e.g., Schrenk et al., 1995; Reed, 1997; Suwa et al., 1997; Wood and Strait, 2004) interpret *P. boisei* sites to have included grassland or open woodland near dependable water sources. Dental microwear and isotopic analyses have not yet resolved these questions. Carbon isotope analysis shows that *P. boisei* had a diet rich in C_4 food items (van der Merwe et al., 2008)—grasses, sedges (including tough papyrus), or animals that eat these plants—but, in contrast to findings made on *P. robustus* (discussed later), microscopic examination of *P. boisei* teeth have not yielded results consistent with a constant diet of hard or tough food items (Ungar et al., 2008). That meat might have been incorporated in the diet of *P. boisei* was suggested by the results of dental strontium-calcium analysis (Boaz and Hampel, 1978). Between these findings and interpretations of its morphology and habitat preferences, it seems reasonable to at least tentatively conclude that *P. boisei* was the "higher primate equivalent of a bushpig" (Wood and Richmond, 2000:38).

PARANTHROPUS ROBUSTUS Broom, 1938
Figure 25.13 and Table 25.2

Partial Synonymy *Paranthropus crassidens* Broom, 1949; *Australopithecus crassidens*, Howell, 1978; *Australopithecus robustus*, Howell, 1978.

Holotype TM 1517, young adult male cranium, Site B, Kromdraai, South Africa (Broom, 1938).

Age and Occurrence Early Pleistocene, southern Africa (table 25.2).

Diagnosis The type specimen was discovered at Kromdraai, South Africa by a schoolboy and subsequently named by Broom in 1938. As the East African species of *Paranthropus* were not yet known, Broom (1938) focused on differentiating *P. robustus* from *"Plesianthropus transvaalensis" (Australopithecus africanus)*, on the criteria of more diminutive anterior teeth, and the large size and morphology of the cheek teeth. Later, Broom (1949) attributed several upper anterior teeth and a mandible with cheek teeth from Swartkrans, South Africa to a new species of *Paranthropus*, *"P. crassidens,"* based on the larger size of its premolars and molars than in the type specimen of *P. robustus*. Comparison of *Paranthropus* crania shows that *P. robustus* can be readily distinguished from *P. aethiopicus* and *P. boisei* by the morphology of its midfacial region and usually by configuration of its zygomatic prominence (see earlier discussion). Compared with *Au. africanus* and *Au. afarensis*, the splanchnocranium of *P. robustus* is deeper vertically (Bilsborough and Wood, 1988), cheek teeth are larger and more disproportionate relative to the size of the anterior dentition, and the midface is more sunken.

Description Based in part on Broom (1939); Broom and Robinson (1952); Howell (1978); Rak (1983); McKee (1989); Susman (1989); Grine and Daegling (1993); Grine and Strait (1994); Keyser (2000); Susman et al. (2001); de Ruiter et al. (2006). Craniodental and mandibular specimens of this species are well represented in the combined sample from Swarkrans, Kromdraai, and Drimolen, South Africa (Grine, 1989; Lockwood et al., 2007). Males appear to comprise a disproportionate percentage of the sample. Similar to *P. boisei*, cranial morphology of *P. robustus* is highly derived and distinctive. The high degree of morphometric variation in the sample has indicated to some the presence of two *Paranthropus* species, *P. crassidens* from Swartkrans and *P. robustus* from Kromdraai (e.g., Broom, 1949; Broom and Robinson, 1952; Howell, 1978; Grine, 1982). Recent discoveries at Drimolen (Keyser, 2000) and interpretive work by Lockwood et al. (2007), however, show that this variation can be accommodated within a single species (see also Kimbel and White, 1988) and accounted for in part by strong sexual dimorphism and bimaturism, in which males continue skeletal growth long after eruption of M3.

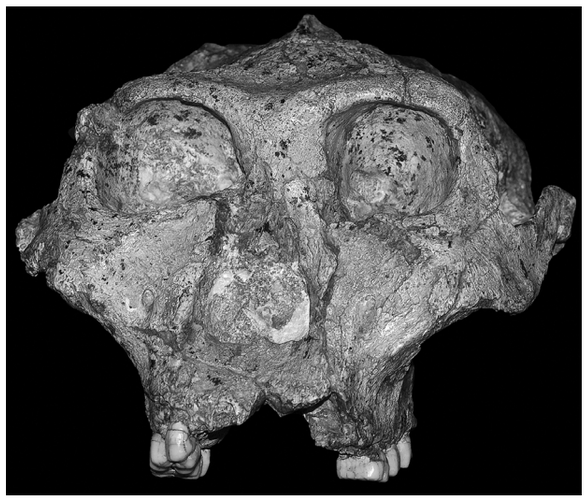


FIGURE 25.13 *Paranthropus robustus* cranium SK 48. Courtesy of the Transvaal Museum (Northern Flagship Institution).

The most complete male cranium of *P. robustus* is SK 48; other notable cranial specimens include the type TM 1517, SK 83, SK 52, SK 46, SK 79, and SKW 18 (de Ruiter et al., 2006; Lockwood et al., 2007). Considered together, these are characterized by a face with a unique maxillary trigon on each side, bordered medially by an anterior pillar, laterally by a zygomaticomaxillary "step," and inferiorly by an obliquely angled zygomaticoalveolar crest. The anterior pillars frame the pyriform aperture and nasoalveolar clivus, which curves smoothly into the nasoalveolar "gutter" at the base of the aperture. The infraorbital foramina open moderately low on the face, and are separated on each side by a subforamen divide from maxillary fossulae.

As noted by Broom (1938, 1939), the *P. robustus* midface is "dished," with its central area depressed relative to the anterior projection of the laterally situated zygomatic prominences. These structures do not flare into visors as in *P. boisei*, but angle sharply posteriorly into the zygomatic arches. The nasals are nearly flat and in the same plane as the maxillae. Glabella is massive, rectangular shaped, and anteriorly prominent, widely separating the orbits. The supraorbital margin on each side is arched into a modest, riblike torus, or costa supraorbitalis (Clarke, 1977); temporal lines running from the midline to these tori enclose a concave frontal trigon that is bounded anteriorly by the glabella. In superior view, postorbital constriction is severe; in lateral view, the cranium does not rise much above the height of the supraorbital tori, and there is no perceptible forehead. In addition, the root of the zygomatic arch and attachment for the masseter muscle are very high and anteriorly placed, relative to the tooth row.

Bizygomatic width in *P. robustus* is great, compared with biorbital breadth, resulting in a large temporal foramen on either side of the cranium. The temporal lines unite posterior to the frontal trigon and are raised in male crania to form a sagittal crest, necessitated by attachment of presumably thick temporalis muscles on a relatively small (and thin-vaulted) braincase. Cranial capacity for SK 1585 is estimated at only 476 cm^3, and features of the endocast such as shape of the frontal and temporal lobes resemble those of apes and other robust australopiths, rather than those of humans, early *Homo*, and *Australopithecus* (Falk et al., 2000).

Flexion of the cranial base in *P. robustus* parallels that of humans and is greater than in *Australopithecus*, and the foramen magnum is situated anterior to the bitympanic line (Dean and Wood, 1981, 1982; Wood and Richmond, 2000). The occipital condyles are relatively small, but the mastoid processes are large, heavily pneumatized, and are inflated laterally such that they constitute the widest points of the cranial base. The nuchal planum is weakly inclined and bordered by a well-developed external occipital crest; however, there is no compound temporal-nuchal crest. The mandibular fossa is deep and backed by a small postglenoid process that is closely adjacent to a cone-shaped tympanic. Intracranially, bony markings suggest that venous blood drained via a supplementary occipitomarginal pathway (Wood and Richmond, 2000).

The palate is shallow anteriorly and deepens posteriorly, is constructed of bone that is thick in cross section (McCollum, 1997; Strait et al., 2007), posteriorly retracted, and is bordered by teeth that form an elongate, U-shaped arcade, with incisors and canines nearly in a straight line transversely. McCollum (1999) linked development of the thickened palate in *Paranthropus* with growth of a vertically expanded mandibular ramus, which she felt was functionally integrated with the expanded occlusal area of the cheek teeth. Compared with the anterior teeth, the premolars and molars are very large—the premolars are somewhat "molarized"—and have bulbous cusps and thick enamel (Grine and Martin, 1988; Zilberman et al., 1990; Conroy, 1991); comprehensive descriptions and information about *P. robustus* tooth morphology are provided by Broom and Robinson (1952) and Grine (1989). In size, the cheek teeth are modally intermediate between those of *Au. africanus* and *P. boisei*, but overlap the range of each (Kimbel and White, 1988). In fact, an m2 from Gondolin, South Africa, probably an outlier of *P. robustus*, is at the upper end of the size range for *P. boisei* (Menter et al., 1999). The permanent tooth formation sequence was apparently I1, M1, I2, C, P3, M2, P4, and M3, in contrast to the modern human pattern of I1, M1, I2, P3, C, P4, M2, and M3 (Broom and Robinson, 1952; Dean, 1985; but see Grine, 1987), and study of enamel apposition in *P. robustus* indicates crown formation timing similar to that in apes, rather than to the developmental rate of modern humans (Dean et al., 1993).

In contrast, female crania, exemplified by the extraordinary DNH 7 specimen from Drimolen, are considerably smaller and lack the cresting seen in adult male crania. Anterior pillars are weakly developed, there are no incisal eminences, and the midface is not as deeply "dished" as in male crania. Although glabella is prominent and borders a depressed frontal trigon, and the postorbital constriction is strong, there are no supraorbital tori. In addition, the mastoid process is small. The anterior teeth (including blunt-tipped canines) are very reduced relative to the size of the cheek teeth, which include molarized, three-rooted premolars. Molar size progression follows the usual pattern seen in *Paranthropus*, with M3 > M2 > M1, and molars are wider than long. These teeth have thick enamel, expanded distal cusps, and are worn flat. When articulated with its mandible, the skull of DNH 7 exhibits a pronounced underbite. Other, less complete female *P. robustus* cranial specimens include SK 21, SK 821, and SKW 8 (Lockwood et al., 2007).

Mandibles of *P. robustus* are characterized by high, anteroposteriorly extensive rami with prominent coronoid processes, a robustly constructed symphysis with heavy inferior and superior transverse tori (but no simian shelf), and a deep genioglossal pit. The anterior margin of the mandible slopes gently backward inferiorly, and is higher than the posterior region of the corpus on each side. The corpora are well buttressed internally and externally, and they have huge extramolar sulci. As in the upper jaw, the lower cheek teeth are disproportionately larger than the anterior dentition, and molar size progression is m3 > m2 > m1. Although *Au. africanus* m2 and m3 approach those of *P. robustus* in size, m1 is generally much larger and molar talonids are relatively expanded in the latter (Suwa et al., 1994). Markings on the mandible for m. masseter, m. temporalis, and the pterygoid muscles are very pronounced. Evidence for substantial sexual dimorphism can be seen in comparison of the mandible from the female skull DNH 7 with male mandibles DNH 8 and SK 12, which have considerably larger dimensions, more massive teeth, and heavier buttressing of tori (Keyser, 2000).

Hominin postcranial elements are well represented in the *P. robustus* sites of Kromdraai and particularly Swartkrans, but specific attribution at the latter site is problematic because of the co-occurrence there of early *Homo* (Brain, 1976, 1988; Wood and Richmond, 2000). Because of the great numerical disparity between the craniodental remains of hominin taxa at Swartkrans, it has been argued that the overwhelming probability is

that most postcrania from the site belong to *P. robustus* (Susman, 1988). Hominin postcranial remains from Swartkrans have been enumerated by Broom and Robinson (1952), Robinson (1970, 1972), Howell (1978), Grine and Susman (1991), McHenry (1994b), Susman et al. (2001), and Susman (1989), and include elements from all regions of the skeleton.

The vertebrae are much smaller than those of modern humans and are similar dimensionally to those of *Au. africanus*. A last lumbar vertebra, SK 3981b, is dorsally wedged, indicative of lumbar lordosis, its pedicles are as robust as those in modern humans, and it has a massive accessory tuberosity on the transverse process for attachment of powerful iliolumbar ligaments, all adaptations to frequent bipedal posture and locomotion (Sanders, 1998). Similarly, configuration of the innominate of *P. robustus* (e.g., SK 3155b; but see Brain et al., 1974) suggests effectiveness in extending the leg and maintaining balance in upright posture. The iliac blade is broad and low, and reflected posteriorly, providing expanded surface area for gluteal muscles and positioning them for better extensor muscle action, as well as lowering the center of gravity and moving it closer in line with the vertebral column and legs (Robinson, 1972). Differences exist between the innominates of this hominin and modern humans. Some of these differences are likely to be primitive retentions in *P. robustus*: the acetabulum is deep but relatively small (e.g., SK 50, SK 3155b), as is the auricular surface for the sacrum; the iliac blades flare more laterally; the well-developed anterior superior iliac spine projects more laterally; and the ischial tuberosity projects farther from the acetabular rim (McHenry, 1975, 1994b). Robinson (1972) felt that this last feature correlated with an ape-like, power-oriented propulsive mechanism and incomplete adaptation to striding bipedalism. The hip joint of *P. robustus* is small, which is an australopith trait, as is the elongation and anteroposterior flattening of the femoral neck (e.g., SK 3121, SKW 19; SK 82, SK 97)(Robinson, 1972; McHenry, 1994b; Susman et al., 2001). In addition, cross-sectional buttressing of *P. robustus* (and *P. boisei*) femoral diaphyses is significantly greater mediolaterally relative to the condition in *Homo* (Ruff et al., 1999). These traits suggest that *P. robustus* may have differed kinematically or mechanically from modern humans in its bipedality. Support for this notion is found in the morphology of the first metatarsal (e.g., SKX 5017, SK 45690, SK 1813), which is not configured for human-like toe-off (Susman and Brain, 1988; Susman, 1989; Susman and de Ruiter, 2004).

Although Susman (1989) generally allocated postcranial fossils from Swartkrans with close similarity to modern humans to *Homo*, manual fossils with a number of derived, modern human-like features from Member 1 were attributed to *P. robustus* (Susman, 1988). These include a pollical distal phalanx (SKX 5016) with a broad apical tuft and muscle marking for a large m. flexor pollicis longus, a first metacarpal (SKX 5020) with a modern human–like lateral marginal crest for a strong opponens pollicis muscle, and a manual proximal phalanx (SKX 5018) with modern human–like shaft curvature. Combined with the proportions of digits II–V, these features indicate modern human–like capabilities for precision grip; based on this interpretation, Susman (1988, 1991a) suggested that the Oldowan stone tools and bone and horn implements found in Member 1 (where *Homo* is very poorly represented) and elsewhere could have been manufactured by *Paranthropus*. This interpretation has not been embraced without some reservations (e.g., Hamrick and Inouye, 1995; Ohman et al., 1995), and has been rejected by others as overly reliant on taphonomic, as opposed to morphological, criteria (e.g., Trinkaus and Long, 1990; but see Susman, 1991b, 1995), and remains controversial. It seems illogical to assume that *Paranthropus*, with its emphasis on craniofacial adaptations to heavy mastication, was the primary maker of stone tools, while *Homo* exhibited a progressive and probably functionally related association of tooth size diminution and improved stone tool manufacture that continued after the demise of its evolutionary cousins.

Remarks The degree of craniodental size differences between females and males suggests gorilla-like levels of sexual dimorphism (Lockwood et al., 2007). Along with the suggestion that older males with higher social rank may have had more exaggerated development of diagnostic features such as anterior pillars, this indicates a social system in which "male reproductive success is concentrated in a period of dominance resulting from intense male-male competition" (Lockwood et al., 2007:1444). Body size in *P. robustus* has been estimated to have ranged from 37.1 to 57.5 kg, or 42.2 to 88.6 kg, depending on the regression employed (Jungers, 1988), and averages between 40.2–49.8 kg for males and 31.9–40.3 kg for females, again depending on the regression used (McHenry, 1992a, 1992b, 1994a). These contrasts are somewhat less than the dimorphism observed in gorillas, so the issue of body size and social structure in *P. robustus* requires further study.

New studies indicate that the derived masticatory apparatus of *P. robustus* may not have been correlated with a narrow dietary specialization. Though most paleoenvironments associated with *P. robustus* are open grasslands, correspondence analysis of faunal assemblages that include this species indicates that it had a woodland habitat preference (de Ruiter et al., 2008). Moreover, carbon isotope analysis of enamel shows that *P. robustus* had a mixed diet primarily of C_3 foods, supplemented by a significant amount of C_4 sources, either grasses, sedges, or animals that consume these plants, and that this diet varied interannually and seasonally (Lee-Thorp et al., 1994, 2000; Sponheimer et al., 2005, 2006; van der Merwe et al., 2008). Thus, it appears that *P. robustus* was a dietary and habitat generalist, perhaps periodically venturing from woodland settings to acquire fallback foods in more open settings, and relying on its powerful occlusal platform to process tough, critical resources.

The dietary adaptations and functional anatomy of the southern African *Paranthropus*, however, are not yet clearly understood. Although bone and horn fragments from Swartkrans have been interpreted as tools for digging up tubers (Brain et al., 1988), subsequent microwear analysis of these tools suggests that they were used to forage for termites (Backwell and d'Errico, 2000). Tooth wear studies do not show microwear features on *P. robustus* teeth consistent with grazing (Grine, 1981; Grine and Kay, 1988), so it is possible that the source of C_4 in these hominins was termites and small vertebrates (Lee-Thorp et al., 2000). The greater incidence of pits, broader wear features, and heterogeneity of scratches observed in dental microwear indicates that *P. robustus* had a different diet than *Au. africanus*, primarily of hard food items (Grine, 1986; Kay and Grine, 1988; Scott et al., 2005). Strontium-calcium ratios in *P. robustus* samples are quite low, however, which is inconsistent with a diet specialized in seeds, roots, and rhizomes. They do fit either with a preference for leaves and shoots of forbs and woody plants, or with omnivory, with substantial intake of animals that graze (Sillen, 1992), including termites, though Sponheimer et al. (2005) have argued that C_4 food other than sedges and

termites might have been important in the diet of *P. robustus*. Nonetheless, it is difficult to imagine hard food items that *P. robustus* might have consumed if not seeds and nuts, and processing such food items is consistent with their heavy jaws, postcanine megadonty, and thick enamel (Lee-Thorp et al., 2000; Lucas et al., 2008).

The relationship of *P. robustus* to East African *Paranthropus* and other australopiths requires further investigation, and it remains possible that that the unique extracranial cresting, dished midfacial configuration, heavy jaws and immense cheek teeth are convergent adaptive responses to similar environmental changes, rather than a shared derived complex (Wood and Constantino, 2007, and references therein); for example, the facial pillars of *P. robustus* have more in common with *Au. africanus* cranial morphology than with the East African *Paranthropus* lineage (if they were not merged into the facial architecture in this group) and could reflect an independent, endemic southern African derivation. Additionally, it has been noted that molar talonid expansion in *P. robustus* occurred via enlargement of the entoconid, whereas it occurred by enlargement of the hypoconid in *P. boisei* (Suwa et al., 1994), suggesting convergence rather than synapomorphy for molar size increase.

Subtribe HOMININA Gray, 1825
Genus *HOMO* Linnaeus, 1758
Table 25.2

Partial Synonymy *Anthropopithecus*, Dubois, 1893; *Pithecanthropus,* Dubois, 1894; *Sinanthropus,* Black, 1927; *Meganthropus,* Weidenreich, 1944; *Atlanthropus,* Arambourg, 1954*; Telanthropus,* Broom and Robinson, 1949.

Age and Occurrence Late Pliocene to Recent (first appearance, eastern and southern Africa; increasingly cosmopolitan following the late Pliocene; table 25.2).

Diagnosis When Leakey et al. (1964) erected the species *Homo habilis*, they presented a diagnosis of *Homo* as follows: postcranium adapted to erect posture and bipedal gait; low intermembral index; fully opposable pollex with well-developed precision and power grips; cranial capacity variable but larger on average than those of australopiths and ranging between ~600 and 1,600 cc; temporal lines do not reach to midline; less postorbital constriction than in australopiths; no concavity in facial profile although degree of orthognathism varies; variation in supraorbital torus development and symphyseal contour; dental arcade parabolic and usually lacking diastema; bicuspid p3; smaller and buccolingually narrower molars than in australopiths; small canines relative to most other hominoids. Wood (1992) published an explicitly cladistic list of eight *Homo* synapomorphies: increased cranial vault thickness; reduced postorbital constriction; increased contribution of the occipital bone to cranial sagittal arc length; increased cranial vault height; more anteriorly positioned foramen magnum; reduced lower face prognathism; buccolingually narrow tooth crowns, especially lower premolars; and shorter molar tooth row. More recently, Wood and Collard (1999; Collard and Wood, 2007) have distilled the criteria for allocation to *Homo* to distinctive features that are adaptively relevant and reliably inferable from the paleontological record: trend toward absolutely larger body size; relatively longer lower limbs; larger brain size relative to body size; prolonged ontogeny; fully committed terrestrial bipedalism; and more gracile masticatory apparatus relative to body size. In addition, they suggest that to be referred to *Homo*, species must be shown to be more closely related to the type species, *Homo sapiens,* than to the type species of any other hominin genus.

Referred Species (partial list) *Homo habilis, Homo rudolfensis, Homo erectus, Homo ergaster, Homo antecessor, Homo heidelbergensis, Homo neanderthalensis, Homo floresiensis, Homo sapiens*.

Remarks See species' sections.

HOMO HABILIS Leakey et al., 1964
Figure 25.14 and Table 25.2

Partial Synonymy *Homo ergaster*, Groves and Mazak 1975; *Homo rudolfensis*, Alexeev 1986; *Homo microcranous*, Ferguson 1995; *Australopithecus habilis*, Wood and Collard, 1999.

Holotype The type specimen OH 7 includes both parietals, partial mandible and hand bones of a juvenile (but see below as to whether the cranial and postcranial remains can be reliably associated). Paratypes referred to *H. habilis* by Leakey et al. (1964) include OH 4, 6, 8, 13; OH 14 and OH 16 were also referred to the species. For additional Olduvai and Koobi Fora specimens, see Wood (1992), Groves (1989), and Schrenk et al. (2007).

Age and Occurrence Late Pliocene to early Pleistocene, East and southern Africa (table 25.2).

Diagnosis Of the characters listed by Leakey et al. (1964) in the original diagnosis, the following remain widely supported: mean cranial capacity greater than that of *Australopithecus* but smaller than *H. rudolfensis* or *H. erectus*; smaller maxillae and mandibles than those of *Australopithecus*, and within the range of *Homo erectus*; premolars that are buccolingually narrower than those of *Australopithecus*, and tendency toward buccolingual narrowness and mesiodistal elongation of all teeth, especially lower premolars and molars; reduced subnasal prognathism compared to *Australopithecus*; and relatively thin molar enamel (see Dunsworth and Walker, 2002; Kimbel et al., 1997). *Homo habilis* also lacks derived features found in *H. erectus* including: frontal and sagittal keeling; mediolaterally narrow temporomandibular joint; angled tympanic-petrous; less postorbital constriction; thick cranial vault; and opisthocranion positioned high on the occipital profile (Spoor et al., 2007).

Description The time period between about 2.4 and 1.8 Ma shows the earliest evidence of major trends in the *Homo*

FIGURE 25.14 *Homo habilis* cranium KNM ER 1813. Courtesy of National Museums of Kenya.

lineages: increase in brain size and decrease in tooth size. However, the non-*Paranthropus* hominins during this interval have high morphological variability in absolute and relative brain size and postcanine occlusal area, and in cranial and facial architecture. Postcranial morphology is also highly variable and further confounded by lack of associations with craniodental material. Consequently, this period is best viewed as a transitional time with a poor fossil record. Nonetheless, current evidence best supports the presence of more than one species of non-*Paranthropus* hominin at Koobi Fora, and possibly elsewhere in Africa.

The following descriptions apply to those Olduvai and Koobi Fora specimens allocated by Wood (1992) to *Homo habilis*. Groves' (1989) allocations coincide with those of Wood, with the exception that the Koobi Fora small forms (KNM-ER 1813, 1805) are considered different from both *H. habilis sensu stricto* and *H. rudolfensis*. Some prefer to refer all or most of these specimens to "early *Homo*" (e.g., Suwa et al., 1996; Asfaw et al., 1999), "habilines" (e.g., Wolpoff, 1999), or species of *Australopithecus* (e.g., Wood and Collard, 1999; see later discussion).

Although 600 cc was the endocranial threshold cited for admittance into *Homo* by Leakey and colleagues (1964), this was lowered considerably from earlier such "cerebral Rubicons." It is now apparent that an absolute endocranial threshold is unworkable and biologically irrelevant in the absence of reliable estimates of body size (Wood and Collard, 1999). Furthermore, small Koobi Fora crania have endocranial volumes below 600 cm^3 [KNM-ER 1813 = 510 cm^3; KNM-ER 1805 = 582 cm^3 (Falk, 1987)], although some Olduvai specimens are larger (OH 7 = 674 cm^3; OH 13 = 673 cm^3; OH 16 = 638 cm^3; Tobias, 1971). Attempts to assess relative brain size using postcranial referents (e.g., McHenry, 1994a; but see below regarding postcranial attributions) and cranial proxies such as orbital area (Wood and Collard, 1999) find that *H. habilis* is only modestly encephalized relative to australopiths. However, although a large brain is correlated with slower maturation, the life history pattern of early *Homo* may have been like that seen in the australopiths. Dean et al. (2001) have shown that the timing of tooth development events resembles those of modern and fossil African hominoids.

Overall, there is reduction in tooth row length, jaw size, and absolute size of the postcanine dentition, but molars fall within the lower range of *Australopithecus* and the upper range of *Homo erectus* (Dunsworth and Walker, 2002). A more rectangular tooth shape (i.e., buccolingually narrow and mesiodistally elongated) is a consistent feature of the taxon, as is thinner (compared with *Australopithecus* and *Paranthropus*) molar enamel.

Supraorbital torus development is variable, but may be described as "incipient" in most specimens. The coronal chord is greater than the sagittal chord in the parietals, upper facial breadth exceeds midface breadth, and the nasal margins are sharp, with an everted nasal sill (Dunsworth and Walker, 2002).

The OH 65 specimen is a maxilla thought by Blumenschine et al. (2003) to have affinities with the KNM-ER 1470 *H. rudolfensis* lectotype, in particular in terms of its broad, flattened naso-alveolar clivus. This is disputed by Spoor et al. (2007), who note similarities between OH 65 and KNM-ER 42703, the youngest known specimen assigned to *H. habilis* (1.44 Ma). For example, both are of similar size and lack the anteriorly placed and forward-sloping zygomatic process found in KNM-ER 1470.

Southern African specimens that may represent *Homo habilis* come from Sterkfontein and Swartkrans, the most complete of which are crania Stw 53 and SK 847 (Grine et al., 1993, 1996; Curnoe and Tobias, 2006), although the former has also been attributed to *Australopithecus africanus* (Kuman and Clarke, 2000) and the latter to *H. erectus* (Kimbel et al., 1997). These two crania have been found to resemble one another more than East African *Homo* specimens KNM-ER 1813, 1470, 3733, OH 24, and KNM-WT 15000, raising the possibility that they represent a geographic variant of *H. habilis* or even a separate species of *Homo* not sampled in East Africa (Grine et al., 1993, 1996). However, the bony labyrinths of the two crania differ. While the semicircular canals of SK 847 resemble those of *Homo sapiens* and *Homo erectus*, suggesting similarity in movement perception to well adapted bipeds, the semicircular canals of Stw 53 were found to have a much less derived configuration (Spoor et al., 1994).

Three *Homo* specimens predating *Homo habilis* from Olduvai and Koobi Fora are securely dated radiometrically. The oldest is a temporal bone from Lake Baringo, Kenya, dated at 2.4 Ma (Hill et al., 1992). It is attributed to *Homo* on the basis of plausible synapomorphies absent in *Australopithecus* and *Paranthropus* temporal bones (although as noted by Asfaw et al. (1999) and Sherwood et al. (2002), comparisons with penecontemporaneous *Au. garhi* are not yet possible), including a medially positioned mandibular fossa, a mandibular fossa containing an anteromedial recess and a flange of tegmen tympani, a reduced temporomandibular tubercle and a sharp petrous crest (Hill et al., 1992; Sherwood et al., 2002). However, given the fragmentary nature of the specimen, it was not assigned to a particular species of *Homo*. A second *Homo* specimen is AL 666-1, a well-preserved maxilla with right P3–M1 crowns and left I2–M2 dated at 2.33 Ma (Kimbel et al., 1996). It has been referred to *Homo* on the basis of 10 characters including relatively broad palate, reduced subnasal prognathism, flat nasoalveolar clivus sharply angled to the floor of nasal cavity, and to a male of *H. habilis* on the basis of dental size and morphology, overall phenetic similarity, large size and lack of derived features found in *H. erectus* (e.g., inclined nasoalveolar clivus) or *H. rudolfensis* (e.g., remodeled subnasal region)(Kimbel et al., 1997). The third specimen is an isolated lower molar of a juvenile from the Nachukui Formation, West Turkana, which was found just above a tuff dated at 2.34 Ma (Prat et al., 2005).

The only postcranial specimens securely associated with early *Homo* craniodental material are OH 62 and KNM-ER 3735, dated to ~1.8 Ma and 1.9, respectively (Häusler and McHenry, 2004). OH 62 has been assigned to *H. habilis* by most workers, but KNM-ER 3735 is referred to *Homo* sp. Remains for OH 62 include maxillary, mandibular, radial, ulnar, humeral, tibial, and femoral fragments, while KNM-ER 3735 is represented by temporal and zygomatic, distal humerus, proximal radius, femoral, tibial and sacral fragments. Although initially thought to possess more primitive limb proportions than A.L. 288-1 (Johanson et al., 1982), it has since been emphasized that femur length cannot be reliably estimated for OH 62 (Asfaw et al., 1999; Dunsworth and Walker, 2002; Reno et al., 2005). Moreover, Häusler and McHenry (2004) have claimed that the OH 62 femur is overall more similar in proportion to an Olduvai specimen (OH 34)(of uncertain age [either Bed II or Bed III] and taxonomic assignment [*Homo* sp.]) than to australopith femora, although the OH 62 femur is small, with a reconstructed body mass of 33 kg (McHenry, 1992a). This finding would be

significant as it would undermine reconstructions of *Homo habilis* as being more primitive in limb proportions, and smaller and more dimorphic than later *Homo erectus* samples, but Ruff (2008) has since provided further evidence that the morphology of OH 62 is not consistent with it being an obligate biped. At present, there is a substantial range of morphology represented in hominin postcranial remains recovered from 1.9 to 1.5 Ma. In the Lake Turkana Basin, *H. erectus* (1.9–1.5 Ma), *H. habilis* (1.9–1.44), *H. rudolfensis* (1.9 Ma), and *P. boisei* (2–1.39 Ma) co-occur. Large, derived postcrania such as the innominate KNM-ER 3228, femora KNM-ER 1481A and 1472 and talus KNM-ER 813 could plausibly belong to any of these taxa. Thus the nature of the transition from an *Australopithecus*-like postcranial grade to the tall, long-legged, and large hindlimb jointed morph (exemplified by the aforementioned postcrania and by *H. erectus* partial skeletons KNM-ER 1808 and KNM-WT 15000) cannot be reliably reconstructed.

The OH 7 hand, OH 35 tibia, and fibula and OH 8 foot, all from Bed I, may represent *Homo habilis* or *P. boisei* (e.g., Gebo and Schwartz, 2006; Susman, 2008; Moyà-Solà et al., 2008). The hand bones are of a juvenile and previous researchers have noted the following: robust, but otherwise humanlike distal phalanges, robust, slightly curved middle and proximal phalanges and a broad, flattened carpometacarpal (CM) joint on the trapezium (Susman and Stern, 1982). These features are compatible with strong grasping, a powerful, mobile thumb, and powerful fingertips. However, Robinson (1972), Dunsworth and Walker (2002) and Moyà-Solà et al. (2008) all doubt whether the hand elements can be reliably associated with the cranial remains, the main grouping argument being the juvenile status of all specimens. The OH 35 tibia has an articular surface that faces inferiorly and limited ability for either dorsiflexion or plantarflexion (Susman and Stern, 1982; DeSilva, 2009). The OH 8 foot has several derived attributes, including a human-like pattern of metatarsal robusticity (i.e., a robust fifth metatarsal, indicating the lateral to medial weight transfer that occurs in modern humans), a lack of abductory capabilities in the hallux and a stiff lateral column, suggestive of a longitudinal arch (Susman and Stern, 1982; DeSilva, 2009). Crocodile and leopard bite marks are present on both the OH 8 talus, and the OH 35 tibia (Njau and Blumenschine, 2007). Citing a "perfect" fit between the OH 8 talus and the OH 35 tibia, Stern and Susman (1982) argued that these bones are not only both from *H. habilis* but possibly from the same individual. Their recovery in different geological horizons makes this hypothesis unlikely (Hay, 1976). Nevertheless, the association of OH 8 and OH 35 was tested by examining the congruence of the talar and tibial articular surfaces of associated human and ape skeletons using a 3-D laser scanner (Aiello et al., 1998; Wood et al., 1998). The results suggested that the articular surfaces of OH 8 and OH 35 were incongruent, and perhaps not only from different individuals but from different species as well (Aiello et al., 1998; Wood et al., 1998). Susman (2008) has recently reiterated the claim (Susman and Stern, 1982) that the OH 8 foot and the OH 7 type mandible belonged to the same, adolescent individual. However, the arthritic lateral metatarsals, and the obliterated epiphyseal line on the base of the first metatarsal indicate an older age for the OH 8 individual than the OH 7 *H. habilis* individual (DeSilva, 2008). Body weight estimates are 32 kg for the tibia and ~31 kg for the talus (McHenry, 1992a). Body weight estimates from orbital area of *Homo habilis* are comparable, ca. 30–35 kg (Aiello and Wood, 1994; Kappelman, 1996).

Remarks *Homo habilis* has been a controversial taxon since its inception—first, either because inclusion of relatively small-brained specimens into the genus (e.g., OH 7) was thought to be unjustifiable (e.g., Holloway, 1965) or because specimens were thought to be subsumable within *Homo erectus* (e.g., Brace et al., 1973). Later, controversy centered on whether *H. habilis* represented either one, highly variable, or two species (see Wood, 1992), with many researchers finding the degree and pattern of variation in *H. habilis sensu lato* to be unlike intraspecific variation found in extant *Homo*, *Pan* or *Gorilla* (Wood, 1991). Troubling to many was the co-occurrence of KNM-ER 1813 and KNM-ER 1470 at 1.9 Ma at Koobi Fora (e.g., Wood, 1985; Lieberman et al., 1988): the former has a small endocranial volume, a small face and teeth, and incipient browridges, while the latter has a larger endocranial volume but a larger facial skeletal, and presumably, dentition, and a transversely flat facile profile. However, an endocranial volume range of 510–750 cc does not exceed the level of variation found in dimorphic extant primates (Miller, 1991), and early *Homo* crania from Dmanisi, Republic of Georgia (~1.77 Ma) have endocranial capacities with almost as wide a range (from 600 to 775 cc)(Gabunia et al., 2000, 2002; Vekua et al., 2002).

Gathogo and Brown (2006) have recently suggested a new age for KNM-ER 1813 of 1.65 Ma, and proposed that this may remove some objections about whether the Koobi Fora sample can be accommodated within one pre-*erectus Homo* taxon (i.e., *Homo habilis sensu lato*). However, the stratigraphic revision on which the new age is based is disputed by Feibel et al. (2007) and is not widely accepted.

While it is very possible that more than one early *Homo* taxon is represented in the Turkana Basin, the same cannot be said for Olduvai, where there is general agreement that only *Homo habilis* has been sampled.

The most significant development in the interpretation of early *Homo* in the last decade is the proposal by Wood and Collard (1999) that inclusion of *Homo habilis* and *H. rudolfensis* in *Homo* produces such poor adaptive coherence that they should be removed, and transferred to genus *Australopithecus*. These authors made the case that the hypodigms for these taxa correspond to an ecological niche or adaptive grade that, overall, more closely resembles those of taxa belonging to *Australopithecus* than to *Homo* (see also Collard and Wood, 2007), but demonstration that these taxa are more closely related to *Australopithecus* than to *H. sapiens* is more equivocal (e.g., Strait et al., 1997; Strait and Grine, 2004). An alternative to placing *H. habilis* and *H. rudolfensis* in *Homo* (which would expand the definition of the genus beyond acceptable limits for many) or *Australopithecus* (already paraphyletic) would be to transfer these taxa to a different genus, or genera (Collard and Wood, 2007). Strait and Grine (2004) advocate leaving these taxa in *Homo*, as they believe the genus retains monophyly with their inclusion, and cladistic arguments should take precedence over gradistic arguments. However, gradistic arguments to remove *H. habilis* and *H. rudolfensis* from *Homo* can still be made, provided the evidence for niche separation is compelling and provided the remaining members retained in *Homo* constitute a monophyletic and holophyletic group. If *H. habilis* and *H. rudolfensis* are shown to be sister taxa (e.g., as in Wood, 1992, Box 4) they could be placed in the same genus. If they are not sister taxa but represent two divergence events that predate the divergence of *Homo erectus* (e.g., as in Strait and Grine, 2004: figures 4 and 5), then they could be removed from *Homo*, but two new genus names would have to be implemented. It has been suggested

that facial similarities between *Kenyanthropus* and KNM-ER 1470 could reflect a close phylogenetic relationship (Leakey at el., 2001). If future finds bear this out, *Homo rudolfensis* may be transferred to *Kenyanthropus rudolfensis*. Given the lack of data to resolve phylogenetic issues, and the likelihood that the degree of niche separation to be inferred from even expanded hypodigms may remain low, many authors prefer to retain *H. habilis* and *H. rudolfensis* within *Homo*, at least for the time being.

Egeland et al. (2007) provide a recent overview of Olduvai Basin Bed I paleoecology. The landscape was dominated by a saline, alkaline paleolake with fluctuating levels; streams drained from volcanoes to the south and east, and the east contained an alluvial fan and plain (Hay, 1976). Paleosol carbonates from trenches in Upper Bed I, between ~1.845 and 1.785 Ma indicate that C_4 plants were a major component of the vegetation, perhaps 40–60% (Sikes and Ashley, 2007). Wooded grasslands/grassy woodlands dominated the edges of the paleolake, and prior to 1.76 Ma, the Olduvai Basin is reconstructed as supporting mixed habitats. Significant aridification takes place between 1.76 and 1.75 ma (Sikes and Ashley, 2007; Egeland et al., 2007).

The Omo Group Plio-Pleistocene deposits of the Turkana Basin are exposed in East and West Lake Turkana, Kenya and Omo Valley, Ethiopia (Feibel et al., 1989; Bobe and Behrensmeyer, 2004). Sediments were deposited by fluvial, lacustrine, and deltaic activity, and the landscape was variously dominated by a large paleolake (between 4 and 2 Ma) or the Omo River. Faunal records of the Turkana Basin indicate that species with adaptations for a continuum of habitats from closed to open persisted between 4.0 and 1.0 Ma (Behrensmeyer et al., 1997) but periods of high faunal turnover occur in intervals from 3.4–3.2, 2.8–2.6, 2.4–2.2, and 2.0–1.8 Ma (Bobe and Behrensmeyer, 2004).

Bobe and Behrensmeyer (2004) demonstrate that large cyclical shifts in the fauna begin at 2.5 Ma in the Turkana Basin, at about the presumed time of the origin of *Homo*, and attempt to link it with environmental change. They note: "The fundamental importance of grasslands [for hominin evolution] may lie in the complexity and heterogeneity they added to the range of habitats available to the early species of the genus *Homo*" (399). Indeed, one of the most seductive environmental scenarios in paleoanthropology has been the idea that increasing seasonality and aridification associated with the late Pliocene was a potent selective force in hominin evolution, linked not just to the origins of genus *Homo* but to encephalization, stone tool manufacture, and a concomitant increase in manual dexterity, and greater commitment to terrestrial bipedality. For example, Vrba's (1985) documentation of a turnover in bovid taxa between 2.7 and 2.5 Ma was thought to occur in synchrony with environmentally driven extinction (*Au. africanus*) and speciation (*P. robustus* and *H. habilis*) among hominins in southern Africa. Support for a pan-African biotic turnover event has not materialized, however (Behrensmeyer et al., 1997), although Reed (1997) has shown that in East Africa, as in the south, *Homo* co-occurs with taxa adapted to more open, arid environments than do australopiths (Reed, 1997). Against this backdrop of evidence for increasingly frequent associations between hominins and more open environments over time, is the recognition that persistent heterogeneity and, particularly, instability (albeit cyclical) in habitat due to factors such as short-term orbitally forced wet/dry oscillations may be a more dominant selective force in hominin evolution (Potts, 1998; Kingston et al., 2007; Kingston, 2007).

The technical skills associated with tool making were long thought to be linked with brain expansion; however, this picture has been complicated by provisional evidence for tool use and manufacture among small-brained australopiths such as *Au. garhi* and *P. robustus*. The oldest Oldowan stone tools from Gona, Ethiopia (2.6 Ma), are not associated with hominin remains and slightly predate the earliest record of *Homo* (table 25.2). Nonetheless, early *Homo* and all subsequent members of the genus are consistently associated with stone tools. Oldowan stone tool manufacture and animal butchery reflect a significant shift in hominin foraging patterns (see Plummer [2004] for a review of the Oldowan sites) and signal the dawn of an ever-increasing dependence on culture as an adaptive strategy. Although an increased dependence on processing animal and possibly plant tissue with stone tools plays a role in the transition from the *Australopithecus* to the *Homo* grade, the nature of this dietary change as inferred from the anatomical, biomechanical, microwear, and isotopic evidence remains ambiguous (Ungar et al., 2006).

HOMO RUDOLFENSIS Alexeev, 1986
Figure 25.15 and Table 25.2

Lectotype This taxon was not formally diagnosed by Alexeev (1986) or later by Groves (1989) and no holotype was assigned, but KNM-ER 1470, an edentulous adult cranium is the lectotype (Wood 1992). Crania KNM-ER 1590 and 3732 and mandibles 1802 and UR 501 are included by some researchers, as are 1.9 Ma large-sized, derived postcrania from Koobi Fora such as KNM-ER 3228 and KNM-ER 1481 (Groves, 1989; Wood, 1992; Dunsworth and Walker, 2002; Schrenk et al., 2007, but see Wood and Richmond, 2000:41).

Partial Synonymy *Pithecanthropus rudolfensis*, Alexeev 1986; *Homo habilis*, Leakey et al., 1964; *Homo ergaster*, Groves and Mazak 1975; *Australopithecus rudolfensis*, Wood and Collard, 1999.

Age and Occurrence Late Pliocene to early Pleistocene, eastern and southern Africa (table 25.2).

Diagnosis Larger endocranial volume (752 cc for KNM-ER 1470 [Wood, 1991], but see the suggestion in Bromage et al. 2008 that the endocranial volume may be smaller than the estimate given here) than *Australopithecus*, *Paranthropus*, and the mean for *H. habilis*; very weak supraorbital tori; moderate

FIGURE 25.15 *Homo rudolfensis* cranium KNM ER 1470. Courtesy of National Museums of Kenya.

postorbital constriction; midface broad relative to upper face; prognathic overall but with an orthognathic lower face; relatively broad, short palate compared to *H. habilis*; anteriorly placed and forward sloping zygomatic process; superior surface of posterior zygoma flat; less everted nasal margins than *H. habilis*; no nasal sill; rounded mandibular symphysis with no internal buttressing; anterior and posterior dentition inferred to be large; more complex premolar root system. Can be distinguished from *H. erectus* by a larger face and dentition and lack of well-developed supraorbital tori (Wood, 1992; Groves, 1989; Dunsworth and Walker, 2002).

Description KNM-ER 1470 was initially referred to *Homo* sp. indet. by Leakey (1973). Although the endocranial capacity clearly aligned it with *Homo*, the face was noted to have similarities with *Australopithecus* and even *Paranthropus* (e.g., Leakey, 1973; Walker, 1976; Wood, 1991); moreover, the orientation of the face was recognized to be uncertain because of expanding matrix distortion of the frontal base (Leakey, 1973; Bromage, 2008). In addition to the features detailed in the diagnosis here, KNM-ER 1470 exhibits anteriorly positioned glenoid fossae and external auditory meati, and weakly developed muscle markings on the occipital and temporal bones (Leakey, 1973). Orbital area and orbital height have been used to reconstruct a body mass of ca. 49 kg (Kappelman, 1996) and 53 kg (Aiello and Wood, 1994) respectively.

Wood (1991) recognized that early *Homo* mandibles from Koobi Fora sort into two types. Those attributed to *H. rudolfensis* (KNM-ER 1482, 1483, 1801, 1802) are noted for their robust corpi, large postcanine crown areas, broad postcanine teeth, p3 molarization including developed talonids, and roots of p3 and p4 that are plate-like (Bromage et al., 1995b).

Wood (1992) tentatively allocated large-sized (and derived) postcrania from Koobi Fora to *H. rudolfensis* but later noted that no postcranial fossils can be reliably linked to *H. rudolfensis* (Wood and Collard, 1999; Wood and Richmond, 2000). KNM-ER 1470 is not directly associated with any postcrania; however, higher in the stratigraphic section in "area 131" where KNM-ER 1470 was found, three separate femora were recovered (KNM-ER 1472, 1475, 1481), one of which (1481) is associated with a tibia and fibula. All four specimens come from below the KBS tuff and are considered to be 1.89 ± 0.05 Ma (Feibel et al., 1989). KNM-ER 1475 is quite fragmentary, but 1472 and 1481 are well preserved. KNM-ER 1481 has some features that resemble australopith femora; for example, its neck is relatively long, and its shaft is anteroposteriorly flattened. However, it is much longer and has an absolutely large femoral head diameter (body weight based on head size is estimated to be 57 kg; McHenry, 1992b), and a similar distribution of femoral subchondral bone as modern humans (MacLatchy, 1996). KNM-ER 1481 may also be from *H. erectus* (Kennedy, 1983), though others find it more likely that this femur is from early *Homo* (i.e., *H. habilis sensu lato*)(Trinkaus, 1984a).

KNM-ER 3228 is 1.95 ± 0.05 Ma (Feibel et al., 1989) and as such is the oldest well-dated postcranial fragment whose size (i.e., body mass based on acetabulum size is estimated to be 62 kg; McHenry, 1992b), and morphology resemble those of *Homo sapiens*. Based on its size, it has been argued that KNM-ER-3228 may represent early *H. erectus* (Antón, 2003), but the only purported *H. erectus* specimen of this antiquity is the occipital fragment KNM-ER 2598 (discussed later) that is contemporaneous with KNM-ER 1470. The enlarged acetabulum on KNM-ER 3228 suggests high joint reaction forces at the hip perhaps as a result of large body mass. There is also a prominent iliac pillar reinforcing the bone and resisting the bending forces that would be imposed on the laterally flaring ilium during bipedal locomotion, and in this way it is similar to the *H. erectus* OH 28 pelvis (Rose, 1984; Aiello and Dean, 1990).

Remarks Other than the Koobi Fora material, the only relatively complete specimens that have been referred to *Homo rudolfensis* by at least some authors are two mandibles: Omo 75-14 from Ethiopia and UR 501 from Malawi. In addition to the mandible, the Omo collection includes upward of 20 isolated teeth of *Homo* affinity (Suwa et al., 1996). Suwa and colleagues have noted that the sizes of the teeth tend to fall above the mean for *H. habilis sensu stricto* and correspond in some respects (e.g., p3 molarization) to the *H. rudolfensis* morphological pattern laid out by Wood (1991, 1992). However, these authors posit that the more robust dentition of *H. rudolfensis* may represent the primitive condition for *Homo*, with rapid gracilization occurring within this lineage (during Upper Burgi Member time), to yield *H. habilis sensu stricto*. Under this model of anagenetic change, the hypodigms of the two early *Homo* taxa would be subsumed into *H. habilis*. However, it has also been suggested that the *H. habilis* morphotype may represent the primitive condition for *Homo* (Kimbel et al., 1997).

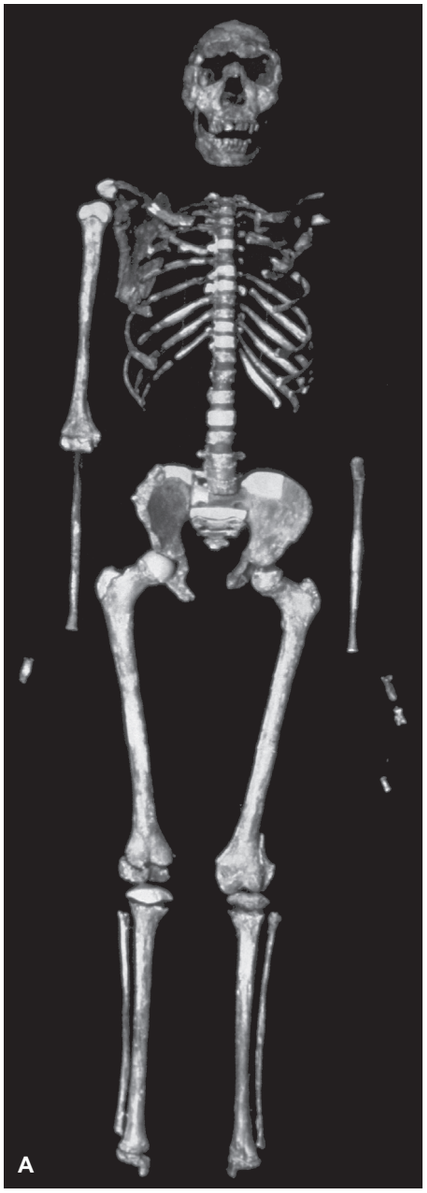
The Malawi mandible is of biogeographic significance in that it is associated with a mostly East African endemic fauna, rather than South African (Bromage et al., 1995b). Schrenk et al. (2002) report a faunal age of 2.5–2.3 Ma for UR 501, largely on the basis that the form of the suid *Notochoerus scotti* from Uraha is reportedly more advanced than those from Member C of the Shungura Formation, which is dated at ca. 2.8 Ma (Feibel et al., 1989) but less advanced than those from Member G, below the KBS tuff at ca. 2.0 Ma (Feibel et al., 1989). Given the ~2,500 km separating Omo and Uraha, a less precise faunal age for the mandible is probably warranted, in the range of 2.7–2.0 Ma. Hill (1995) has also suggested caution in attaching too narrow a faunally based date to this specimen.

HOMO ERECTUS (Dubois, 1893), Weidenreich, 1940

Figure 25.16 and Table 25.2

Partial Synonymy *Anthropopithecus erectus*, Dubois, 1892; *Pithecanthropus erectus*, Dubois, 1894; *Sinanthropus pekinensis*, Black, 1927; *Homo* (*Javanthropus*) *soloensis*, Oppenoorth, 1932; *Homo primigenius asiaticus*, Weidenreich, 1933; *Homo neanderthalensis soloensis*, von Koenigswald, 1934; *Homo soloensis*, Dubois, 1936; *Homo erectus javensis*, Weidenreich, 1940; *Homo erectus pekinensis*, Weidenreich, 1940; *Pithecanthropus robustus*, Weidenreich, 1945; *Meganthropus palaeojavanicus*, Weidenreich, 1945; *Pithecanthropus pekinensis*, Boule and Vallois, 1946; *Telanthropus capensis*, Broom and Robinson, 1949; *Pithecanthropus modjokertensis*, von Koenigswald, 1950; *Paranthropus palaeojavanicus*, Robinson, 1954; *Atlanthropus mauritanicus*, Arambourg, 1954; *Australopithecus capensis*, Oakley, 1954; *Pithecanthropus capensis*, Simonetta, 1957; *Pithecanthropus palaeojavanicus*, Piveteau, 1957; *Pithecanthropus sinensis*, Piveteau, 1957; *Homo leakeyi*, Heberer, 1963; *Homo sapiens soloensis*, Campbell, 1964; *Sinanthropus lantianensis*, Woo, 1964; *Tchadanthropus uxoris*, Coppens, 1966; *Homo ergaster*, Groves and Mazák, 1975; *Homo modjokertensis*, von Koenigswald, 1975; *Pithecanthropus soloensis*, Jacob, 1978; *Homo erectus trinilensis*, Sartono, 1982; *Homo palaeojavanicus sangiranensis*, Sartono, 1982; *Homo palaeojavanicus mojokertensis*, Sartono, 1982; *Homo palaeojavanicus robustus*, Sartono, 1982; *Homo erectus ngandongensis*, Sartono, 1982; *Homo georgicus*, Gabounia et al., 2002.

Holotype Trinil 2. Calotte discovered along the Solo River, Java in 1891.



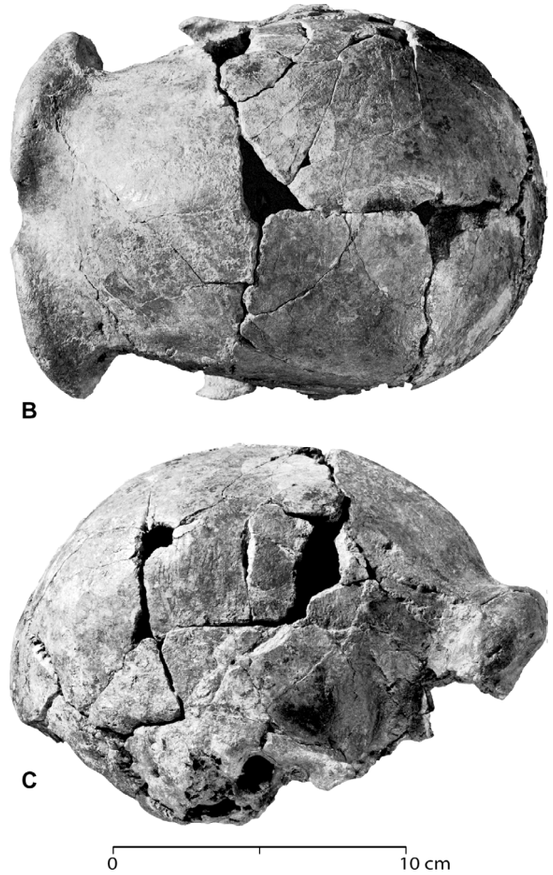


FIGURE 25.16 A) *Homo erectus* partial skeleton KNM WT 15000. Courtesy of National Museums of Kenya. B) *Homo erectus* calvaria BOU-VP-2/66. Courtesy of Tim White.

Age and Occurrence Early to middle Pleistocene Africa, Asia, Europe. Perhaps into later Pleistocene in sites in China and Indonesia (table 25.2).

Diagnosis The Trinil calvaria was the first fossil to demonstrate the existence of a small-brained hominin in the human fossil record. Compared to *H. sapiens*, the type specimen has a smaller cranial capacity (~850 cc); a low, sloping frontal bone with a thick, continuous supraorbital torus; moderate postorbital constriction; a midline keel; a strongly angled occipital with a thick transverse occipital torus; and less flexed basicranium. Fossils from Swartkrans, South Africa (Broom and Robinson, 1949), Olduvai Gorge, Tanzania (Heberer, 1963), Lake Turkana, Kenya (Leakey and Walker, 1976; Walker and Leakey, 1993), and Middle Awash, Ethiopia (Asfaw et al., 2002; Gilbert and Asfaw, 2008), have greatly expanded our knowledge of *H. erectus*. Compared to *H. sapiens*, *H. erectus* has a wider face; moderate subnasal prognathism; does not possess a mental eminence though the mandibular corpus is more robust, the ramus is mediolaterally wide, and the bicondylar breadth large; and a relatively larger third molar. Postcranially, *H. erectus* had six lumbar vertebrae; a longer femoral neck with associated broader pelvis; and thicker cortical bone in long bone midshafts. Compared to *Australopithecus* and earlier *Homo*, *H. erectus* has a larger average cranial capacity; vertically oriented parietals; thicker supraorbitals; overall thicker cranial bones especially in inner and outer tables; a strongly angled occipital region; reduced temporal fossa; a narrow but deep temporomandibular fossa; smaller postcanine teeth (especially M3) relative to body size; mesiodistally reduced upper M3; more platymeric femora; thicker cortical bone in lower limbs; more modern human–like intermembral index; and an overall larger body height and weight.

Description *Homo erectus* crania tend to be quite broad relative to their height, with parallel-sided parietals when viewed posteriorly, a robustly built occipital region often with an occipital torus, and a supraorbital torus that varies in projection and thickness, perhaps as a function of sexual dimorphism. Above the supraorbital torus is often a shelflike supratoral sulcus. The crania are typically thick and possess keeling along the midline and often a postbregmatic eminence. There is usually a degree of subnasal prognathism. The robusticity of the occipital and supraorbital region of the cranium may scale allometrically (Spoor et al., 2007). The thickened cranial vaults, expanded nuchal plane, and prominent supraorbitals may be a suite of characters functionally related to the increased anterior loading of the skull during mastication (Wolpoff, 1999). *Homo*

erectus is more modern human–like in craniodental morphology and postcranial anatomy than earlier *Homo* or australopiths.

The average cranial capacity in eight African fossils assigned to *H. erectus* is 870 cm^3 ± 129 cm^3 (range 691 cm^3–1067 cm^3; Holloway et al., 2004). These fossils include the relatively complete crania KNM-ER 3733, KNM-ER 3883, KNM-WT 15000, KNM-ER 42700, OH 9, UA 31 (Buia), BOU-VP-2/66 (Daka), and OH 12. Perhaps the earliest evidence for cranial expansion is the 1.9 Ma KNM-ER 2598 occipital fragment, which has a wide posterior cranial fossa, an angled occipital with a transverse occipital torus, but some claim this fossil may not be 1.9 Ma, and instead may have weathered from more recent deposits (White, 1995). *Homo erectus* has midfacial anatomy different from earlier hominins, including the presence of larger orbits and larger nasal regions. The large nasal regions may have been selected to increase the volume of air, and to retain water during expiration (Franciscus and Trinkaus, 1988). Other important craniodental fossils of *H. erectus* include KNM-ER 730, an associated mandible, frontal, and occipital of an older adult female. Consistent with other presumed female *H. erectus* fossils, the supraorbital is not markedly tall, and there is a weak nuchal torus. Craniodental remains of *H. erectus* may also be present in the later Sterkfontein cave deposits (SE 1508 and SE 1937) and at Swarkrans cave (SK 15 mandible and SK 847 partial cranium preserving part of the face)(Clarke, 1994a; Curnoe and Tobias, 2006).

The craniodental remains of *H. erectus* show a substantial range of variation, perhaps related to a persistence of *Australopithecus*-like levels of sexual dimorphism. A roughly 950,000-year-old frontal and temporal fossil (KNM-OL 45500) from the archaeologically rich site of Olorgesailie is quite gracile (Potts et al., 2004). Though the glabella region is prominent, the frontal breadth is reduced and the supraorbital thinner than all known *H. erectus* specimens except perhaps OH 12 (Potts et al., 2004). Recently described fossils from Ileret, Kenya, are consistent with the hypothesis that *H. erectus* displayed marked sexual dimorphism (Spoor et al., 2007). The 1.55 Ma calvarium KNM-ER 42700 has the smallest cranial capacity (691 cm^3) of any definitive *H. erectus* from Africa, and like in KNM-OL 45500, the supraorbitals are thin. The cranial vault is thinner than most *H. erectus* fossils, and the occipital not as strongly angled and lacks a strong occipital torus. A recent morphometric study of KNM-ER 42700 found it to be quite distinct from known *H. erectus* crania and perhaps not attributable to that species (Baab, 2008a; but see reply in Spoor et al., 2008). Despite this substantial range of variation in cranial morphology, Suwa et al. (2007) have found morphological continuity in the dental remains of *H. erectus* from 1.65 to 1.0 Ma, with a slight tendency toward dental gracility after 1.4 Ma. This may be correlated with the appearance of Acheulean tool technology, first preserved in 1.4 Ma deposits at the *H. erectus* site of Konso-Gardula (Asfaw et al., 1992).

The postcranial anatomy of *H. erectus* is known primarily from the remarkably complete skeleton of the young male from Nariokotome, KNM-WT 15000 (Brown et al., 1985; Walker and Leakey, 1993). Most of the skeleton is preserved; the specimen lacks some of the cervical and thoracic vertebrae, the left humerus, both radii, and hand and foot bones. Readers are referred to the Nariokotome volume (Walker and Leakey, 1993) for a detailed treatment of this specimen. The morphology of the ribs suggests that *H. erectus* was as barrel chested as modern humans (Jellema et al., 1993). The femora and tibiae are elongated, the proximal femur has a long femoral neck and the ilia flare laterally, though the ilia are poorly preserved in this specimen. Latimer and Ward (1993) believe that the vertebrae and sacrum have relatively small, australopith-like centra (but see Sanders, 1998), a modern human–like lumbar lordosis, and by inference strong erector spinae. The shoulder of the Nariokotome Boy possesses a combination of derived morphologies, including a modern human–like scapula, with a less cranially oriented glenoid than those found in apes and australopiths; primitive morphologies including a short clavicle and humerus with reduced torsion (Larson et al., 2007).

Brown et al. (1985) estimate that KNM-WT 15000 was roughly 12 years old at death, but others use perikymata to suggest that he was only 8 years old (Dean et al., 2001). Nevertheless, at the age of 8–12, he already had a thicker supraorbital torus and more robust facial morphology than the adult KNM-ER 3733. He was also already 1.66 m and roughly 48 kg (Ruff and Walker, 1993). Dean et al. (2001) have suggested that if this young *H. erectus* male had already attained this size within only 8 years, then *H. erectus* may have had an accelerated life history relative to modern humans, including an earlier weaning age, a rapid period of growth, and an earlier age of first reproduction.

Other possible postcranial remains from *H. erectus* have been described from Koobi Fora, Olduvai Gorge, and from sites in southern Africa. These include KNM-ER 1808, a pathological skeleton of a tall female *H. erectus*. Walker et al. (1982) found that the pattern of bone formation on the KNM-ER 1808 skeleton was similar to skeletal material from individuals who had consumed large quantities of raw liver, and in consequence had suffered from an overdose of vitamin A. The authors concluded that the morphology of the KNM-ER 1808 skeleton was evidence not only for the consumption of meat in *H. erectus*, but for conspecific care, as well (Walker and Shipman, 1996). Skinner (1991) argued that hypervitaminosis A could also result from eating too much honey, and Rothschild et al. (1995) most recently argued that the 1808 skeleton is more consistent with this individual suffering from yaws, not from hypervitaminosis A. Nevertheless, both KNM-ER 1808 and KNM-WT 15000 display modern human body proportions. This differs from earlier australopiths, which tend to have a relatively higher intermembral index (Aiello and Dean, 1990). Another specimen, KNM-ER 803 preserves parts of both upper and lower limb morphology, though this skeleton is quite fragmentary.

Other postcranial remains suggested to be from *H. erectus* include femora KNM-ER 736, KNM-ER 737, BOU-VP-1/15, BOU-VP-2/15, BOU-VP-19/63; tibiae KNM-ER 741, KNM-ER 19700, BOU-VP-1/109, StW 567; tali KNM-ER 5428 and BOU-VP-2/95, and the OH 28 femur and pelvis (Walker, 1994; Antón, 2003; Gilbert and Asfaw, 2008). These fossils collectively suggest that *H. erectus* was a large, muscular hominin. Body size estimates from the tibia and femora range from 45–68 kg (Antón, 2003). Using human-based regression equations, the large talus KNM-ER 5428 would be from an 86.7-kg individual (McHenry, 1992b). *Homo erectus* femora are characterized by thick midshaft cortical bone, subtrochanteric platymery, and a distal position of the minimum shaft breadth (Kennedy, 1983; Gilbert and Asfaw, 2008). The lower limb postcranial anatomy of *H. erectus* is consistent with a bipedal locomotor gait similar, if not indistinguishable, from that of modern humans. This assertion has recently been supported by an analysis of 1.52-Ma footprints presumably left by *H. erectus* at Ileret, Kenya (Bennett et al., 2009).

An *H. erectus* female pelvis and lumbar vertebra (BSN49/P27a-d) have recently been described from 0.9- to 1.4-Ma deposits in Gona, Ethiopia (Simpson et al., 2008). The pelvis is from a small, presumably female, individual (1.2–1.46 m in height) and retains the laterally flaring ilia characteristic of the australopith pelvis. However, the dimensions of the birth canal

suggest that *H. erectus* females were capable of delivering infants with large (300- to 315-cc) brains, suggesting that *H. erectus* had evolved a modern human–like prenatal brain growth pattern.

Remarks Readers are advised to consult Antón (2003) for a more detailed treatment of the biology and evolution of *Homo erectus*. As already discussed, the allocation of unassociated postcrania is problematic; however the partial skeletons KNM-ER 15000 and 1808 are evidence that *H. erectus* is a consistently larger hominin than the australopiths or perhaps early *Homo*.

Bramble and Lieberman (2004) have suggested that evolution of the body proportions and anatomies first seen at 1.9 Ma and present in KNM-ER 15000 and 1808 are adaptations for long-distance running and may have been selected for to increase hunting or scavenging success. Relatively long legs provide an elongated stride and energy conserving tendons increase the efficiency of long-distance travel. Modern humans have important physiological differences when compared to chimpanzees that are related to heat dispersal, such as sweat glands and reduced body hair. Adoption of diurnal hunting, scavenging, and long-distance travel would impose such a selection pressure against body hair. However, with the removal of body hair, selection would act fiercely on modern human skin color. Jablonski and Chaplin (2000) have elegantly shown that under an equatorial African sun, light skin color would result in folic acid destruction, whereas dark skin pigmentation would protect folic acid, while still allowing enough ultraviolet radiation to maintain sufficient vitamin D production. Rogers et al. (2004) sequenced the MC1R gene in modern humans and other primates and found that this gene, which helps regulate pigmentation, coalesced in hominins at roughly 1.5 Ma. These data suggest a selective sweep in a gene partially responsible for skin color variation in hominins near the time that *H. erectus* appeared. *Homo erectus* may therefore have been the first hominin with reduced body hair, perhaps as a result of long-distance diurnal travel related to hunting and scavenging.

Homo erectus specimens also indicate a shift in dietary strategies compared to earlier hominins. Australopith postcanine teeth are both relatively and absolutely larger than either early *Homo* or early *H. erectus* teeth. However, there is an increase in incisor size in *H. erectus*, suggesting a greater emphasis on anterior tooth loading. The evidence for an increase in meat consumption around 2 million years ago is supported by genetic studies on the tapeworm, which presumably evolved a relationship with hominins after being consumed as part of an animal carcass (Hoberg et al., 2001). Finally, a species cannot become reliant on meat if that food source is not present in the environment. The evolution of *H. erectus* and evidence that this species began to consume more meat tissue than its predecessors is supported by paleoecological evidence for faunal evolution in Africa between 2.5 and 1.8 million years ago during a time of variable climates with the trend toward drier and a greater variety of habitats (Behrensmeyer et al., 1997). These conditions would support the evolution of many of the prey animals found in *H. erectus* assemblages.

The pattern of stone tool sites on the African landscape changes during the early evolution of *H. erectus* (Cachel and Harris, 1998). These authors have noted that at that time archaeological sites begin to increase in volume, and the distances that hominins traveled to obtain the raw material for their stone tools increased. The patterns of stone tools thus indicate an increase in the home range occupied by *H. erectus*. This has also been reported in the later *H. erectus* locality of Olorgesailie, which reflects a shift toward greater use of the landscape and a more deliberate selection of stone tool raw materials (Potts, et al. 1999). These archaeological data are consistent with work by Antón et al. (2002) who have shown that an increase in body size and a change in diet correlate with an increase in home ranges across primates. Critically, the increase in home range is not just within Africa, but *H. erectus* is presumably the first hominin species to migrate out of Africa. This occurred shortly after the first fossil evidence for *H. erectus* (~1.95 Ma), as fossils likely assignable to this species have been found in 1.77-Ma sites in Dmanisi, Georgia (Gabunia and Vekua, 1995; Gabunia et al., 2000; Vekua et al., 2002; Lordkipanidze et al., 2006, 2007), and in 1.8-Ma sites in Indonesia (Swisher et al., 1994).

Related to an increase in big-game hunting, long-distance travel, and stone-tool sophistication is the tantalizing, but difficult-to-test, question of whether *H. erectus* possessed language. Based on the reduced size of the thoracic vertebral canals in the Nariokotome skeleton, MacLarnon (1993) suggested that *H. erectus* might have lacked the precise motor control of the intercostal and abdominal muscles necessary for modern human–like speech. However, the vertebrae of the Nariokotome skeleton may be pathological (Latimer and Ohman, 2001), and vertebrae from other *H. erectus* skeletons suggest that the size of the vertebral canals are within the modern human range and do not preclude *H. erectus* from possessing language (Meyer, 2006).

Based on morphological differences between the African and Asian *Homo* fossils from the early Pleistocene, some have suggested that *H. erectus* be reserved for fossils from Asia, and the majority of African fossils from this time period be allocated to *H. ergaster* (Groves and Mazák, 1975). This hypothesis of taxonomic diversity in the *H. erectus* sample has other supporters (e.g., Wood and Richmond, 2000; Schwartz and Tattersall, 2003). However, fossils of *H. erectus* crania from Eritrea dated to 1.0 Ma (Abbate et al., 1998) and remains from 1.4- to 1.0-Ma sites in Ethiopia (Asfaw et al., 2002; Suwa et al., 2007) overlap in variation with Asian and African *H. erectus* specimens, suggesting that *H. erectus* is a single, morphologically diverse taxon as suggested earlier (Rightmire, 1993). Results of a 3-D geometric morphometric study of variation in *H. erectus* found that a single-species hypothesis best fit the data (Baab, 2008b).

Recently, a 1.44 Ma maxilla KNM-ER 42703 was assigned to *H. habilis* (Spoor et al., 2007). If the taxonomic assignment is correct, then *H. habilis* and *H. erectus* were contemporaries, challenging the view that *H. habilis* evolved into *H. erectus* via anagenesis.

HOMO HEIDELBERGENSIS Schoetensack, 1908
Figure 25.17 and Table 25.2

Partial Synonymy *Palaeanthropus heidelbergensis*, Bonarelli, 1909; *Homo rhodesiensis*, Woodward, 1921; *Cyphanthropus rhodesiensis*, Pycraft, 1928; *Homo* (*Africanthropus*) *helmei*, Dreyer, 1935; *Homo florisbadensis* (*helmei*), Drennan, 1935; *Paleoanthropus njarensis*, Kohl-Larsen and Reck, 1936; *Homo steinheimensis*, Berckhemer, 1936; *Africanthropus njarasensis*, Weinert, 1939; *Homo marstoni*, Paterson, 1940; *Homo swanscombensis*, Kennard, 1942; *Homo saldanensis*, Drennan, 1935; *Homo sapiens rhodesiensis*, Campbell, 1964; *Homo sapiens steinheimensis*, Campbell, 1964; *Homo sapiens steinheimensis*, Campbell, 1964; *Homo erectus petraloniensis*, Murrill, 1983; *Homo antecessor*, Bermúdez de Castro et al., 1997; *Homo cepranensis*, Mallegni et al., 2003

Holotype Mauer Mandible, complete adult mandible from Rösch sandpit in the village of Mauer, near Heidelberg, Germany (Schoetensack, 1908).

Age and Occurrence Middle Pleistocene, Europe, Asia, Africa (table 25.2).

FIGURE 25.17 *Homo heidelbergensis* cranium from Kabwe, or "Broken Hill." Courtesy of Philip Rightmire.

Diagnosis A nearly complete mandible from Germany described by Schoetensack (1908) and reevaluated by Howell (1960) and more recently by Mounier et al. (2009) differentiated *H. heidelbergensis* from *H. erectus* and from *H. sapiens*. Compared to *H. erectus* mandibles, the Mauer mandible has a broader ramus; a taller anterior corpus; a posteriorly positioned mental foramen; a truncated gonial angle; an enlarged buccal cusp on the third premolar; and taurodontism of the molar pulp cavities. Unlike *H. sapiens*, the Mauer mandible has a thick symphysis with no projecting mental eminence; an extended planum alveolare; and the second molar is larger than the first. Similarities between the Mauer type mandible and mandibles and a cranium from the Arago site in France has led Rightmire to amend the diagnosis to include features shared in common by the Arago specimen, and fossils from Africa including Kabwe, Bodo, and Ndutu (Rightmire, 1998, 2008). In comparison with *H. erectus*, *H. heidelbergensis* possesses a larger cranial capacity achieved through an expanded parietal region and reduced postorbital constriction; a longer, more vertical occiput and shorter, more horizontally oriental nuchal plane; increased flexion of the anterior cranial base; larger frontal sinuses; a thinner tympanic plate; discontinuous supraorbital tori with a shallower supratoral sulcus; a shallower mandibular fossa; an anteriorly positioned incisive canal; and a more vertically oriented nasal margin. In comparison with *H. sapiens*, *H. heidelbergensis* possesses less parietal expansion; superior-inferiorly thicker and more projecting supraorbital tori; thicker cranial bones; midline keeling of a less vertically oriented frontal bone; an angular torus on the parietals; and a large, broad face.

Description Based on Rightmire (2008). *Homo heidelbergensis* possesses an interesting mixture of primitive features found in *H. erectus* and more derived features found in later *H. sapiens* specimens. These include a large, broad face, with a brain size that is within the range of modern humans. The brain is encased in a differently shaped and more robust cranium. The frontal bone is low, and there is a distinctive sagittal keel. The cranial vault is thick, particularly in the occipital region. There is also some subnasal prognathism. The supraorbital tori are projecting, superoinferiorly tall and discontinuous. The tori achieve their maximum thickness in the mid-orbit region, and appear everted or twisted laterally (Wolpoff, 1999). However, relative to earlier *H. erectus* crania, *H. heidelbergensis* has expanded parietals, a broader frontal, and a more rounded occiput, all features consistent with a larger brain volume. Postcranially, *H. heidelbergensis* shares with *H. sapiens* the same limb proportions; however, the long bones are more robustly built. The three most complete crania from Bodo, Kabwe, and Ndutu will be discussed here.

The earliest African specimen that may belong to *H. heidelbergensis* is the 600 ka (Clarke et al., 1994) Bodo cranium recovered in the Middle Awash, Ethiopia in 1976 (Conroy et al., 1978). The Bodo cranium consists of most of the face, and 41 cranial fragments pieced together to form most of the frontal bone, parietals, some of the anterosuperior aspect of the temporals, and some of the right aspect of the superior occipital. There is also a missing portion of the left maxilla and zygomatic. None of the teeth are preserved well enough to discern any occlusal detail. Bodo possesses a very large face, with massive zygomatics, a broad nasal opening, and a robustly built arched supraorbital torus. The supraorbital height is approximately 17.5 mm, slightly less than the 21 mm thick supraorbitals on the Kabwe skull. The breadth of the face (15.8 cm) is matched only by the large Indonesian *H. erectus* skull Sangiran 17. Bodo possesses a gently sloping frontal bone, with limited postorbital constriction. There is also a keel running along the sagittal aspect of the cranium. The cranial bones of the Bodo specimen are extremely thick, approaching 13 mm at the bregma position—greater than in any known *H. erectus* specimen (Conroy et al., 1978). Using a CT reconstruction of the skull, Conroy et al. (2000b) estimated a cranial capacity of 1,250 cc. Distinct cutmarks on the frontal and maxilla may be evidence of the deliberate defleshing and potential cannibalism of Bodo (White, 1986b).

In many ways, the Bodo cranium is similar to another large Middle Pleistocene cranium from Kabwe (or "Broken Hill"). Both skulls are considered to be from males (Rightmire, 1998; Wolpoff, 1999). The Kabwe cranium was the first major discovery of a fossil human on the continent of Africa and thus holds important historical significance. It was discovered in 1921 in the Broken Hill Mine in Zambia. Kabwe is nearly complete, missing only a region consisting of the right temporal and the right side of the basicranium (Woodward, 1921). Like Bodo, the Kabwe cranium is robustly built, with a broad face, and a thick, arched supraorbital torus. Also like Bodo, Kabwe has a gently receding forehead, and a midline keel. However, Kabwe possesses more gracile zygomatics than those found on the Bodo cranium. All of the maxillary teeth are preserved and they show considerable wear, with many of the teeth littered with cavities. The cranial capacity of Kabwe is estimated to be ca. 1,300 cm^3 (Holloway et al., 2004). Postcranial remains recovered from the Broken Hill Cave include several femora, a complete tibia (E 691), and an innominate (E 719) that all show modern human proportions, though are more robustly built than modern human lower limbs (Pearson, 2000). This postcranial robusticity is evident as well in a large Middle Pleistocene femur from Berg Aukas, Namibia (Grine et al., 1995), and KNM-ER 999, a large femur from Koobi Fora, Kenya (Day and Leakey, 1974; Trinkaus, 1993b).

Similar in morphology to Bodo and Kabwe, though slightly more gracile, the fragmentary Ndutu cranium is probably from a female (Rightmire, 1998; Wolpoff, 1999). Ndutu has a projecting supraorbital torus, though it is thinner than that found on either Bodo or Kabwe. The Ndutu cranium also has expanded parietals and a long vertical occiput (Clarke, 1976, 1990). The cranial capacity is estimated by Holloway et al. (2004) to be 1,100 cm^3.

Temporally younger specimens, such as those from Guomde, Florisbad, and Lake Eyasi, are more similar morphologically to modern *Homo sapiens* than early members of *H. heidelbergensis,* and thus it is difficult to confidently assign these fossils to a taxon, and the absence of accurate and precise information about the age of these fossils (Millard, 2008) currently limits our ability to accurately assess the tempo of evolutionary change from a *H. heidelbergensis*–like ancestor to the earliest definitive *H. sapiens*.

Remarks The legitimacy of *Homo heidelbergensis* as a taxonomic unit is controversial. Some regard *Homo heidelbergensis* as a late version of the evolving lineage *Homo erectus* that ultimately gave rise to our own species *Homo sapiens* in Africa (White et al., 2003). This view necessarily evokes transitional fossils with intermediate morphologies. Formerly, these fossils were regarded as "archaic" *Homo sapiens*, but most paleontologists now refer to them as *H. heidelbergensis*. Two studies have recently tested the distinctiveness of *H. heidelbergensis* and both have supported its taxonomic validity (Rightmire, 2008; Mounier et al., 2009).

Since *H. erectus*, *H. heidelbergensis*, and *H. sapiens* may represent a single evolving lineage, some have argued that the former two taxonomic distinctions should be sunk into *H. sapiens sensu lato* (Tobias, 1995; Wolpoff, 1999). However, this approach is untenable given overwhelming morphological and genetic (e.g., Stringer, 2002; White et al., 2003; Green et al., 2006; Wall and Kim, 2007) evidence that Neanderthals are a distinct lineage of extinct hominins. The most recent common ancestor of *H. sapiens* and *H. neanderthalensis* requires a name that is neither *H. sapiens* nor *H. neanderthalensis*. Some have given that distinction to *H. erectus* (e.g., White et al., 2003), while others suggest that middle Pleistocene hominins are sufficiently and consistently different from earlier *H. erectus* to warrant a separate species, that would be *H. heidelbergensis* (e.g., Tattersall, 1986; Rightmire, 2008). The taxonomic murkiness in the middle Pleistocene is further complicated by suggestions that European *H. heidelbergensis* fossils (represented perhaps by the crania from Petralona, Arago, and Atapuerca) are morphologically distinct from African fossils from Bodo and Kabwe, and that the European specimens of *H. heidelbergensis* form a chronospecies with *H. neanderthalensis* (Stringer, 1996). Nonetheless, the coefficient of variation for over 20 features of all crania assigned to *H. heidelbergensis* is within the expected range for a single species (Rightmire, 2008). If future studies find the European and African *H. heidelbergensis* fossils different enough to warrant species distinction, the African fossils will be regarded as *Homo rhodesiensis*, with the Kabwe cranium as the type specimen (Rightmire, 2008).

HOMO SAPIENS Linnaeus, 1758
Figures 25.18 and 25.19; Table 25.2

Partial Synonymy *Homo capensis*, Broom, 1918; *Palaeoanthropus palestinensis*, McCown and Keith, 1939; *Homo sapiens neanderthalensis*, Howell, 1978; *Homo sapiens afer*, Howell, 1978; *Homo sapiens capensis*, Galloway, 1937a, 1937b; *Homo helmei*, McBrearty and Brooks, 2000; *Homo sapiens idaltu*, White et al., 2003; *Homo idaltu*, Basell, 2008.

Diagnosis Because of the gradual accumulation of features that today characterize our own species, *Homo sapiens* (considered here to be synonymous with "humans"), it has proven difficult to construct a diagnosis applicable to all members of the lineage, or to identify the point at which the species began (Howell, 1978). If a criterion for inclusion in *H. sapiens* was the possession of features described in some literature as "anatomically modern," this would exclude some extant humans (Lieberman et al., 2002) and much of the late middle through late Pleistocene African hominin sample many would attribute to *H. sapiens*. Although Howell (1978) provided a thorough summary of modern human skeletal anatomy, including many features uniquely found in *Homo sapiens*, but not in *H. neanderthalensis*, or in other species of *Homo*, he emphasized that he was not offering a diagnosis of *H. sapiens*. Subsequent studies have attempted to identify and quantify autapomorphies of *Homo sapiens* (e.g., Day and Stringer, 1982; Stringer et al., 1984; Lieberman, 1995; Lieberman et al., 2002); however, because these features arose sequentially, it is preferable to adopt a lineage-based definition of the species, in which descendants of *H. heidelbergensis* subsequent to the separation from the *H. neanderthalensis* lineage are considered humans, and to view the accumulation of autapomorphies in this context (Lieberman et al., 2002).

Among the autapomorphic traits identified as characteristic of, or unique to, the *Homo sapiens* lineage are limb bones with thin cortical bone and small articular surfaces, presence of a canine fossa, large endocranial capacity, cerebral asymmetry, elevated cranial vault with a high, vertical forehead and greatest width biparietally, and inferred associated expansion of the prefrontal cortex and parietal lobes, with parietal bossing and loss of sagittal keeling and parasagittal flattening, high frontal angle, narrow, high, rounded occipital planum of the occipital bone, strong basicranial flexion with the foramen magnum tucked well under the braincase, expanded middle cranial fossa, associated with inferred expansion of lateral and inferior areas of the temporal lobes that relate to language, reduced, orthognathic face, separation of the supraorbital region from glabella and subdivision of the superior orbital margin into supraorbital and supraciliary portions, inferior orbital plane tilted down and back from the inferior orbital margin, extreme lateral placement of the styloid processes, reduced dental crown size and concomitant reduction in size of alveolar processes of the upper and lower jaws, reduction of cranial robustness, including thinner cranial bones, and expansion of the mental trigon and mental fossae of the mandible to form a bony chin (Howell, 1978; Day and Stringer, 1982; Arsuaga et al., 1999; Lieberman, 1998; Spoor et al., 1999; Lieberman et al., 2002; Schwartz and Tattersall, 2003; Bastir et al., 2008; Pearson, 2008).

Description Survey of the fossil record shows that the features characteristic of anatomically modern humans accumulated progressively in a mosaic fashion, beginning in the late middle Pleistocene and reaching full expression only by the end of the late Pleistocene (Howell, 1978; Habgood, 1989; Stringer, 2002; Trinkaus, 2005; Bräuer, 2008; Pearson, 2008). These features appeared first in Africa and the geographically closely linked Levant at the same time that the distinctive Neanderthal morphological pattern was developing in Europe and western Asia (Stringer, 2002) and when more archaic hominins (i.e., *H. erectus*) still inhabited eastern Asia (Klein, 1995). The fossil record of *Homo sapiens* in Africa is copious, particularly from localities dated to the end of the late Pleistocene and Holocene, making it impossible to comprehensively list and describe all the relevant specimens within the scope of this overview. Table 25.2 provides instead a representative sampling of fossil *Homo sapiens* occurrences on the continent and several from the Levant. Specimens are described as exemplars of archaic, near-modern, and modern human categories, with greatest emphasis on the earlier phases of the lineage, though it should be noted that these phases grade into one another without clear demarcations and that there was considerable morphological heterogeneity at any particular time (Foley and Lahr, 1992).

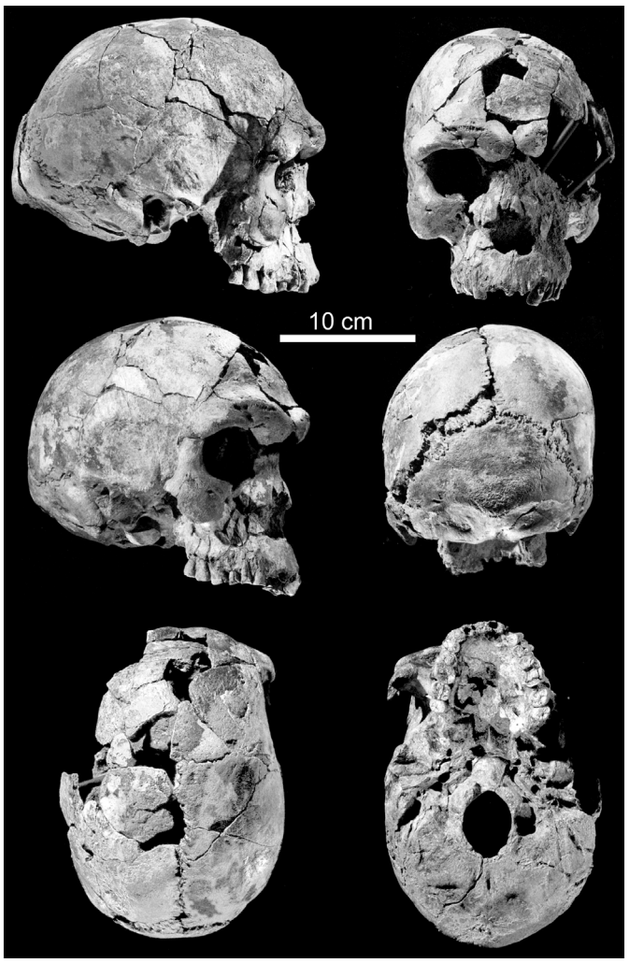


FIGURE 25.18 Holotype of *Homo sapiens idaltu*, cranium BOU-VP-16/1. Courtesy of Tim White.

Archaic humans (early fossil *H. sapiens*) typically exhibit some of the morphological configuration of extant humans, while retaining varying degrees of structural primitiveness. They date from the late middle to early late Pleistocene, and their cultural context is usually Mousterian or Middle Stone Age (McBrearty and Brooks, 2000; Basell, 2008). The oldest of these hominins may be from the Omo Kibish deposits (table 25.2). Omo I, comprised of parts of the skull, dentition, and postcranial skeleton, has a cranium that is robust in comparison with modern human crania, with a prominent glabella, slightly receding forehead, prominent supraorbital torus, and large teeth, accompanied by more derived features such as a rounded occipital profile, contracted nuchal planum with modest muscle markings, a relatively high vault, expanded parietal region and widest point high on the vault, and absence of a sagittal keel and parasagittal flattening (Day, 1969). Its skeleton is morphometrically within the modern human range (but see Pearson, 2000), though it is robustly built with strong muscle markings (Day, 1969; Rightmire, 1976; Stringer, 1978; Day and Stringer, 1982). In contrast to the condition of the Omo I cranium, the Omo II calvaria has greater resemblance to specimens of *Homo heidelbergensis* and is more heavily constructed, with strong muscle markings; it has a receding forehead, large, flat nuchal plane, greater occipital angulation, modest sagittal keel, and shallow parasagittal depressions, and a massive occipital torus accompanied by a transverse supratoral sulcus; nonetheless, its cranial capacity is estimated to be 1,435 cm^3 (Day, 1969; Day and Stringer, 1982). The Omo I postcranials and other remains from Omo Kibish indicate that individuals from the site were of medium to tall stature (ca. 162–182 cm; Pearson, 2000; Pearson et al., 2008a, 2008b). Though Omo I clearly belongs in *Homo sapiens* and neither specimen has anatomical affinities with Neanderthals (Day and Stringer, 1982; *contra* Brose and Wolpoff, 1971), its relationship to Omo II and the phylogenetic position of the latter remain unclear (Fleagle et al., 2008).

An extraordinary set of archaic *H. sapiens* crania, penecontemporaneous with the Omo fossils (table 25.2), was recovered from Herto, Ethiopia. The most complete of these is BOU-VP-16/1, which has a long, high vault. Its more archaic morphology includes a modestly receding forehead, strongly flexed occipital with a prominent external occipital protuberance, large teeth, large, flared pterygoid plates, broad, deep glenoid fossa, very well-developed temporal lines, robust supraorbital region, and great distance between the articular eminence and occlusal plane; however, it also exhibits the advanced features of a divided supraorbital torus, greatest breadth high on the vault, relatively little prognathism, and modest-sized orbits and malars (White et al., 2003). Typical of *H. sapiens* from this

time period, BOU-VP-16/1 and the other adult (BOU-VP-16/2; BOU-VP-16/43) and immature (BOU-VP-16/5) cranial remains from Herto have no special morphometric affinity with any regional modern *H. sapiens* population, but they demonstrate that modern human morphology was developing in Africa prior to the disappearance of Neanderthals from Europe and western Asia (White et al., 2003). Cut marks on these crania reveal the earliest evidence for nonutilitarian defleshing and mortuary practices (Clark et al., 2003).

Also from this time period are hominin remains from Jebel Irhoud, Morocco (table 25.2), including two partial crania (Irhoud 1 and 2), and a juvenile mandible and humerus (Irhoud 3 and 4)(Hublin and Tillier, 1981; Hublin et al., 1987). Although the Irhoud specimens have been considered by some to have Neanderthal affinities (e.g., Ennouchi, 1962, 1963, 1969; Mann and Trinkaus, 1973), this has been largely discounted as only a superficial resemblance (e.g., Briggs, 1968; Hublin and Tillier, 1981; Hublin et al., 1987; Hublin, 1992, 2001). Instead, the Irhoud specimens are typical of other late middle Pleistocene *H. sapiens* from Africa, in exhibiting a mix of archaic and advanced features that anticipates the morphology of modern humans. Irhoud 1 has a long, low cranial vault and large upper face. It also possesses a weak occipital torus and moderately elongate nuchal planum. The interorbital distance is broad. Cranial capacity was recalculated at a modest 1,305 cm^3 (Holloway, 2000), after an initial estimate of 1,480 cm^3 by Anthony (1966). However, the forehead is only slightly receding, the frontal attains a great vertical dimension at bregma, and the lower face is gracile. In addition, although the supraorbital tori are arched, robust, and continuous across glabella, they thin out laterally. The parietals rise vertically and are expanded superiorly (Hublin, 1992), so the greatest width is high on the cranium, and in posterior view the cranial vault has a pentagonal profile (Hublin, 2001). Alveolar prognathism is pronounced but not outside the modern human range, and there is no midfacial prognathism (Hublin, 1992). Irhoud 2 has an even more modern-looking frontal profile, and its supraorbital tori are more separated by glabella than in Irhoud 1. Conversely, Irhoud 2 appears more primitive in the posterior outline of the cranial vault and extent of the nuchal planum (Hublin, 1992). X-ray synchrotron microtomography of the teeth in Irhoud 3 shows that dental development and tooth eruption were like that of modern humans, the oldest evidence of modern life history parameters such as prolonged growth and a correlated increased juvenile learning period (Smith et al., 2007). This mandible has a true chin, small condyle, and the height of the corpus decreases posteriorly, but primitively it has large teeth, a genioglossal fossa, and a planum alveolare (Hublin, 2001).

Hominin remains from the Levantine sites of Jebel Qafzeh and Skhul (Israel) provide further evidence of the development of *H. sapiens* features in the late middle Pleistocene–earliest late Pleistocene (table 25.2), and represent the first known migration of *Homo sapiens* out of Africa proper. At Skhul, at least 10 individuals were recovered (Schwartz and Tattersall, 2003), most from intentional burials (Garrod and Bate, 1937). The best-preserved adult skull is Skhul V, which exhibits a high, rounded vault, vertical forehead, diminished nuchal planum (compared with *Homo heidelbergensis* crania), expanded parietal eminences, a posteriorly placed lateral origin of the petrotympanic crest, and large mastoid processes, in combination with more archaic features such as barlike supraorbital tori that continue across an anteriorly prominent glabella, large teeth, and a very broad interorbital area (McCown and Keith, 1939; Howells, 1970; Harvati, 2003; Schwartz and Tattersall, 2003). The mandible of this individual has no incisive alveolar planum, the corpus decreases in height posteriorly, and although it has a projecting "chin," the jaw lacks a proper mental trigon or mental tubercles (Schwartz and Tattersall, 2003), its ramus is quite high and vertical, and the coronoid process is very high. Other crania (e.g., Skhul II, IV) also show archaic features, with greater development of the supraorbital region, thicker bones, and lower crania with longer nuchal planes and more receding foreheads. The juvenile cranium Skhul I has a comparatively more modern aesthetic about it: it has a vertical forehead, raised cranial vault, and parietal expansion producing a pentagonal outline in posterior view. Estimated brain sizes of the more complete adult crania are impressive, ranging from 1,520 to 1,590 cm^3 (Holloway, 2000).

Fourteen hominin individuals have been recovered from Jebel Qafzeh, most from intentional graves in Mousterian contexts (Vandermeersch, 1981). There is some variation in this sample in the degree of development of supraorbitals and mental trigons, but the overall expression of anatomically modern *H. sapiens* features is unmistakable (Vandermeersch, 1981; Stringer, 1974; Trinkaus, 1984b; *contra* Brose and Wolpoff, 1971). The crania are generally long, high vaulted, with vertical to near-vertical frontals and rounded occipital profiles. Parietal expansion and bossing is obvious, as is reduction of the lower face. In some individuals (Qafzeh 9, 11), the supraorbital region is bipartite, the mastoid process is large and juxtamastoid eminence small, and the mandible exhibits a true mental trigon or chin (Harvati, 2003; Schwartz and Tattersall, 2003). Endocranial volume is capacious, calculated as 1,568 cm^3 for Qafzeh 6 and 1,508 cm^3 for Qafzeh 9 (Vandermeersch, 1981; Holloway, 2000). In contrast to penecontemporaneous Neanderthals from the region, postcranial features of the Skhul and Qafzeh hominins are far more like those of modern humans (e.g., higher neck-shaft angles of the femur, short, stout superior pubic rami, position of the external obturator groove, lower limb cross-sectional anatomy; Ben-Itzhak et al., 1988; Smith et al., 1983, 1984; Rak, 1990; Trinkaus, 1992, 1993a). The differences in femoral angles have a high correlation with varying activity levels during development, and from this it can be implied that adults endured less femoral strain and juvenile individuals from the Qafzeh-Skhul population(s) underwent lower levels of locomotor activity and greater age-grade division of activities than Neanderthal juveniles from the region (Ruff and Hayes, 1983; Trinkaus, 1993a). In addition, principal components analysis of crania demonstrate that Qafzeh 6 and Skhul 5 fall within a grouping of *Homo sapiens* crania from northern Africa dated between 35,000 and 5,000 y, and not with the Neanderthal sample (Bräuer and Rimbach, 1990). Dental analysis of prey species shows that these Levantine *H. sapiens* may have had a more efficient strategy of resource exploitation than Neanderthals from the same region and hunted more seasonally, demonstrating that similarities in stone tool cultures did not necessarily correlate with identical behaviors (Lieberman and Shea, 1994). Measurements estimated from the ratio of femoral length to stature indicate that the Qafzeh-Skhul hominins were reasonably tall, with adult heights of between 164 and 193 cm (Feldesman et al., 1990).

The persistence of archaic features and considerable morphological heterogeneity in the African late Pleistocene (Stringer, 2002) is evidenced in specimens such as those from Klasies River Mouth in South Africa, and L.H. 18 from the Ngaloba Beds at Laetoli, Tanzania. Though not as old geologically as the Herto hominins (table 25.2), L.H. 18 has a more primitive appearance, with a relatively low vault, small mastoid process,

marked recession of the forehead, slight keeling of the frontal, inferred facial prognathism, occipitomastoid crest, thick cranial bones, central occipital torus, and low cranial capacity (1,200 cm^3)(Day et al., 1980; Rightmire, 1984). More advanced traits in the specimen include a rounded occipital profile, low position of inion, parietal bossing, presence of a nasal spine, canine fossa, absence of parasagittal flattening, and a divided supraorbital torus (Day et al., 1980; Rightmire, 1984).

Fossils from Klasies River Mouth, South Africa, are close in age to the Ngaloba hominin (table 25.2), and derive from Middle Stone Age contexts (Singer and Wymer, 1982). These have been prominent in the debate about the antiquity of the emergence of modern humans in Africa, with some workers stressing their modern human features (e.g., Singer and Wymer, 1982; Rightmire and Deacon, 1991; Bräuer et al., 1992) and others denying their modernity (e.g., Wolpoff et al., 1994). The debate is fueled in part by the degree of variation in the sample, particularly in mandibular morphology (Grine et al., 1998). Mandibular specimen KRM 41815 (SAM-AP 6222) is small but robust, with remnants of evidently modest-sized teeth. The ramus has an anteriorly projecting expansion of the coronoid process, and a broad, shallow sigmoid notch. The corpus decreases in height posteriorly. Although the chin is not anteriorly prominent, nonetheless it is well demarcated, with a clear mental trigon flanked by shallow depressions. In contrast, the anterior profile of the symphyseal region of mandible SAM-AP 6223 is nearly vertical, and its mental trigon is more weakly demarcated (Schwartz and Tattersall, 2003). Detailed comparative morphological examinations of the malar (KRM 16651 = SAM-AP 6098) and temporal (SAM-AP 6269) specimens from the site show that they are within the range of variation observed in modern humans (Bräuer and Singer, 1996; Grine et al., 1998). The supraorbital region of the frontal fragment from Klasies River Mouth (KRM 16425) is divided into supraorbital and superciliary portions and is essentially modern (Grine et al., 1998). Variability in the hominin sample from this site extends to the postcranium, which is described as exhibiting a mix of modern and archaic features (Churchill et al., 1996; Pearson and Grine, 1997; Pearson, 2000).

The partial cranium (M.A.R. 89.4.1.3, or Dar es Soltane 5) from Dar es Soltane II, Morocco is reminiscent of the Ngaloba specimen, though it may be much younger geologically (table 25.2). It clearly is not anatomically modern in all respects, attesting to the persistence of archaic morphology in *H. sapiens* well into the late Pleistocene. Its frontal is slightly receding and bounded by thick, arched supraorbital tori, which project more anteriorly than glabella, it has a broad interorbital area, the nasals are deeply set under glabella, the articular fossa is deep, and cranial bones are moderately thick, imparting a primitive aspect to the cranium (Ferembach, 1976a; Bräuer, 1984). Nonetheless, the supraorbitals are each faintly subdivided into medial and lateral segments, it has canine fossae, and the frontal vault rises to impressive height near bregma (Schwartz and Tattersall, 2003; Trinkaus, 2005).

By the latter half of the late Pleistocene in Africa, hominins were near-modern human anatomically, but usually still relatively robust in build and dimensions and generally not morphometrically affiliated with a particular modern human population. The skeleton from Nazlet Khater, Egypt (table 25.2), is typical of this group of hominins. The postcranial anatomy of this specimen is indistinguishable from that of modern humans, but the skull exhibits strong alveolar prognathism, a robust mandibular corpus, very great breadth of the mandibular ramus, and "does not display clear affinities with modern Negroid populations" (Thoma, 1984; Pinhasi and Semal, 2000, p. 282; Trinkaus, 2005). Nonetheless, in principal components analysis of cranial variables, Nazlet Khater and Dar es Soltane 5 fall within the range or closer to anatomically modern humans than to Neanderthals, or closer than Neanderthals are to modern humans, including Upper Paleolithic Europeans (Bräuer and Rimbach, 1990). Some of the features found in the Nazlet Khater skull (anteriorly positioned zygomatic; exceptionally wide mandibular ramus) are shared with the oldest known early modern human in Europe, Pestera cu Oase 2, from Romania, dated to ca. 40,000 y (Rougier et al., 2007).

A cranium from Hofmeyr, South Africa, is of similar antiquity to Nazlet Khater (table 25.2). This specimen is large, robust, and retains primitive features such as a broad nasal opening, glabellar prominence, a continuous, moderately well-developed supraorbital torus, large molars, and a broad frontal process of the maxilla (Grine et al., 2007). Though it also exhibits many modern human features, such as a steeply vertical frontal, high, rounded braincase with parietal expansion and greatest width high on the parietals, and has an associated mandibular fragment lacking a retromolar gap, its overall construction does not match that of crania from extant African populations; however, 3-D geometric and linear morphometric analyses show a close affinity between the Hofmeyr specimen and Upper Paleolithic European crania (Grine et al., 2007). This supports the idea that the ancestry of Upper Paleolithic Eurasians was rooted in Africa, as previously indicated by the work of Bräuer and Rimbach (1990). While Wolpoff (1989) has argued to the contrary that early humans from Africa exhibit features linking them closely with contemporary African populations, the evidence for this is unconvincing (Habgood, 1989).

Hominin fossils from Border Cave, South Africa also belong in this group of near moderns. A very fragmentary cranium, BC 1, has thick, arched supraorbital tori that are not subdivided and that project anterior to glabella, resembling the Dar es Soltane II cranium in this regard. It has a wide interorbital region, and prominent mastoid and supramastoid crests. However, the frontal rises steeply vertically and is "bulging," glabella is little developed, and the vault is large (cranial capacity ca. 1,510 cm^3; Holloway, 2000) and high (Cooke et al., 1945, de Villiers, 1973; Rightmire, 1979; Habgood, 1989). The mandibles have moderately developed chins, corpora that recede in height posteriorly, and lack retromolar gaps, but they have anteroposteriorly expanded rami with high, shallow notches between the coronoid processes and condyles. Statistical analyses showing close affinity between BC 1 and modern African populations such as southern African Negro and Khoisan (e.g., de Villiers 1976; Rightmire, 1979; de Villiers and Fatti, 1982) are statistically suspect and flawed by comparatively including only modern African populations that it was assumed a priori had a phylogenetic relationship with the Border Cave hominin (Campbell, 1980; Habgood, 1989).

A slightly older *H. sapiens* specimen is the juvenile skeletal burial from Taramsa Hill, Egypt (table 25.2). The long bones are slender, and the cranium exhibits a number of modern features such as a high, vertical forehead, rounded occipital, divided supraorbital, and expanded parietals, but it retains a relatively large, prognathic face and large teeth (Vermeersch et al., 1998). This appears to be the oldest known intentional burial north of the equator in Africa (Vermeersch et al., 1998).

By the end of the late Pleistocene–early Holocene, most hominins (the exceptions are *H. neanderthalensis* in Europe, and late-surviving *H. erectus* and *H. floresiensis*, both in Indonesia) were essentially anatomically modern, and their accompanying

archeological record of Late Stone Age or Upper Paleolithic and Epipaleolithic cultures exhibits the signs of modern human–like cognitive skills and behaviors (including, at Wadi Kubbaniya, Egypt, and Jebel Sahaba, Sudan, evidence of murder or warfare; Wendorf, 1968; Wendorf and Schild, 1986; Thorpe, 2003). Hominins from this time period include a number of specimens from the Upper Semliki Valley, Democratic Republic of Congo, dated to the late Pleistocene (e.g., Is 11 fossils) and Holocene (e.g., Is 1-1 and 1-2; Ky 2), respectively (table 25.2; Boaz et al., 1990). The most complete of these, Is 1-1, includes a cranium (figure 25.19), mandible, and partial skeleton from an adult male. In all respects, the morphology of this individual matches that of anatomically modern humans, and the results of multivariate discriminant analysis show that it closely resembles modern Bantu or Central African Negroid populations in its cranial anatomy (Boaz et al., 1990). This fits a pattern in which other African fossil *Homo sapiens* from this interval (table 25.2) routinely have strong morphometric affinities with extant African populations (Rightmire, 1975).

Remarks A number of models have been advanced to explain the origin and phylogeny of *Homo sapiens*, including the African Replacement Model, which states that *H. sapiens* first arose in Africa, migrated to other regions of the Old World, and replaced archaic, indigenous populations in these regions with little or no interbreeding; the African Hybridization and Replacement Model, which allows for some degree of genetic exchange between African emigrants and populations being replaced; the Assimilation Model, which posits an African origin for humans and subsequent significant gene flow between regions, but denies an important role for migratory replacement; and the Multiregional Evolution Model, which denies a recent African origin for modern humans, emphasizing instead regional genetic and morphological continuity over time and gene flow between regions, with humans emerging contemporaneously in different regions (Aiello, 1993; Stringer, 2002).

As shown, the African (and Levantine) fossil record supports an African origin for *Homo sapiens*. Skeletal traits associated with modern humans first appeared in Africa during the late middle Pleistocene–early late Pleistocene, long before evidence for this morphology in other parts of the Old World (Foley and Lahr, 1992), and well before the disappearance of Neanderthals in Europe (Aiello, 1993). In addition, the earliest *H. sapiens* populations outside Africa resemble contemporaneous African *H. sapiens* cranially and postcranially (Bräuer and Rimbach, 1990; Holliday and Trinkaus, 1991; Ruff, 1994; Holliday, 1997, 1998, 2000; Pearson, 2000; Grine et al., 2007), suggesting that migration "out of Africa" played an important role in regional populational transformations from archaic hominins to *Homo sapiens* (McBrearty and Brooks, 2000).

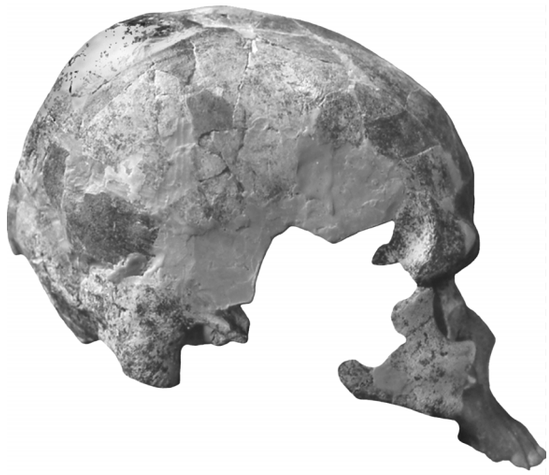


FIGURE 25.19 Lateral view of anatomically modern Homo sapiens cranium Is 1-1 from Ishango, Democratic Republic of Congo. Courtesy of Noel Boaz.

The central importance for Africa in the establishment of *H. sapiens* throughout the Old World in the Pleistocene is further supported by genetic studies, which indicate that all modern humans share a late Pleistocene African ancestor (e.g., Wainscoat et al., 1986; Cann et al., 1987, 1994; Mountain et al., 1993; Stoneking, 1993; Stoneking et al., 1993; Bowcock et al., 1994; Cavalli-Sforza et al., 1994; Nei, 1995; Tischkoff et al., 1996; Ingman et al., 2000; Pearson, 2004; but see Templeton, 1993; Relethford, 1995). Study of the mitochondrial (mt) haplogroup M, originally thought to be an ancient marker of East Asian origin, demonstrated that this haplogroup is rooted in eastern Africa; its distribution and variation indicate migration of *H. sapiens* from Africa to Asia via western India around 50,000 years ago (Quintana-Murci et al., 1999). In contrast, mtDNA studies of Neanderthals reveal an ancient separation time of their lineage from the one leading to modern humans, within the interval 741,000–317,000 years ago (Krings et al., 2000; Ovchinnikov et al., 2000). Furthermore, the amount of gene flow needed to spread modern human morphology among small peripheral populations is incompatible with the maintenance over time of regional features in those populations (Stringer, 2002). Thus, the balance of evidence does not support the Assimilation and Multiregional Evolution Models. Genetic evidence also does not generate much support for the Hybridization and Replacement Model (Pearson, 2004).

The *Homo sapiens* lineage in Africa forms a good paleospecies: it is morphologically more advanced than *Homo heidelbergensis* and *Homo erectus*, differs anatomically substantially from the penecontemporaneous Neanderthal lineage, and exhibits progressive accumulation of features that characterize modern humans. As with many other basal segments of mammalian clades, however, recognition of the earliest members of the lineage is difficult because of the retention of a great number of plesiomorphies. Moreover, taxonomic "splitters" may prefer to emphasize the primitive features in these early modern humans by subdividing the lineage formally (cf. McBrearty and Brooks's [2000] use of *"Homo helmei"* and *"Homo sapiens"*). Nonetheless, it appears that the *Homo sapiens* lineage emerged in the latter part of the middle Pleistocene, close in time to the beginnings of Middle Stone Age (MSA) culture, which was distinguished by prepared core technology, and flake and blade tools including unifacial or bifacial projectile points (McBrearty and Brooks, 2000). Although the first appearance of the MSA is dated by $^{40}Ar/^{39}Ar$ in the Ethiopian Rift to >276,000 years (Morgan and Renne, 2008), older than the corpus of fossil evidence for archaic *Homo sapiens* (table 25.2), specimens such as Florisbad (Dreyer, 1935; Grün et al., 1996), and possibly the Guomde hominin, KNM-ER 3884 (Bräuer et al., 1992b)(closer in age to the beginning of the MSA; table 25.2), seem more advanced than other specimens assigned to *Homo heidelbergensis* and could represent the beginnings of the *Homo sapiens* lineage.

While the origin of *Homo sapiens* may have been coincident with the beginning of MSA culture, the connection between these cultural and anatomical changes is obscure, since Mousterian and MSA stone tool kits found with early *H. sapiens* are technologically identical to stone tool industries of Neanderthals (Klein, 1995). There is ongoing debate about the

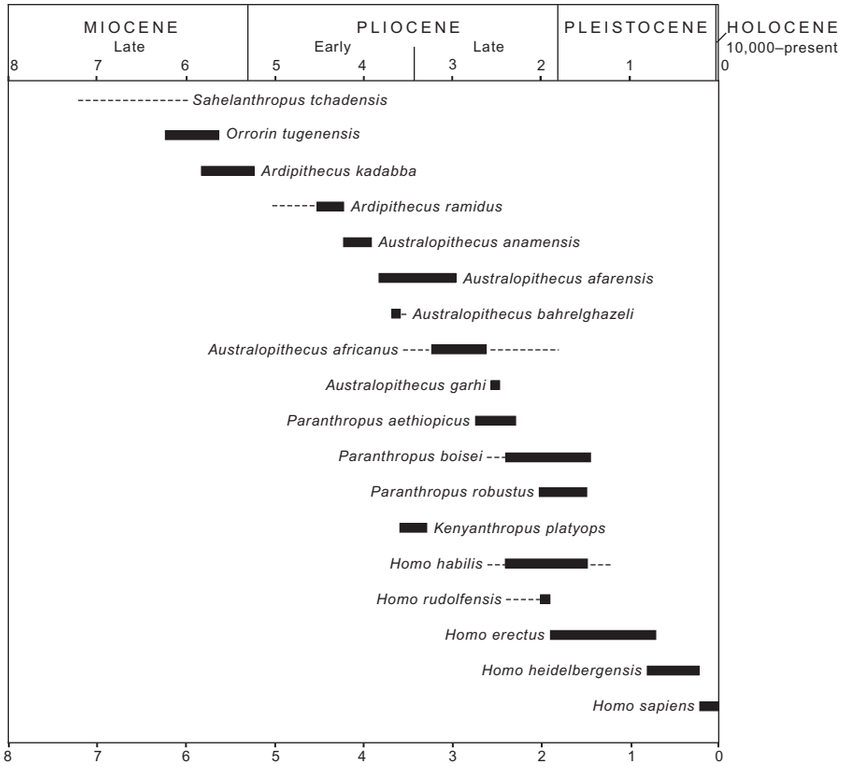


FIGURE 25.20 Time line of hominin species' ranges.

relationship between the emergence of modern human features and cultural change. Changes in African *H. sapiens* cranial anatomy seem to have started with increased brain size and expansion of the frontal, parietal, and perhaps temporal regions, implying a significant reorganization of the brain and cognitive abilities, as well as with diminution of the lower face. This was followed by "modernization" of the occipital profile, lessening of midfacial robusticity, and thinning and bipartite division of supraorbital tori. Tooth size reduction and lessening of mandibular robustness occurred more recently, toward the end of the late Pleistocene. Some of the most recent transformations of human morphology were probably associated with new methods of processing food. If the acquisition of modern human morphology was not causally related to equally unique and modern behaviors, what was the reason for anatomical transformation into *H. sapiens*, and when did modern human behavior begin?

In the current debate, the Human Revolution Model posits that the first unequivocal signs of fully modern cognitive and communicative abilities occurred in the African archeological record relatively late, around 50–40,000 years ago, driven by largely undetectable reorganization of human neurological networks (e.g., Klein, 1992, 1995, 2000). The evidence for this relatively recent cognitive and technological shift is found in cultural factors associated with the Late Stone Age (LSA) and Upper Paleolithic, including customary shaping of bone, antler, shell, and ivory into formal artifact types; expression of ritual in art and elaborate graves; spatial organization of camp floors; greater diversity and standardization of artifact types; capability of blade and microlithic production; increased geographic range and widespread trade networks; personal ornamentation; and capability of fishing (Klein, 1992, 1995, 2000). In contrast, others (e.g., Lahr and Foley, 1998; McBrearty and Brooks, 2000) have argued that the African Middle Stone Age was not just a regional variant of Mousterian culture, and that modern cultural features had been gradually accumulating throughout the duration of the MSA, in phase with the mosaic development of modern human morphology. If this view is correct, *H. sapiens* cognitive changes, increased utilization of coastal resources (e.g., Walter et al., 2000), and migratory patterns may have been driven by cycles of cooling and aridity, correlated with Northern Hemisphere glacial cycles (Carto et al., 2009). These climatic pulses are connected to episodic emigrations of humans from Africa throughout the late Pleistocene, leading to establishment of *Homo sapiens* as a global species by the end of the epoch (Carto et al., 2009).

Summary

The three earliest purported hominin species (*Sahelanthropus tchadensis*, *Orrorin tugenensis*, and *Ardipithecus kadabba*) are characterized by subtly modified canines relative to fossil and extant hominoids, molars as large or slightly larger than those of *Pan*, slightly thicker enamel than is found in extant African apes, and provisional evidence for bipedality. Paleoenvironmental contexts suggest at least some heterogeneity with grassland, woodland and forest represented at hominin-bearing sites. The specific ecological niches of hominins within these mosaic environments, however, remain unknown.

Haile-Selassie et al. (2004a, 2004b) have suggested that only one genus may be sampled thus far in the late Miocene, and it is not unexpected that the systematics of the late Miocene taxa are debated, given such sparse material. The record in the early Pliocene is less ambiguous taxonomically and craniodental evidence supports three time successive species with ancestor-descendant relationships possible: *Ardipithecus ramidus* (itself a

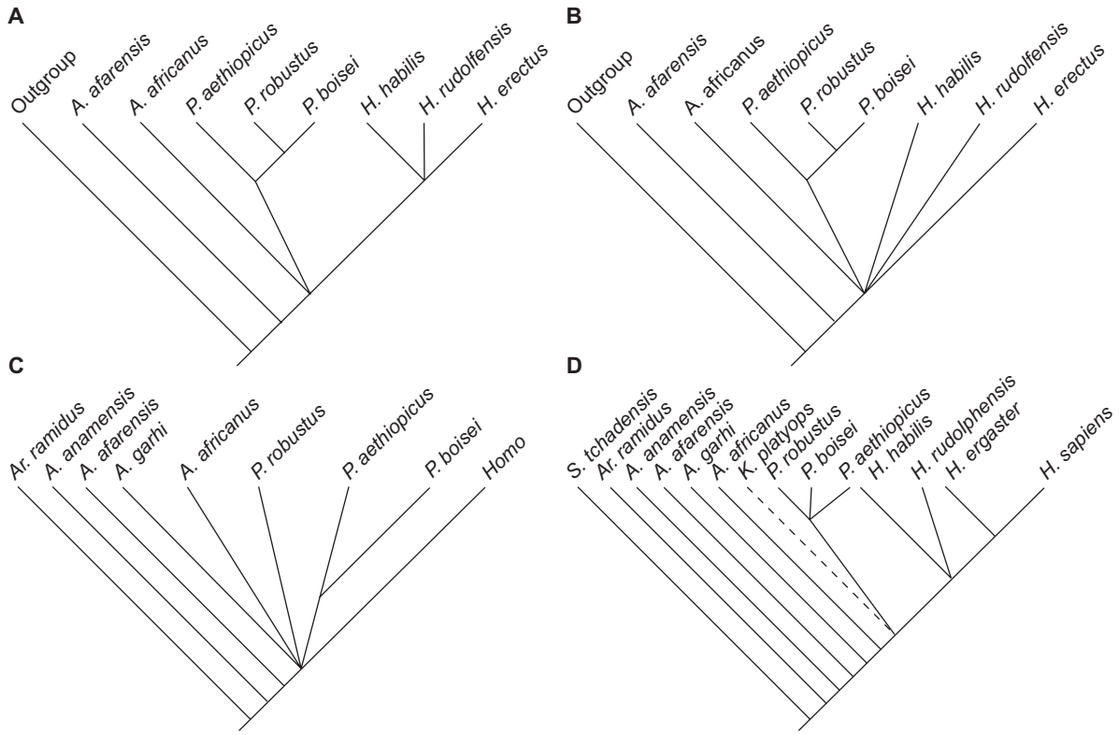


FIGURE 25.21 A) Strict consensus of the three shortest trees found by PAUP's branch and bound algorithm in phylogenetic analysis published by Kimbel et al., 2004. B) Strict consensus of the five shortest trees found by PAUP's branch and bound algorithm in phylogenetic analysis published by Kimbel et al., 2004. C) Cladogram published by Asfaw et al., 1999, showing an unresolved polychotomy as a major feature. D) Strict consensus of the most parsimonious cladograms published by Strait and Grine, 2004. The dashed line reflects these authors' uncertainty as to whether *Kenyanthropus* is a distinct species.

likely descendant of *Ardipithecus kadabba*), *Australopithecus anamensis*, and *Australopithecus afarensis*. If these taxa are related, it suggests that over time there was directional selection for postcanine megadonty, and a concomitant change in canine function and morphology (i.e., canines become more incisiform) as the premolars became molarized. Postcranially, *Ardipithecus* can now be distinguished in numerous respects from *Australopithecus*, raising the possibility of rapid aquisition of bipedal features. Alternatively, *Ardipithecus* may not be the sister taxon to *Australopithecus*.

The mid-Pliocene finds the first record of hominins in southern Africa. *Australopithecus africanus* is craniodentally derived relative to *Au. afarensis* in several respects, and shares features of the jaw, face, and basicranium with later hominins. Both *Au. afarensis* and *Au. africanus* are well represented postcranially and are incontrovertibly terrestrial bipeds, although the details of their gait and degree of commitment to bipedalism are subjects of ongoing discussion. The mid-Pliocene also has two controversial taxa, *Kenyanthropus platyops* and *Au. bahrelghazeli*, considered by some to be conspecific with *Au. afarensis*.

As figure 25.20 reveals, the late Pliocene/early Pleistocene is the only part of the African hominin record where multiple lineages clearly co-occur in time and possibly space, in southern and East Africa. This runs counter to prevailing notions of the hominin diversification being rather bushy (see also White, 2003, 2009) although future finds may increase evidence for cladogenesis. Overlap of multiple taxa makes attribution of fossil postcrania and stone tools with dental remains problematic, however, it is apparent that hominins of this time were experimenting with new and different adaptive pathways. Both *Au. garhi* and *Paranthropus* evolve even larger masticatory apparatuses than found in earlier australopiths, allowing these taxa to puncture, crush and grind food with abrasive and/or hard mechanical properties. Encephalization and reduction in tooth size also evolve during this period, and fossils exhibiting these traits are almost invariably associated with stone tool manufacture and placed in one of three recognized species of early *Homo* that, somewhat ambiguously, co-occur as early as 1.9 Ma. More long-legged and bipedally efficient body plans also appear in the late Pliocene, but while *Homo erectus* is known to possess derived postcrania due to associated skeletal material, *Homo habilis*, *Homo rudolfensis*, and *Paranthropus* have few postcrania definitively assigned to them.

Environmental mosaicism is associated with all hominins during this period, although there is a general trend of increasingly frequent associations between hominins and more open environments over time. The instability and variability of such habitats is itself a likely selective force in hominin evolution contributing to behavioral plasticity and a generalist strategy associated with the tribe's success in Africa and worldwide.

Phylogenetic hypotheses abound for this period (figure 25.21). Monophyly of South and East African *Paranthropus* species is supported by most parsimony-based analyses but it remains plausible that the forms evolved independently. There is no clear candidate among known australopith-grade hominins for an ancestral relationship to genus *Homo*, although *Au. africanus* and *Au. garhi* seem more closely related than *Au. afarensis*. *Paranthropus* is deemed too derived to have played an ancestral role, but some analyses (figure 25.21) place *Paranthropus* as the sister clade to *Homo*. Finally, if *Homo habilis* and

Homo rudolfensis are two different species, then it is presently unclear which is more closely related to *Homo erectus*.

There is general agreement that *Homo erectus*, *Homo heidelbergensis*, and *Homo sapiens* represent an evolving lineage within Africa, although the species boundaries on either side of *H. heidelbergensis* are obscure. Behaviorally, this lineage became ever more complex, as brain size increased dramatically and tools became more sophisticated. Many have argued that behavioral evolution took a punctuated leap sometime after the origin of *H. sapiens* ca. 200,000 years ago, so that humans were acquiring anatomically modern features before exhibiting fully modern behavior. Archeological evidence in Africa suggests that modern behavior may have accreted slowly initially, then exploded after a critical threshold was reached. Africa was thus the crucible that selected for virtually all of the adaptations that allowed one hominin taxon to spread into every biome on Earth.

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