

Early *Homo*

Who, When, and Where

by Susan C. Antón

The origin of *Homo* is argued to entail niche differentiation resulting from increasing terrestriality and dietary breadth relative to the better known species of *Australopithecus* (*A. afarensis*, *A. anamensis*, *A. africanus*). I review the fossil evidence from ~2.5 to 1.5 Ma in light of new finds and analyses that challenge previous inferences. Minimally, three cranial morphs of early *Homo* (including *Homo erectus*) exist in eastern Africa (1.9–1.4 Ma), with at least two in southern Africa. Because of taphonomic damage to the type specimen of *Homo habilis*, in East Africa two species with different masticatory adaptations are better identified by their main specimen (i.e., the 1813 group and the 1470 group) rather than a species name. Until recently, the 1470 group comprised a single specimen. South African early *Homo* are likely distinct from these groups. Together, contemporary early *H. erectus* and early *Homo* are bigger than *Australopithecus* (~30%). Early *H. erectus* (including recently discovered small specimens) is larger than non-*erectus Homo* (~15%–25%), but their size ranges overlap. All early *Homo* are likely to exhibit substantial sexual dimorphism. Early *H. erectus* is less “modern” and its regional variation in size more substantial than previously allowed. These findings form the baseline for understanding the origin of the genus.

The origins of the genus *Homo* and the factors that may have led to its appearance remain murky. In the past two decades, the idea of increased behavioral flexibility in our early forebears (Potts 1988) and increased diet quality and ranging (Antón, Leonard, and Robertson 2002; Shipman and Walker 1989) have become cornerstones of how we understand the origin and evolution of *Homo* before we left Africa. These ideas in turn have emphasized the importance of enlarging brain and body size, decreases in sexual dimorphism, somewhat expanded ontogenetic periods, increases in energetic requirements, and increased cooperation during the first million years or so of our history (Aiello and Key 2002; Dean and Smith 2009; Dean et al. 2001). Yet more recent fossil finds call into question some of these trends. New fossils in East Africa, Georgia, and Indonesia suggest large ranges of size and perhaps shape variation in *Homo erectus* sensu lato and hint at local adaptation and short-term accommodation as an important yet underappreciated contributor to the morphological picture seen in the fossil record (Antón et al. 2007; Potts et al. 2004; Rightmire, Lordkipanidze, and Vekua 2006; Simpson et al. 2008; Spoor et al. 2007). Although the record is patchier, there is also considerable variation among earlier *Homo*, and arguably several species are represented (Curnoe 2010; Leakey, Tobias, and Napier 1964; Leakey et al. 2012;

Schrenk, Kullmer, and Bromage 2007; Stringer 1986; Wood 1991) even if there is little agreement as to their composition.

Any understanding of the origin and evolution of *Homo* must build from the primary data of the fossil record. To frame what comes later in this special issue, here I discuss how the genus may be defined relative to other hominin genera. And within our genus I consider the morphology, location, and age of the individual representatives of early *Homo* up to and including *H. erectus*. The taxa of interest here are those commonly referred to as *Homo habilis* sensu lato and *H. erectus* sensu lato (table 1; fig. 1). The former group is often split into multiple taxa, usually *H. habilis* and *Homo rudolfensis*, but others, such as *Homo microcranus* (for KNM-ER 1813) and *Homo gautengensis* (for Stw 53) have also been suggested. The *H. erectus* group is also sometimes split into *Homo ergaster* for the early African and Georgian material and *H. erectus* for the Asian, although a consensus seems to be building for recognizing just one species, *H. erectus* (Antón 2003; Baab 2008; Rightmire 1990). Given this flux in species composition, I advocate that particular attention must be paid to individual fossil data and ranges of variation in size and shape in order to build an explicit picture of what we can and cannot know about fossil taxa and how what we think we know changes depending on the included data points of a taxon.

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Recognizing Early *Homo*

A biological genus comprises closely related species, and although the protocol for doing this is not strictly codified in

Table 1. Fossils attributed as type specimens to named species of early *Homo*

Umbrella species and type specimen	Species name	Publication	Country of type
<i>Homo habilis</i> sensu lato:			
OH 7	<i>Homo habilis</i>	Leakey, Tobias, and Napier 1964	Tanzania
KNM-ER 1470	<i>Homo rudolfensis</i>	Alexeev 1986	Kenya
KNM-ER 1813	<i>Homo microcranous</i>	Ferguson 1995	Kenya
Stw 53	<i>Homo gautengensis</i>	Curnoe 2010	South Africa
<i>Homo erectus</i> sensu lato:			
Trinil 2	(<i>Pithecanthropus</i>) <i>erectus</i>	Dubois 1894	Indonesia
Zhoukoudian 1	<i>Sinanthropus pekinensis</i>	Black 1927	China
Ngandong 1	<i>Homo soloensis</i>	Openoorth 1932	Indonesia
Perning 1	<i>Homo modjokertensis</i>	Von Koenigswald 1936	Indonesia
Swartkrans 15	<i>Telanthropus capensis</i>	Broom and Robinson 1949	South Africa
Ternifine 1	<i>Atlanthropus mauritanicus</i>	Arambourg 1954	Algeria
OH 9	<i>Homo leakeyi</i>	Heberer 1963	Tanzania
KNM-ER 992	<i>Homo ergaster</i>	Groves and Mazek 1975	Kenya
Dmanisi 2600	<i>Homo georgicus</i>	Gabunia et al. 2002	Georgia

Note. Species listed by umbrella taxon in chronological order of publication. The most commonly used species appear in bold.

zoological nomenclature, it has been argued that a genus “should be defined as a species, or monophylum, whose members occupy a single adaptive zone” (Wood and Collard 1999: 66). Such a definition combines the cladistic requirement of monophyly for genera with a means of deciding (the adaptive zone) where to recognize the base of the genus. Such a definition is thus both prudent and pragmatic if somewhat problematic to apply. The main problem is how to assess the “adaptive zone,” especially in light of the probability that the full suite of characters associated with such a zone is likely to have evolved in a mosaic fashion rather than appearing full blown at the base of the genus.

Several morphological differences distinguish fossil members of the genus *Homo* from those of *Australopithecus* and *Paranthropus*,¹ including reduction in tooth and jaw size, reorganization of craniofacial morphology, and perhaps changes in body shape and size (Kimbel 2009; Rightmire and Lordkipanidze 2009; Wood 2009). And these physical differences have been taken to suggest underlying adaptive shifts at the origin of the genus *Homo*, most or all of which have energetic and life history implications (e.g., McHenry and Coffing 2000). Thus, the adaptive zone of *Homo* has been variously defined, implicitly or explicitly, to relate either to cranial expansion and masticatory diminution (e.g., Kimbel 2009; Kimbel, Johanson, and Rak 1997; Kimbel et al. 1996; Leakey, Tobias, and Napier 1964) and/or to increased locomotor efficiency and ranging (Wood 2009; Wood and Collard 1999) relative to *Australopithecus*.

Using the above definition of a genus, Wood and Collard (1999; see also Collard and Wood 2007; Wood 2009; Wood

and Baker 2011) proposed to remove two species, *Homo habilis* and *Homo rudolfensis*, from the genus and place them into *Australopithecus*. Their criteria for distinguishing species of *Homo* from those of *Australopithecus* were based on finding six classes of characteristics that were more similar to the condition in *Homo sapiens* than to that of *Australopithecus africanus* (the type species of each genus). The first criterion is monophyly. The last is an extended period of growth and development. The remaining four criteria are more explicitly related to the adaptive zone; three to reconstructions of body mass, shape, and proportions and one to jaw and tooth proportions as scaled to body-size-adjusted brain size. Three of the six are not assessable in *H. rudolfensis*. And those that are assessable in *H. rudolfensis* or *H. habilis* are contested (see Holliday 2012). That aside, judging inclusion in a genus based on the association with its most derived member would seem to preclude the possibility of mosaic evolution in its earlier members. Thus, the specific ways in which *H. rudolfensis* and *H. habilis* are like other members of the genus, such as relative brain size, are trumped by their dissimilarity to *H. sapiens*.

While monophyly must be maintained and identifying adaptive zones will always be somewhat subjective, I favor recognizing and fully weighting the incipient characters of the adaptive zone; Wood and Baker (2011) refer to this as a “bottom-up” approach. Genus *Homo* is recognized, then, on the basis of the following mostly derived craniodental characters relative to *Australopithecus* as have been outlined and more fully described by others.

1. *Cranial expansion*. Size-adjusted capacity relative to orbit size is above 2.7 (Collard and Wood 2007; Wood and Collard 1999). In addition or independently, there may be evidence of endocranial expansion or asymmetry relative to *Australopithecus* (LeGros Clark 1964; Rightmire and Lordkipanidze 2009).

2. *Shape of the face and palate*. The palate is deep and broad. The anterior maxillary profile, as seen from above, is round

1. While it is recognized that *Australopithecus* may be paraphyletic, for the purposes of the comparisons in this paper, the genus is considered to exclude *Paranthropus* species but to include the best represented species commonly assigned to *Australopithecus*, that is, *A. anamensis*, *A. afarensis*, *A. garhi*, *A. africanus*, and *A. sediba*. When the data for specific comparisons come from a single species, that species is indicated by name.

to square (not triangular). The subnasal prognathism is mild, the nasoalveolar clivus is sharply angled to the nasal floor, and the nasal margin is everted (Kimbel 2009; Kimbel, Johanson, and Rak 1997; Kimbel et al. 1996).

3. *Size and shape of the dentition.* The canine crown is symmetrical. Premolars lack substantial molarization in crown and root form (buccolingually narrow) but are not sectorial. The molars, especially the first, are somewhat mesiodistally elongated but may retain a large crown-base area. M² is “rhomboidal” in shape (dominated by mesial cusps; Bromage, Schrenk, and Zonneveld 1995; Johanson et al. 1987; Kimbel 2009; Kimbel, Johanson, and Rak 1997; Kimbel et al. 1996; Wood 1991).

Postcranial differences are not used here to distinguish *Homo* and *Australopithecus* because few postcranial remains are certainly associated with species-diagnostic cranial remains of early *Homo*. Additionally, those that do not support a major locomotor difference between *H. habilis* sensu lato on the one hand and *H. erectus* (= *ergaster*) on the other (see Holliday 2012 contra Wood and Collard 1999). Using this standard, *H. habilis* and *H. rudolfensis* are recognized as *Homo* because both differ in distinct craniodental ways from *Australopithecus* (see below). In these differences, *H. habilis* and *H. rudolfensis* trend toward the condition in later members of genus *Homo*.

Homo before 2 Ma

A small number of fossil remains of older than 2 Ma in East Africa satisfy the above criteria; however, none of these can be confidently attributed to species (fig. 1). The oldest fossil *Homo* is likely to be the A.L. 666 maxilla from Hadar, Ethiopia, which is minimally 2.33 Ma (Kimbel et al. 1996). This specimen differs from *Australopithecus* in the anatomical suites of characters mentioned in items 2 and 3 above. A similarly aged isolated molar from West Turkana, Kenya, is also likely early *Homo* (Prat et al. 2005). Both have some affinities with later early *Homo* from Kenya, such as KNM-ER 1813. Isolated dental remains from the Omo, Ethiopia (2–2.4 Ma), also likely represent early members of *Homo* and bear some similarities to later teeth of KNM-ER 1802 from Kenya (Suwa, White, and Howell 1996). The Uraha-501 (UR-501) mandible from Malawi has been argued to be of similar or slightly older age; its age, based on faunal correlations, may be as young as 1.9 Ma or as old as 2.5 Ma (Bromage, Schrenk, and Zonneveld 1995; Kimbel 2009). The inclusion of UR-501 in *Homo* is based on both molar and premolar morphology (item 3) and mandibular anatomy. This specimen has strong morphological affinities of the symphysis and corpus with the KNM-ER 1802 mandible (Schrenk, Kullmer, and Bromage 2007). These similarities suggest the two are likely to belong to the same species of *Homo*, whatever that may be.

In South Africa, fewer fossils from the period 2.6 to 2.0 Ma or older have been suggested to represent either early *Homo* or a species of *Australopithecus* derived in the direction

of *Homo* (Curnoe 2010; Dean and Wood 1982; Kimbel and Rak 1993; Moggi-Cecchi, Tobias, and Beynon 1998). These include the cranial base, Sts 19, and juvenile cranial fragments, Stw 151, from Sterkfontein. However, both are commonly attributed to *Australopithecus africanus* (Dean and Wood 1982; Spoor 1993).

It is unclear which species is directly ancestral to *Homo* (Kimbel 2009). However, the origin of the lineage is likely to be at 2.5 Ma or earlier given that by 2.3 Ma there is incipient evidence of two dental morphs. Based on the current record, the earliest accepted *Homo* appear to be in the northern part of eastern Africa; however, this does not preclude an ancestor from another part of the continent.

Non-*erectus* Early *Homo* (2.0–1.44 Ma)

Members of “non-*erectus*” *Homo* are better represented after 2 Ma and range in age from about 2.0 to 1.44 Ma (Feibel, Brown, and McDougall 1989; Spoor et al. 2007). They are best known from Kenya and Tanzania, although at least one South African morph also appears to be present (Curnoe 2010; Grine 2005; Grine et al. 2009; Hughes and Tobias 1977; Moggi-Cecchi, Grine, and Tobias 2006).

Early Homo: Taxa, Individuals, and Anatomy

Homo habilis (Leakey, Tobias, and Napier 1964) was the first non-*erectus* species of early *Homo* to be recognized, and for many scholars it represents a single species that is larger brained and smaller toothed than *Australopithecus* yet smaller brained and slightly larger toothed than early African *Homo erectus*. Apart from size, the teeth differ in shape from *Australopithecus* and *Paranthropus* in the ways discussed in the definition above, among others. For a time, all other early, relatively small-brained African *Homo* specimens were lumped into this species (e.g., Boaz and Howell 1977; Hughes and Tobias 1977; Johanson et al. 1987; Leakey, Clarke, and Leakey 1971; Wood 1991).

The discussion in the mid-1980s regarding whether the *H. habilis* hypodigm varied too much to constitute a single species is well known (Lieberman, Pilbeam, and Wood 1988; Stringer 1986; Wood 1985). The debate has focused heavily on issues of brain size, with the most complete of the Koobi Fora specimens, KNM-ER 1470 and 1813, representing the extremes of cranial capacity (750 vs. 510 cm³). For those who include these fossils in a single species, the size and shape differences between the two are explained as sexual dimorphism (Howell 1978; Tobias 1991); however, the very different facial structures are more problematic than is absolute size for the inclusion of both specimens in a single species (Leakey et al. 2012; Wood 1991, 1992).

Subsequently, these fossils have been used as type specimens for other species. In 1986, KNM-ER 1470 became the type of *Australopithecus rudolfensis* (Alexeev 1986); Wood (1991, 1992) provided substantial anatomical reasoning to support

Table 2. Elements commonly associated with KNM-ER 1470 as *Homo rudolfensis*

Specimens	Element	Main attributes and reasons for previous association with KNM-ER 1470 ^a
Type specimen: KNM-ER 1470	Cranium + partial tooth roots	Large cranial vault (750 cm ³); flat face with anterior placement of zygomatic takeoff (mesial end M1); P3 with three roots “incompletely divided double root”; P4 probably double rooted (Wood 1991: 74).
Craniodental specimens: KNM-ER 1590	Upper dentition and cranial fragments	Large vault size and shape and large tooth crown size (Wood 1991:251). <i>However, root form cannot be compared as these are yet to form in this subadult, and crown form is not preserved in 1470. This specimen formed the basis for arguments of large crown size in H. rudolfensis (see Leakey et al. 2012).</i>
KNM-ER 3732	Partial calotte and left zygoma	Large vault size, size and robusticity of the frontal bone’s contribution to the face, and the anterior inclination of the malar region (Wood 1991:251). <i>However, no teeth are present and supraorbital and orbital region differs from 1470. Zygomatic and palatal portions are incompletely preserved. Does not add to our knowledge of crown morphology.</i>
KNM-ER 3891	Cranial fragments including maxilla fragments	Anterior takeoff of the zygomatic at distal P4; three-rooted P3 and P4; large entoglenoid (although construction differs from that of 1470; Wood 1991:135, 251). <i>This fragmentary specimen may affiliate with 1470 but does not add to our knowledge of crown morphology or cranial size.</i>
Mandibulodental specimens: ^b KNM-ER 819	Mandible fragment	Similar in size and shape to 1802, sharing everted base and P roots. Superficial resemblance to <i>Paranthropus boisei</i> , but lacks extreme specializations (Wood 1991:251). <i>Ties to KNM-ER 1802 but not necessarily 1470 (see Leakey et al. 2012).</i>
KNM-ER 1482	Mandible	Similar in size and shape to 1802. Similar superficial association with <i>P. boisei</i> as above (Wood 1991: 251). <i>Ties to 1470 (see Leakey et al. 2012).</i>
KNM-ER 1483	Mandible fragment	Large corpus size, and symphysis align with mandible 1802, but premolar roots are simpler (Wood 1991:251). <i>Ties to KNM-ER 1802 less strong for corpus shape and premolar form.</i>
KNM-ER 1801	Mandible fragment	Similarities to KNM-ER 1802 in corpus, symphysis, P roots and M3 (Wood 1991). <i>Homo + Australopithecus boisei</i> -like features affine it with 1802 (Wood 1991:189). <i>Ties to 1470 (Leakey et al. 2012).</i>
KNM-ER 1802	Mandible	Mandibular robusticity and dental size and root complexity consistent with the inference that 1470 was adapted to a heavy masticatory pattern (Wood 1991:251). <i>No direct tie to KNM-ER 1470; but, as noted by Wood, Stringer argued, “The anterior placement of the root of the ascending ramus and extramolar sulcus may be consistent with KNM-ER 1470 zygoma position” (Stringer 1986). However, see Leakey et al. (2012).</i>
UR-501	Mandible	Mandibular morphology similar to KNM-ER 1802 with especial reference to the broad Ps and plate-like P roots (Bromage, Schrenk, and Zonneveld 1995). <i>Strong ties to KNM-ER 1802 but not necessarily 1470.</i>
Postcranial specimens: KNM-ER 813	Talus	More similar to human than australopithecine tali (Wood 1992). <i>Tie to KNM-ER 1470 is based on presumed size. Could be other early Homo.</i>
KNM-ER 1472	Femur	Larger size and more humanlike anatomy than femora from Olduvai (Wood 1992). <i>Tie to KNM-ER 1470 is based on presumed size. Could be other early Homo.</i>
KNM-ER 1481A, B	Femur/tibia	Larger size and more humanlike anatomy than femora from Olduvai (Wood 1992). <i>Tie to KNM-ER 1470 is based on presumed size. Could be other early Homo.</i>

Note. The list of referred specimens is taken from the most commonly followed delineation of *H. rudolfensis*, that presented by Wood (1991, 1992), with the additional inclusion of UR-501, the mandible from Malawi that is considered nearly identical to but with smaller premolars than KNM-ER 1802 (Bromage, Schrenk, and Zonneveld 1995).

^a Main attributes or reason for association with KNM-1470 as provided by original author. Italicized comments provided by Antón and/or Leakey et al. (2012).

^b Note added in proof: I consider the newly described cranial (KNM-ER 62000) and mandibular (KNM-ER 60000 and 62003) specimens to associate with KNM-ER 1470 to the exclusion of KNM-ER 1802 for the reasons articulated by Leakey et al. (2012).

the specific designation and its association with genus *Homo*. He also suggested the possibility that a number of other cranial, mandibular, dental, and postcranial remains from Koobi Fora might be included as well (see table 2). In 1995, KNM-ER 1813 became the type specimen of *Homo microcranous* (Ferguson 1995). Because the issue of affinity of OH 7, and hence the *H. habilis* name, has never been adequately addressed (see below), it is most prudent to set it aside for the moment and work from the specimens that are more complete. So as not to confound the argument, I will refer here to these specimens and any associated fossils as the 1813 and 1470 groups, respectively. The main specimens assigned to these groups and their earlier attributions are listed in table 3.

As was argued in the initial proposal for two taxa, there are important differences in facial structure and perhaps dental size between the two specimens (Wood 1991, 2009). Regardless of how it is hafted to the vault (Bromage et al. 2008), the KNM-ER 1470 face is quite flat, with a forward-facing malar region and relatively deep and tall zygomatics that are anteriorly inclined. The anterior tooth row and the maxillary bone that holds it are somewhat retracted and narrow across the canines (Wood 1985, 1991). Although the anatomy shows superficial similarities to the *Paranthropus* face, zygomatic position causes the facial flatness in *Paranthropus*, whereas the midface itself is flat in KNM-ER 1470. Wood suggested additional parallels between the two, including postcanine megadontia (albeit less marked in KNM-ER 1470). He thus described the 1470 morph as a large-brained but large-toothed early *Homo*. Alternatively, the KNM-ER 1813 face is more conservative in its structure, with a moderately prognathic midface, a rounder anterior maxilla, and somewhat more posteriorly positioned but more vertical zygomatic arches. The KNM-ER 1813 face also houses relatively smaller teeth.

If we accept that the structural differences in the face indicate two different species, the constituents of the groups can only be built based on direct anatomical associations between other fossils and either 1470 or 1813. KNM-ER 1470, while preserving a face and vault, lacks maxillary dental crown morphology and does not preserve a mandible. Table 2 delineates the specimens typically associated with KNM-ER 1470 (aka *Homo rudolfensis*) and the original reason for so doing (mostly after Wood 1991, 1992). The large size of the vault, tooth roots, and flat anterior face suggested that large individuals with a “heavy” masticatory pattern might be the best fit. However, there are no discrete, derived anatomical arguments beyond vault size and inferred dental size for linking KNM-ER 1470 with KNM-ER 1590, until recently the only complete maxillary dentition assigned to *H. rudolfensis*. Alternatively, the table highlights the strong arguments, including premolar root form, for linking some of the mandibular remains (e.g., KNM-ER 819, UR 501) with one another and with the more complete mandible KNM-ER 1802. However, there are again no linkages between these mandibles and KNM-ER 1590 or 1470 except for size. Despite this, KNM-

ER 1590 and KNM-ER 1802 have become the de facto examples for *H. rudolfensis* maxillary and mandibular dental morphology, respectively (e.g., Schrenk, Kullmer, and Bromage 2007; Spoor et al. 2007; Wood and Richmond 2000). While parsimony may suggest that this KNM-ER 1802/UR-501 group of mandibles may go with the 1470 face, there is no particular anatomical argument that they must.²

Alternatively, because of the better preservation of KNM-ER 1813, the 1813 morph can be extended to include other maxillae from Kenya and Tanzania (e.g., OH 13, OH 62, OH 65, KNM-ER 1805). OH 65 was initially aligned with KNM-ER 1470 largely on the basis of size and malar position (Blumenshine et al. 2003; Clarke 2012). However, zygomatic root position, midfacial prognathism, anterior maxillary contours, arcade shape, and tooth position differ so markedly between the two as to preclude their inclusion in the same group to the exclusion of the 1813-group specimens (see Rightmire and Lordkipanidze 2009; Spoor et al. 2007).³ Thus, if two morphs are accepted, OH 65 must be placed with the 1813 group. Because KNM-ER 1813 also retains some maxillary teeth, the maxillary dental anatomy of the group is known and can be compared for consistency with those dentitions that are housed in the maxilla mentioned above. And because some of these other maxillae have associated mandibles (e.g., OH 13; KNM-ER 1805), the mandibular dental anatomy and bony morphology can be directly seen and linked to isolated mandibles. The 1813 group can thus be formed on the basis of direct anatomical ties.

The affinity of the type of *H. habilis*, OH 7, to either of these groups remains unclear. OH 7 is a difficult type from which to judge the anatomy of the species because it comprises a subadult, a partial mandible that is also deformed taphonomically, a set of parietals that indicate approximate vault size but provide little definitive anatomy, and some isolated hand bones presumed to be the same individual. The scenario that has found the most favor links OH 7 with the 1813 group, thus named *H. habilis* (e.g., Schrenk, Kullmer, and Bromage 2007; Wood 1991). The 1470 group (which according to those authors includes the 1802/UR-501 mandibles) is then *H. rudolfensis*. OH 7 has often been suggested to align with the 1813 group on dental crown anatomy, al-

2. Note added in proof: Recently described Kenyan fossils (KNM-ER 60000, 62000, 62003) confirm facial differences between KNM-ER 1470 and 1813 but not absolute molar size differences. These fossils also seem to exclude the 1802 group of mandibles from the 1470 group (Leakey et al. 2012).

3. The main issue here is the contention that OH 65's lower nasal region; roots of the zygoma; and broad, flat, nasoalveolar clivus were most similar to KNM-ER 1470's. However, this is not the case. OH 65 is much more prognathic subnasally and has more posteriorly positioned zygomatic roots than does KNM-ER 1470. Additionally, OH 65's nasoalveolar clivus is arched at the alveolar margin where 1470 is flat, and its canine alveoli are not part of the anterior tooth row, whereas those of 1470 are. In short, OH 65 is a large version of KNM-ER 1813 and shows none of the structural features that are critical to erecting the 1470 morph.

Table 3. Main fossil specimens attributed to earliest or early *Homo* by original attribution and species group in this paper

Specimen	Element	Common attribution	Species/group
>2.0 Ma:			
East Africa:			
A.L. 666-1	Palate	<i>Homo</i> sp. aff. <i>H. habilis</i> (Kimbel et al. 1996)	Early <i>Homo</i>
KNM-WT 42718	Molar	<i>Homo</i> sp. aff. <i>H. habilis</i> (Prat et al. 2005)	Early <i>Homo</i>
Omo E-G teeth	Miscellaneous teeth	<i>Homo</i> sp. aff. <i>H. rudolfensis</i> (Suwa, White, and Howell 1996)	Early <i>Homo</i>
UR-501 ^a	Mandible	<i>H. rudolfensis</i> (Bromage, Schrenk, and Zonneveld 1995)	1802 group
KNM-BC 1	Temporal	<i>Homo</i> sp. indet. (Hill et al. 1992), Hominidae gen. sp. indet. (Martyn and Tobias 1967)	?
South Africa:			
Sts 19	Cranial base	<i>Homo</i> sp. (Kimbel and Rak 1993)	?
Stw 151	Cranial fragments—juvenile	Derived toward an early <i>Homo</i> condition (Moggi-Cecchi, Tobias, and Beynon 1998)	?
2.0–1.5 Ma non-<i>erectus Homo</i>:			
East Africa:			
KNM-ER 1470	Cranium	<i>H. (A.) rudolfensis</i> (Alexeev 1986)	1470 group
KNM-ER 1590	Cranial fragments/teeth	<i>H. rudolfensis</i> (Wood 1991)	Early <i>Homo</i>
KNM-ER 3732	Partial cranium	<i>H. rudolfensis</i> (Wood 1991)	Early <i>Homo</i>
KNM-ER 3891	Cranial fragments/maxilla	<i>H. rudolfensis</i> (Wood 1991)	Early <i>Homo</i>
KNM-ER 819	Mandible fragment	<i>H. rudolfensis</i> (Wood 1991)	1802 group
KNM-ER 1482 ^b	Mandible	<i>H. rudolfensis</i> (Wood 1991)	Early <i>Homo</i> ^b
KNM-ER 1483	Mandible fragment	<i>H. rudolfensis</i> (Wood 1991)	1802 group
KNM-ER 1801 ^b	Mandible partial	<i>H. rudolfensis</i> (Wood 1991)	Early <i>Homo</i> ^b
KNM-ER 1802	Mandible	<i>H. rudolfensis</i> (Wood 1991)	1802 group
KNM-ER 1501	Mandible partial	<i>H. habilis</i> (Wood 1991:270)	1813 group
KNM-ER 1813	Cranium	<i>H. habilis</i> (Howell 1978; Wood 1991)	1813 group
KNM-ER 1805	Calvaria + maxilla + mandible	<i>H. habilis</i> (Wood 1991)	1813 group
KNM-ER 3735	Cranial fragments + partial skeleton	<i>H. habilis</i> (Leakey et al. 1989)	Early <i>Homo</i> ; ?1813 group
KNM-ER 42703 ^c	Maxilla fragment	<i>H. habilis</i> (Spor et al. 2007)	1813 group
OH 7	Mandible + cranial fragments	<i>H. habilis</i> (Leakey, Tobias, and Napier 1964)	<i>H. habilis</i>
OH 13	Maxilla, mandible, teeth, cranial fragments	<i>H. habilis</i> (Leakey, Tobias, and Napier 1964)	1813 group
OH 16	Maxillary and mandibular teeth + cranial fragments	<i>H. habilis</i> (Leakey, Tobias, and Napier 1964)	Early <i>Homo</i>
OH 24	Cranium trampled	<i>H. habilis</i> (Leakey, Clarke, and Leakey 1971)	1813 group
OH 62	Maxilla + fragmentary skeleton	<i>H. habilis</i> (Johanson et al. 1987)	1813 group
OH 65	Maxilla + dentition	Similar to 1470, which they include in <i>H. habilis</i> (Blumenshine et al. 2003; Clarke 2012)	1813 group

though it should again be noted that no dental remains are firmly associated with the 1470 group (the calvaria retains only partial roots), and it is unclear, therefore, how or whether the groups differ in dental occlusal anatomy or size. Alternatively, OH 7's roughly estimated cranial capacity (690 cm³; Tobias 1991) perhaps aligns it with KNM-ER 1470. If OH 7 is so placed, that group (= KNM-ER 1470 only + OH 7) then becomes *H. habilis*, leaving the 1813 group as *H. microcranous*. Present data are, in my opinion, insufficient to choose between these scenarios or to show to which the 1802/UR-501 group links. While future evidence may prove convincing, it is also possible that 1802/UR-501 represents a third morph and that the affinities of OH 7 are with any of the three (see also Leakey et al. 2012).

It is generally agreed that there is some fossil evidence for at least one member of non-*erectus* early *Homo* in South Africa; however, there is no consensus concerning which species are present or whether these also occur in East Africa (see also Grine 2005; Grine et al. 2009). The remains in question date (roughly) between 2.0 and 1.5 Ma and come from Sterkfontein, Swartkrans, and Drimolen. The Swartkrans remains are most frequently linked with *H. erectus* and are discussed below. The Sterkfontein remains include isolated teeth, two partial mandibles, and the cranium Stw 53, whose taxonomic identification and reconstruction is heavily contested (e.g., Curnoe 2010; Curnoe and Tobias 2006; Grine 2001; Grine et al. 2009; Kuman and Clarke 2000). The Sterkfontein cranial remains have been variously affiliated with *Homo* (aff. *habilis* or sp. indet.; Kuman and Clarke 2000 for the mandibles; Curnoe and Tobias 2006; Grine et al. 2009) or *Australopithecus* (Kuman and Clarke 2000 for StW 53; Clarke 2012). The isolated teeth from Sterkfontein and Drimolen lend strong support to the identification of an as yet unnamed early non-*erectus* *Homo* in South Africa (Grine et al. 2009). Because they do not affiliate strongly with the East African teeth, following Grine (2001; Grine et al. 2009) they are considered here simply as early non-*erectus* *Homo*.

Postcranial remains of early East African *Homo* are few, and fewer still are certainly associated with one of the cranial morphs (table 4). OH 7 has a partial hand. The OH 62 partial skeleton can be associated with the 1813 group on the basis of maxillary morphology. The KNM-ER 3735 fragmentary skeleton is *Homo*, based on anatomy of the posttoral sulcus, mandibular fossa, and zygomatic, but of uncertain affinity. Isolated elements of the lower limb—such as OH 8 (foot), OH 35 (distal tibia), and various hind limb fragments from Koobi Fora—have been tentatively assigned to *Homo*. However, for these isolated remains there is always some question as to which hominin they belong (see Gebo and Schwartz 2006; Wood and Constantino 2007). If OH 8 is early *Homo*, the ankle and “close-packed” arches may indicate a pattern of bipedalism similar to *Homo sapiens* (see Harcourt-Smith 2007; Harcourt-Smith and Aiello 2004), although primitive elements are retained as well. The OH 7 hand retains the primitive condition of the carpals and curvature of the pha-

langes, which presumably indicate some arboreal behavior (Tocheri et al. 2007). However, other aspects of especially the thumb suggest precision grip abilities more derived toward human than ape capabilities (Susman and Creel 1979). The sizes and proportions of the limbs of the associated skeletons are discussed below.

Non-erectus Early Homo: Size and Proportions

Given that at least two different facial morphs seem to coexist in time and space in East Africa, what can be said about size and shape of non-*erectus* *Homo*? As currently constructed, the 1470 group has a larger cranial capacity (750 cm³) than does the 1813 group (510–675 cm³) with the caveat that OH 7 has not been assigned to either group (tables 5, 6). Additionally, more fragmentary remains, such as the OH 65 maxilla, conform well to the shape of the KNM-ER 1813 palate and teeth but are quite a bit bigger and could (but are not required to) imply a larger cranial capacity for that group. Similarly, KNM-ER 1590, a fragmentary juvenile specimen whose parietals suggest a large cranial capacity, has been included by some in the 1470 group based on size and the presumption that this group is large and the 1813 group small, but it could instead affiliate with the 1813 group if size differences are not substantiated. Yet even without such size extension of the 1813 group, brain size among the well-preserved early *Homo* individuals (KNM-ER 1805; OH 13, 16, 24) is fairly continuously distributed between the two end members, KNM-ER 1813 and 1470 (table 6). Such distribution suggests that average ranges of cranial capacity will vary depending on who is included in each group. On the basis of facial morphology, KNM-ER 1805 and OH 13 and 24 should be included in the 1813 group (OH 16 does not preserve facial anatomy), and thus the upper end of this group is as much as 670 cm³, substantially larger than KNM-ER 1813. Regardless of whether there is one or more species of early non-*erectus* *Homo*, brain size across the entire group ranges from 510 to 750 cm³.

Dental size cannot be compared between the groups because only the 1813 group has complete teeth that are certainly associated with it; however, dental size can be assessed across the entire early *Homo* sample and for the 1813 group alone (table 7). KNM-ER 1470 has been inferred to be large toothed on the basis of preserved tooth roots. However, this inference is overstated given that especially the postcanine roots are observed low on the root and in oblique section. The maxillary dental metrics generally quoted for this species are from KNM-ER 1590, which has extremely large teeth but as discussed above has no firm anatomical tie to KNM-ER 1470. Similarly, the mandibular dental metrics are from KNM-ER 1802, which has large teeth but also has no firm anatomical tie to KNM-ER 1470. Thus, the argument that the 1470 group is large toothed is circular because it is made on the basis of specimens that have been placed in the group because of large dental size resulting in the conclusion that the group has large

Table 4. Main postcranial specimens attributed in this paper to earliest or early *Homo* in Africa and Georgia by original attribution and species group used in this paper

Specimen	Element	Common attribution	Species/group	Body mass estimate (kg) ^a
East Africa:				
KNM-ER 1472	Femur	<i>Homo rudolfensis</i> (Wood 1992)	?Early <i>Homo</i>	49.6
KNM-ER 1481A, B	Femur, tibia	<i>H. rudolfensis</i> (Wood 1992)	?Early <i>Homo</i>	57
KNM-ER 3228	Os coxae	<i>Homo ?erectus</i> (Rightmire 1990) or <i>H. rudolfensis</i> (McHenry and Coffing 2000)	Early <i>Homo</i>	63.5
OH 35	Tibia, distal	<i>H. habilis</i>	Early <i>Homo</i>	31.8
OH 62	Maxilla + fragmentary skeleton	<i>H. habilis</i> (Johanson et al. 1987)	1813 group	?
OH 28	Os coxae	<i>H. erectus</i> (Rightmire 1990)	<i>H. erectus</i>	54
OH 34	Femur	<i>H. erectus</i> (Rightmire 1990)	<i>H. erectus</i>	51
KNM-ER 736	Femur	<i>H. erectus</i> (Rightmire 1990)	<i>H. erectus</i>	68.4
KNM-ER 737	Femur	<i>H. erectus</i> (Rightmire 1990)	<i>H. erectus</i>	?
KNM-ER 1808	Multiple cranial and postcranial elements	<i>H. erectus</i> (Walker, Zimmerman, and Leakey 1982)	<i>H. erectus</i>	63.4
KNM-WT 15000	Skeleton + skull	<i>H. erectus</i> (Walker and Leakey 1993)	<i>H. erectus</i>	51
Gona	Pelvis	<i>H. erectus</i> (Simpson et al. 2008)	? <i>Homo</i>	39.7
South Africa:				
SK-1896	Femur, distal	<i>Homo</i> aff. <i>erectus</i> (Susman, de Ruiter, and Brain 2001)	<i>Homo</i> aff. <i>erectus</i>	57
SK-2045	Radius, proximal	<i>Homo</i> aff. <i>erectus</i> (Susman, de Ruiter, and Brain 2001)		53–58
SKX-10924	Humerus, distal (small)	<i>Homo</i> aff. <i>erectus</i> (Susman, de Ruiter, and Brain 2001)	<i>Homo</i> aff. <i>erectus</i>	(30)
SKW(SKX) 34805	Humerus, distal (large)	<i>Homo</i> aff. <i>erectus</i> (Susman, de Ruiter, and Brain 2001)	<i>H. aff. erectus</i>	?
Georgia:				
Dmanisi (small)	Multiple elements	<i>H. erectus</i> (= <i>H. ergaster</i> ; Gabunia et al. 2000; Rightmire and Lordkipanidze 2009)	<i>H. erectus</i>	40.7
Dmanisi (large)	Multiple elements	<i>H. erectus</i> (= <i>H. ergaster</i> ; Gabunia et al. 2000; Rightmire and Lordkipanidze 2009)	<i>H. erectus</i>	48.8

Note. Only those bones useful in establishing stature or body weight are listed. Hand and foot elements excluded.

^a In addition to sources in a previous column of this table, body mass estimates follow table 8, Holliday (2012), Pontzer (2012), and Ruff, Trinkaus, and Holliday (1997).

Table 5. Comparative brain and body size of *Australopithecus* and *Homo*

	South Africa		East Africa		South Africa	East Africa/Georgia
	<i>A. sediba</i>	<i>A. africanus</i>	<i>A. afarensis</i>	Early non-erectus <i>Homo</i>	<i>H. aff. erectus</i>	Early <i>H. erectus</i>
Brain size ^a	420 (MH 1)	571 (Stw 505) 485 (Sts 5) 443 (MLD 37/38) 385 (Sts 60) 410 (Sts 71)	550 (A.L. 444-2) 485 (A.L. 333-45) 400 (A.L. 162-28)	510 (1813) 580 (1805) 595 (OH 24) 630 (OH 16) 660 (OH 13) 680 (OH 7) 750 (1470)	...	638 (D3444) 655 (D2282) 690 (42700) 727 (OH 12) 775 (D2880) 804 (3883) 848 (3733) 909 (15000) 995 (Daka) 1,067 (OH 9)
Mean	420	454–461	478	629	...	810 (w/Dmanisi) 863 (East Africa only)
CV	...	15.9	15.7	12.2	...	17.8 (w/Dmanisi) 15.9 (East Africa)
Body mass/femur length ^b	35.7 (MH 2) 31.5 (MH 1)	45.4/433.5 (Stw 99) 41.3 (Stw 443) 40.7 (Stw 311) 38.4 (Sts 340) 37.9 (Stw 389) 34.2 (Stw 25) 32.7 (Stw 392) 32.5 (TM 1513) 30.5 (Stw 102) 30.3/276 (Sts 13, 34) 27.5 (Stw 347) 23.3 (Stw 358)	50.1/382 (A.L. 333-3) 48.2 (A.L. 333x-26) 45.6/375 (A.L. 827-1) 45.4 (KSD-VP-1/1) 42.6 (A.L. 333-7) 41.4 (A.L. 333-4) 40.2 (A.L. 333-w-56) 33.5 (A.L. 333-8) 28/281 (A.L. 288-1) 27.1 (A.L. 129a)	63.5 (3228) 49.6/401 (1472) 57/396 (1481) 31.8 (OH 35) 31 (OH 8) —/315 (OH 62)	57 (SK 1896) 53–58 (SK 2045) [30] (SKX 10924)	68.4 (736) 63.4/485 (1808) 54/456 (OH 28) 51/429 (15000) 51/432 (OH 34) 48.8 (Dmanisi large) 40.7 (Dmanisi small) 39.7 (Gona)
Mean body mass	33	34	40	44	44	52 (w/Dmanisi) 55 (East Africa only)
CV body mass/femur length	9/—	18.7/—	20.2/16.3	33/13	32/—	19.3/8.7 (w/Dmanisi) 18.8/5.8 (East Africa)

Note. Specimen numbers are in parentheses. Brain size in cm³; mass in kilograms; femur length in millimeters.

^a Endocranial capacity for *A. sediba* from Berger et al. (2010), for *A. africanus* from Neubauer et al. (2012), for *A. afarensis* from Holloway and Yuan (2004), and individually for *Homo* as indicated in table 6 of this paper.

^b Body mass estimates follow Pontzer (2012) and tables 4 and 8 of this paper. Femur length CVs are raw values not corrected for dimensionality.

teeth. Across all of early *Homo*, then, molar size is somewhat diminished over the condition in *Australopithecus* and somewhat, but not significantly, larger than the condition in early *H. erectus* (table 5; Antón 2008). There is some suggestion that there may be a large-toothed morph, but it is unclear whether this morph belongs to the 1470 group or not (see note in table 7).

Dental proportions and occlusal morphology can also be described for the 1813 group, which differs from *Australopithecus* and *H. erectus*. Whether this morphology is unique to this group of early *Homo* is unknown. The 1813 group shows buccolingual narrowing of its cheek teeth, especially the molars, relative to *Australopithecus*, and its M2s are mostly rhomboidal in form. The third molar is large relative to M2, however, in contrast to the condition in *H. erectus* (Spoor et

al. 2007). There is also some evidence of difference between the 1802 group and the 1813 group in both dental and mandibular morphology. The former have relatively broader premolars with greater talonid development and differently shaped roots, and the base of the mandible is everted and the symphysis more vertical than the apparent condition in the 1813 group (Antón 2008; Schrenk, Kullmer, and Bromage 2007, table 9.1); however, it is unclear to what extent these differences may reflect intraspecific idiosyncratic variation in mandibular size and robusticity.

Body size cannot be compared between the groups because only the 1813 group has associated postcranial remains (i.e., OH 62 on maxillary form; table 3). OH 62 has been interpreted as small bodied and with relatively long and strong arms, but the specimen is very fragmentary (Haeusler and

Table 6. Size comparisons of individual fossils of *Homo habilis* sensu lato and early *Homo erectus* sensu lato

Specimen ^a	Group (1813 or 1470)	Geological age (Ma)	Presumed sex ^b	Brain size (cm ³)	Mean body mass (kg) from orbit area (k/a) ^c	Range body mass (kg) from orbit area (k/a) ^c	Mass (kg) from postcrania			
							M ¹ area	M ₁ area	M ² area	M ₂ area
<i>Homo habilis</i> s.l.:										
KNM-ER 1813	1813	1.9	Female	510	34.9/31.0	24.3–50/36.9–35.5	1,560	...	1,640	...
KNM-ER 1805	1813	1.9	Male	580	1,770	...	1,730	...
OH 24	1813	1.8	Female	595	30.3/36.3	21.1–43.4/31.5–41.8	1,790	...	1,890	...
OH 16	?	1.8	?	625–638	2,010	1,870	2,020	2,330
OH 13	1813	1.6	Female	650–675	1,640	1,510	1,810	1,700
OH 7 <i>Homo habilis</i>	?	1.8	Male	647–690	1,760	...	2,110
KNM-ER 60000	1470	1.8	?	1,460	...	1,790
KNM-ER 1590	?	1.85	?	2,090	...	2,570	...
KNM-ER 62000	1470	1.9	Female	1,850	...	2,016	...
KNM-ER 1470 <i>Homo rudolfensis</i>	1470	2.03	Male	750	45.5/77.4	33.8–69.9/64.1–93.6
<i>Homo erectus</i> s.l.:										
Dmanisi D3444		1.7	Male	638
D2282/D211		1.7	Female	655	1,560	1,550	1,560	1,420
KNM-ER 42700		1.55	Female	690
OH 12		1.2	Male	727
D2280		1.7	Male	775
KNM-ER 3883		1.5	Male	804	57.4/83	39.9–57.5/68.2–101 kg
KNM-ER 3733		1.8	Female	848	59.2/88.8	41–85.3/72.5–108.7 kg	1,860	...
KNM-WT 15000		1.5	Male	909	59.9/...	41.5–86.4/...	...	1,490	1,410	1,500
Daka		1.0	?	995
OH 9		1.5	Male	1,067

Note added in proof. Data from recently described fossils from the 1470 group (Leakey et al. 2012) are included here but could not be included in text discussion.

^a Species names for which these serve as type specimens are noted by the specimen number.

^b The sex of all specimens is unknown. These estimates represent the most frequent inferences and should be considered uncertain at best.

^c Body mass estimates from orbital area are from k = Kappelman (1996) and a = Aiello and Wood (1994).

Table 7. Dentognathic summary statistics for *Homo habilis* sensu lato and early *Homo erectus* from Africa and Georgia

	Africa				Africa and Georgia
	KNM-ER 1590	KNM-ER 1802	1813 group	<i>Homo habilis</i> sensu lato	Early <i>Homo erectus</i>
M ₁ buccolingual	...	130	119.3/6.7 (3)	123.8/9.0 (8)	119.2/7.6 (5)
M ₁ mesiodistal	...	148	137.6/0.6 (3)	138.5/6.1 (8)	132.2/6.5 (5)
M ₁ area	...	1,920	1,610/118 (3)	1,705/181 (8)	1,592/131 (6)
M ¹ buccolingual	148	...	132.3/2.9 (6)	134.9/6.0 (8)	129.2/6.8 (4)
M ¹ mesiodistal	142	...	128.3/5.1 (6)	132.3/8.7 (8)	126.2/3.8 (5)
M ¹ area	2,090	...	1,695/88 (6)	1,784/181 (8)	1,630/127 (5)
Corpus height M ₁	...	38	29.3/2.7 (3)	32.6/4.3 (11)	29.4/2.9 (6)
Corpus breadth M ₁	...	23	18.3/2.3 (3)	20.8/3.68 (10)	20.1/0/9 (6)
Symphyseal height	...	36	25	33.2/6.0 (5)	33.4/2.6 (4)
Symphyseal depth (labiolingual)	...	24.5	18	21.7/3.2 (5)	18.5/2.4 (4)

Note. Individual fossils KNM-ER 1590 and 1802 and the 1813 group are also presented. Measurements in millimeters; mean/SD; (*n*).

Note added in proof. Teeth of the 1470 group are now known from recently described fossils, and, while dental proportions differ, teeth are not always large. See Leakey et al. (2012) for discussion. New fossils are not included in these statistics, but see table 6 for some raw measures.

McHenry 2004; Richmond, Aiello, and Wood 2002; see also Holliday 2012). KNM-ER 3735 is larger than OH 62 but more fragmentary and is not definitively assigned to either subgroup (Haeusler and McHenry 2007; Leakey et al. 1989). The range of body weights in these two specimens is 30–46 kg (66–101 lb.), respectively (tables 5, 8; Johanson et al. 1987; Leakey et al. 1989). Inferred stature is very approximately 118–145 cm (3'11"–4'8"). Three other relatively large femora may be assigned to *Homo* sp. and would support the larger end of this size range (149 cm/57 kg; Holliday 2012) if their attribution is correct. However, two of the femora (KNM-ER 1472 and 1481) are often attributed either to the 1470 group (because they are large; Wood 1992) or *H. erectus* (because they are somewhat flattened in the subtrochanteric area and are large; Kennedy 1983a, 1983b; but see Trinkaus 1984), and they are also attributed to *H. habilis* sensu stricto by others (e.g., Schrenk, Kullmer, and Bromage 2007). One large partial os coxae (KNM-ER 3228) has a geological age of 1.95 Ma. This specimen is usually considered *Homo* and possibly *H. erectus* (Antón 2003; Rightmire 1990), although McHenry and Coffing (2000) suggest it may represent a large-bodied non-*erectus* *Homo* (their *H. rudolfensis*). Based on estimates of femoral head size, a body mass estimate of 60–65 kg has been suggested (Ruff, Trinkaus, and Holliday 1997). Collectively, these remains suggest that the largest end of the non-*erectus* early *Homo* body size range is just under 5 ft. tall (150 cm), and the average weight is 44 kg (range 31–65; tables 4–6, 8; see Holliday 2012; Pontzer 2012).

There is much discussion as to whether the limb proportions of early *Homo* are as or even more primitive than *Australopithecus afarensis* and therefore whether they differentiate early *Homo* from *H. erectus*. Based on cross-sectional strength measures, the OH 62 humerus is relatively stronger compared with its femur than is true of recent humans and is like those of *Pan* (Ruff 2010; see also Richmond, Aiello, and Wood 2002). Thus, OH 62, but not later *Homo*, likely participated in substantial arboreal locomotion as well as terrestrial (bipedal) locomotion. This would be supported by the OH 7

wrist bones, if they are of the same taxon (Tocheri et al. 2007). Alternatively, hind-limb elongation remains debated because of uncertainties in reconstructions of long bone lengths from the highly fragmentary OH 62 and KNM-ER 3735. At least one set of researchers argues that hind-limb elongation may have been present (Haeusler and McHenry 2004; Reno et al. 2005; but see Korey 1990; Richmond, Aiello, and Wood 2002). And the relatively long distal tibia of OH 35 may support this idea (Harcourt-Smith 2007). However, others have reconstructed the lengths differently and found the primitive condition (i.e., long humerus, short femur; Richmond, Aiello, and Wood 2002). More recent work, however, suggests that hind-limb length proportions do not actually differ between *Australopithecus* and *Homo* (see Holliday 2012; Pontzer 2012). So, while strength proportions appear to link OH 62 with *Australopithecus* rather than later *Homo*, hind-limb elongation relative to body size would appear to be the same in all genera.

It will be clear from the small number of fossils in each group and the disagreement about taxonomic assignments that assessing sexual dimorphism will be nearly impossible for early *Homo*. Ideally, we should identify males and females by focusing on discrete characters that are independent of overall body size, such as canine size and robusticity, and then assess male and female mean values from these independently assigned subgroups. The 1813 group is the only one in which it is possible to try to assess sexual dimorphism in this way, but such characters are few. Historically, the development of cranial crests in KNM-ER 1805 over the condition in KNM-ER 1813 has been used to suggest the former is male and the latter female (Wood 1991:84). None of the other known specimens in the group exhibit crests, leaving KNM-ER 1805 as the only male candidate at the moment. Cranial capacity differs little between the two specimens (510 vs. 580 cm³). However, molar occlusal areas are larger in KNM-ER 1805. Yet they are no larger than, say, OH 24, which lacks crests and is thus a presumed female. Here we face the issue of the possibility of large females and small males and the inadequate sampling of the fossil record. For the postcranial skeleton, if

Table 8. Body size in East African adult early non-*erectus* *Homo* and early East African and Georgian *Homo erectus* individuals and isolated elements

Taxon	Africa					Georgia	
	Early <i>Homo</i> adult OH 62	Early <i>Homo</i> adult KNM-ER 3735	Adult isolated <i>Homo</i> sp. ^a	<i>H. erectus</i> adult KNM-ER 1808 ^b	<i>H. erectus</i> adult individuals ^c	Inferred <i>H. erectus</i> isolated elements ^d	<i>H. erectus</i> adult individuals ^e
Brain size (cc)	510–750 $x = 629$...	909 ±	690–1,067 $x = 863$	638–775 $x = 686$
Femur length (mm)	[280–374]	...	350 (1503) 400 (1472) 395 (1481) $x = 383.75$	480	386
Range (<i>n</i>)	[280–374] (1)	...	350–400 (4)	480 (1)	$x = 498$ 473	$x = 454.5$...
Stature (cm):							
Mean	118	...	145	173	179 170	174	155
Range (<i>n</i>)			173–185 (2) 168–173 (2)	161–186 (4)	145–166
Body mass (kg):							
Mean orbit	36.9 k 48.2 a	58.8 k 85 a	...
Femur head mass estimates	49.6 (1472) 57 (1481)	63.4	51 (15000)		49.6 (D4507)
Mean postcrania	33	46	48	59 63	64.5 (2) 57 (2)	54.75	48.8 large 40.2 small
Range (<i>n</i>)	21–77	...	63–68 (2) 55–63 (2)	51–68 (4)	40–49.6 (3)

^a KNM-ER 1503 is assigned to either *Homo habilis* or *Australopithecus boisei*, as are most specimens of this age from Koobi Fora (McHenry 1991); “k” and “a” refer to orbitally estimated mean body masses from Kappelman (1996) and Aiello and Wood (1994); femur head estimates from Holliday (2012); parenthetical number next to femur value is the specimen number providing that value. Square brackets are estimates.

^b KNM-1808 mean body mass values from Ruff and Walker (1993), top, or Ruff, Trinkaus, and Holliday (1997), bottom.

^c Adult individuals are KNM-1808, and adult estimates for KNM WT 15000 femur, stature, and body mass following either Ruff and Walker (1993), top, or Graves et al. (2010); Ohman et al. (2002) provide even smaller stature estimates for KNM-WT 15000.

^d Femora: KNM-ER 736 and 737, OH 28 and 34.

^e Mass data are for large and small adult individuals (see Pontzer 2012), and range estimates include other elements (Holliday 2012).

the small OH 62 skeleton is female and the larger KNM-ER 3735 is male, then if they are typical of their sexes, sexual dimorphism in body mass could be as much as 1.5 (male/female weight dimorphism as compared with chimpanzees at about 1.3 and *H. sapiens* about 1.1). Alternatively, one could use CVs from the certain members of the 1813 group, although this may give an artificially low value because it is not clear how to handle some of the larger specimens, such as KNM-ER 1590. And using the overall CV also implicitly assumes that size differences and sex differences are the same thing. In the absence of discrete characters to indicate sex, this may be a necessary assumption, but it is worth noting the confounding issue (see also Plavcan 2012). CVs for upper and lower first molar area are 5.2 and 7.3, respectively, and CVs for capacity are 9.9. These values are lower than those for early African and Georgian *H. erectus*, particularly for cranial capacity. If we take instead all the early non-*erectus* *Homo*, regardless of group affiliation, the cranial CVs are still lower than those for *H. erectus*, but their body mass CVs are

significantly greater (table 5). Plavcan (2012) provides a fuller discussion of the options for considering size dimorphism in these taxa.

Homo erectus sensu lato (1.9–? Ma)

In the early part of its range with which we are concerned, *Homo erectus* overlapped for nearly half a million years with other groups of early *Homo* in Africa, principally the 1813 group, whose last appearance datum is 1.44 Ma (fig. 1; see Spoor et al. 2007). The earliest *H. erectus* (at about 1.8–1.9 Ma) are found in Koobi Fora, Kenya, and the species persists in Africa until about the Brunhes-Matuyama boundary (0.78 Ma; fig. 1; Asfaw et al. 2002; Feibel, Brown, and McDougall 1989; Potts et al. 2004). *Homo erectus* is best known from Kenya and Tanzania, although Ethiopian and South African specimens also exist (e.g., Asfaw et al. 2002; Robinson 1953). The earliest African *H. erectus* quickly dispersed into Asia by 1.7–1.8 Ma (Gabunia et al. 2000; Swisher et al. 1994). The

species persists in Asia and Island Southeast Asia through at least the middle if not the late Pleistocene (Indriati et al. 2011; Shen et al. 2009; Swisher et al. 1996).⁴ Given interest here in the origin and evolution of *Homo*, I consider only the early African and Georgian record.

Homo erectus: Taxa, Individuals, and Anatomy

Like *Homo habilis*, *H. erectus* sensu lato is an umbrella taxon that may include nested sets of other taxa (table 1). Those who split the larger taxon in two usually refer to the African/Georgian members as *Homo ergaster* based on the type specimen KNM-ER 992 (Groves and Mazek 1975).⁵ Most recently, *Homo georgicus* (Gabunia et al. 2002) was named to accommodate morphology in the Georgian remains that is argued to combine more primitive traits (especially of the face and brain size) than in the earliest African *H. erectus*. However, this variation is easily encompassed within early African *H. erectus* (Antón 2003; see also Baab 2008; Rightmire and Lordkipanidze 2009), which also shows clear signs of size-related shape changes with cranial capacity (Antón et al. 2007; Spoor et al. 2007). And the derived characters shared by the Georgian and recently discovered small-brained African specimens unite them taxonomically (Spoor et al. 2007). For the purpose of discussion here, it makes little difference whether the Far East Asian and African/Georgian hominins are seen as regional demes of one species, as two distinct species, or even multiple species, although I favor the former interpretation (table 3; Antón 2003).

As will be clear from the discussion of the genus, *H. erectus* is now considered to take the first major anatomical and behavioral steps in the direction of a “modern human” body plan (Antón 2003; Antón et al. 2007; Walker and Leakey 1993). Although the species was not identical to *Homo sapiens* in size or shape, *H. erectus* bodies and brains were larger and their teeth and especially jaws were somewhat diminished in size, on average, compared with those of earlier members of *Homo* (Antón 2008). However, their teeth were larger and their brains smaller than in later *Homo*. Their lower-limb skeleton was relatively elongated compared with body mass over the condition in *Pan*, and their upper limbs were somewhat foreshortened over the condition in *Australopithecus* and perhaps other early *Homo* (Holliday 2012; Pontzer 2012). That said, newly discovered small-sized individuals from

Georgia, Kenya, Tanzania, and perhaps Ethiopia suggest substantial overlap in absolute size with earlier *Homo* species (tables 5–7; Antón 2004; Gabunia et al. 2000; Potts et al. 2004; Rightmire 1979; Simpson et al. 2008; Spoor et al. 2007; Vekua et al. 2002).

Although absolutes of size do not differ, some proportions do, and so individuals of *H. erectus* are relatively easy to differentiate from all other early *Homo* on the basis of craniodental remains. Early *H. erectus* tends to have somewhat smaller occlusal areas and fewer roots than other early *Homo* but relatively larger crowns and more complex roots (especially premolar) than do modern humans (table 7; Gabunia et al. 2000, 2001; Indriati and Antón 2008). Crowns, especially molars, tend to be buccolingually narrower compared with length and less bulbous than in early *Homo*, with cusp apices closer to the outer margins of the tooth than in other early *Homo* (Antón 2008; Indriati and Antón 2008). *Homo erectus* also shows size reduction along the molar row with the third molar reduced or similar in size to M² (Spoor et al. 2007). And early *H. erectus* jaws are relatively more lightly built with narrower extramolar sulci than in early *Homo* (Grine 2001). The *H. erectus* symphysis is thinner (anteroposterior), the genioglossus pit is relatively lower, and the postincisive plane, although obliquely oriented, is not quite so pronounced as in other early *Homo* (Antón 2008).

Although general vault thickness scales with cranial capacity in *H. erectus* and other early *Homo*, *H. erectus* shows species-typical examples of thickening (Antón et al. 2007; Spoor et al. 2007). These include (1) essentially continuous supraorbital tori of variable thickness associated with a posttoral shelf/sulcus that may be continuous, (2) occipital tori that are continuous but somewhat variably expressed, often continuous with the angular tori and mastoid crests and often associated with a supratoral sulcus, (3) angular tori, and (4) midline (sagittal, bregmatic, and frontal) keels.

Homo erectus also differs from other early *Homo* and modern humans in other aspects of the cranium. The occipital squama is relatively short, and the petrous temporal is more sagittally oriented and angled relative to the tympanic portion (i.e., petrotympanic angle reduced; Rightmire and Lordkipanidze 2009; Weidenreich 1943; although the base of earlier *Homo* is not well known). The glenoid fossa is relatively broader anteroposteriorly (compared with mediolaterally) than in other early *Homo* (Spoor et al. 2007). The face is described as more similar in proportions to modern humans than with other early *Homo* (Bilsborough and Wood 1988; Wood and Richmond 2000); however, the positioning and form of the zygomatics and supraorbital torus is more similar to the 1813 group than to KNM-ER 1470, as is relative facial breadth, which is greatest at the midface in 1470 but at the superior face in the other groups.

While there again is some difference of opinion as to taxonomic affinities of the South African fossils, craniodental remains from Swartkrans are likely to represent either *H. erectus* (as discussed above) or something very *erectus*-like.

4. Throughout the paper I use the traditional chronological delineation of the Plio/Pleistocene boundary as occurring at 1.8 Ma, the onset of severe northern hemispheric glaciation.

5. While this is the most common nomen, it should be noted that many of the often included specimens represent types for earlier named species (i.e., *Homo (T.) capensis* [Swartkrans 15; Robinson 1953]; *Homo (At.) mauritanicus* [Ternifine 1; Arambourg 1954], and *Homo leakeyi* [OH 9; Heberer 1963]; table 1); thus, the earliest of those included should provide the group name. This has not been the case, however, because these earlier types were not included when the species was named and are not consistently included in *Homo ergaster* by all scholars (e.g., Wood 1991:276).

Two mandibles, SK 15 and SK 45, were the first at Swartkrans to be recognized as *Homo* (originally as *Telanthropus capensis*; Broom and Robinson 1949; Grine 2001; Grine et al. 2009; Robinson 1961). The most compelling evidence, however, is the SK 847 partial face that shows strong affinities with early East African *H. erectus* (Antón 2003; Clarke, Howell, and Brain 1970; Kimbel, Johanson, and Rak 1997; Walker 1981). Given this strong resemblance, the postcranial remains at Swartkrans that differ from those of *Paranthropus* are most usually assigned to *Homo* aff. *erectus* (Susman, de Ruiter, and Brain 2001).

The postcranial record for early East African *H. erectus* is far better than that of other early *Homo*. In Africa, a single well-preserved skeleton, KNM-WT 15000, is the main data point, but this information is augmented by a second partial skeleton, KNM-ER 1808, and a number of large isolated elements (tables 4, 8). We should be cautious that the isolated elements could, however, represent other early *Homo*. Additionally, in Georgia both adult and subadult skeletal elements, some associated, are known. Although little that is species specific can be attributed to the postcrania of *H. erectus*, there is much that differs from *Australopithecus*. For example, *H. erectus* has enlarged articular surface areas of long bones, thick cortical bone particularly in the lower limb, and an anteroposteriorly flattened (platymeric) femur (Weidenreich 1941), deep trochlea of the distal femur (Tardieu 1998, 1999), double meniscal attachments of the proximal tibia (but see Dugan and Holliday 2009), reoriented pelvis that are perhaps less broad (but see Holliday 2012) but certainly more capacious (Ruff 2010), a marked iliac pillar (i.e., acetabulocrystal buttress), and medial torsion of the ischial tuberosity (Day 1971; Rose 1984). Thus, postcranially, *H. erectus* differs from modern humans mostly in primitive characters, some of which are derived relative to nonhuman primates and others of which may originate at the origin of *Homo* (e.g., McHenry, Corruccini, and Howell 1976; Trinkaus 1984). Alternatively, a number of aspects of the postcranial skeleton—including most of the hand and foot—are better known in other early *Homo* than in *H. erectus*.

Homo erectus: Size and Proportions

Early *H. erectus* from Georgia and East Africa are moderately bigger brained than other early *Homo* in East Africa. Adult cranial capacity ranges from 638 cm³ to a maximum of 1,067 cm³ (tables 5, 6; Holloway 1983; Spoor et al. 2007; Vekua et al. 2002). Several characters scale with cranial capacity, including cranial vault shape; smaller crania are more globular (see Antón et al. 2007; Spoor et al. 2007). Although their ranges overlap, the Georgian sample is smaller (638–775 cm³) than the African (690–1,067), which may speak to issues of resource scarcity, extrinsic mortality, or climatic adaptation (seasonality).

Dental and mandibular size are smaller in early *H. erectus* than in the entire early *Homo* group (table 7). However, the

differences are smaller between early *H. erectus* and the 1813 group (excluding KNM-ER 1802 and 1590) and are not statistically significant for individual teeth in any event (Antón 2008). Relative molar cusp proportions and molar size relationships do, however, sort early *H. erectus* from early *Homo* (Grine et al. 2009; Spoor et al. 2007).

Body size range is quite substantial as well (tables 4, 5, 8). South African and East African *H. erectus* are similar in size, although there are only a few South African remains for which body size can be estimated. The Georgian remains are 17%–24% smaller (40–50 kg, 146–166 cm) on average than early East African *H. erectus* (51–68 kg, 160–185 cm) depending on whether the Gona pelvis is included. This difference may be the result of a categorization bias in Africa that has tended to place smaller isolated postcrania into early *Homo* and larger into *H. erectus*. The Gona pelvis (Simpson et al. 2008), if substantiated as *H. erectus*, would lower the body size range for Africa to perhaps as little as 120 cm/39.7 kg. In light of the small-headed remains from Ileret (Spoor et al. 2007), Olorgesailie (Potts et al. 2004), and Olduvai Gorge (OH 12; Antón 2004), a small-bodied *H. erectus* in Ethiopia seems plausible. However, the Gona pelvis is not associated with cranial remains, and Ruff (2010) argues that the pelvis is more likely *Australopithecus* or *Paranthropus*. Without Gona, early *H. erectus* stature estimates range from 145 to 185 cm (5'3"–6'1") and body mass estimates from 40 to 68 kg (88 to 150 lb.). It should be noted, however, that although the remains are fragmentary, Susman, de Ruiter, and Brain (2001) have suggested that female *Homo* aff. *erectus* at Swartkrans may be as small as 30 kg (table 4).

Several lines of evidence suggest that early *H. erectus* was an accomplished striding biped with little arboreal locomotion in its repertoire. Hind-limb elongation is present in the associated skeletons from Africa (McHenry and Coffing 2000) and Georgia (Lordkipanidze et al. 2007). Whether this elongation began with *H. erectus*, at the base of the genus, or even at the base of the hominins, is a matter of debate (see Holliday 2012; Pontzer 2012), although it now seems likely that this is a hominin adaptation. However, the forelimb is at least somewhat reduced in length compared with overall body size in *H. erectus* and with the condition in *Australopithecus* and perhaps early *Homo*. Cross-sectional properties of the hind limb and forelimb indicate different patterns of strength between *Australopithecus afarensis* and early *H. erectus* (Ruff 2008, 2009), suggesting that like humans, *H. erectus* was a predominantly terrestrial biped. The foot of *H. erectus*, which is recently known from Dmanisi, supports this notion by showing evidence of both transverse (metatarsal torsion) and longitudinal (first metatarsal base width) arches (Lordkipanidze et al. 2007; Pontzer et al. 2010). The hand skeleton is largely unknown.

The shoulder and trunk appear to exhibit both primitive and derived conditions. The shoulder girdle retains an intermediate condition: The glenoid fossa of the scapula is oriented more superiorly (Dmanisi and KNM-WT 15000), the clavicle

is relatively short compared with body size (proxied by humeral length), and humeral torsion is not as great as in modern humans. Thus, the scapula was likely placed relatively less dorsally than in recent humans (Larson et al. 2007), which has implications for throwing and possibly suggests less stability while running (Larson 2009). Like *Australopithecus*, the lumbar vertebral bodies of both Dmanisi and Nariokotome are small relative to body weight, unlike the condition in modern humans (Latimer and Ward 1993; Lordkipanidze et al. 2007). Additionally, the African remains may suggest the primitive condition of diaphragmatic placement (Williams 2011) even though they appear to retain five lumbar vertebrae, as is the modal condition in humans (Haeusler, Martelli, and Boeni 2002; Haeusler, Schiess, and Boeni 2011; Williams 2011).

Other thoracic and pelvic features appear derived. The thorax is broad superiorly and narrow inferiorly (based on the angulation of KNM-WT 15000's ribs to thoracic vertebrae; Jellema, Latimer, and Walker 1993). This shape suggests that *H. erectus* had a relatively small gut (Aiello and Wheeler 1995), which has implications for diet quality and possible foraging shifts. Additionally, a number of pelvic features of *H. erectus* have been argued to be more similar to *H. sapiens* than to *A. afarensis* and possibly *H. habilis* (Ruff and Walker 1993). However, some of these features are from os coxae of indefinite species attribution, such as KNM-ER 3228, and may also be seen in non-*Homo* pelvises such as the *A. sediba* adult, MH 2. Furthermore, Holliday (2012) contends that pelvic narrowing is not seen until *H. sapiens*.

Until recently, sexual dimorphism was thought to be smaller in *H. erectus* than in *Australopithecus* because of differentially large *H. erectus* females (Aiello and Key 2002; Leonard and Robertson 1997; McHenry 1992; McHenry and Coffing 2000; Ruff 2002; but see Susman, de Ruiter, and Brain 2001). Current evidence suggests, however, that cranial and body mass dimorphism may have been as large as in earlier hominins (Pontzer 2012; Spoor et al. 2007). However, this conclusion is dependent on the frame of comparison. Plavcan (2012) shows that there is a significant temporal component-to-size variation in *Homo*. And he shows that when compared with intraspecific variation in extant apes, *H. erectus* size variation (and perhaps dimorphism) is not particularly remarkable. To complicate matters, the assemblages make clear that not all small-sized individuals are females. In the small-sized Dmanisi population, some cranially robust probable male remains (D3444; 638 cm³) are absolutely small (Lordkipanidze et al. 2006). Similarly, at Olduvai, OH 9 (1,067 cm³) and OH 12 (727 cm³) differ greatly in size but not robusticity (i.e., cranial thickness, superstructure development), which I interpret as within-sex variation. Nonetheless, cranial and body mass CVs are similar to one another (around 15%–19%) and not substantially different than species of *Australopithecus* or early *Homo* (12%–20%; table 5). Given small and uncertain samples, the values should not be weighed too heavily; none-

theless, they do not suggest a reduction of dimorphism in *H. erectus* over other groups.

Given that by 1.8 or 1.9 Ma *H. erectus* coexists with two groups of early *Homo*, the origin of the taxon must predate this by some time. Craniofacial affinities are strongest with the 1813 group, suggesting that the A.L. 666 maxilla is one possible source population.

Summary of Shifts in *Homo*

Early *Homo* appears in the record by 2.3 Ma. By 2.0 Ma at least two facial morphs of early *Homo* (1813 group and 1470 group) representing two different adaptations are present (table 3). The 1813 group survives until at least 1.44 Ma. Early *Homo erectus* represents a third more derived morph yet and one that is of slightly larger brain and body size but somewhat smaller tooth size. South African remains of early *Homo* are present; however, they likely represent a separate species from those in East Africa (see Grine et al. 2009).

Small cranial remains from Georgia and Africa provide evidence of substantial individual and perhaps populational size variation within early *H. erectus* and indicate overlapping ranges of brain size with other early *Homo*. However, even with these new discoveries, *H. erectus* had a larger range (638–1,067) and average ($x = 810$ cm³) of cranial capacity than did other early *Homo* (510–750, $x = 629$ cm³; Antón et al. 2007). Currently, the overlap of cranial ranges is greater than is the body size overlap; however, this may reflect sampling bias between cranial and postcranial remains.

Although the fossil evidence is limited, average body and brain size increase appears to be an important shift between early *Homo* and *Australopithecus* and again between *H. erectus* (sensu lato) and other early *Homo* (*H. habilis* sensu lato). Holliday (2012) and Pontzer (2012) document ~33% increase in average mass estimates between the genera *Australopithecus* and early *Homo* (all taxa from 2.0 to 1.5 Ma inclusive of *H. erectus*) and about a 10% increase between early non-*erectus* *Homo* and *Australopithecus*. Body size estimates from postcranial specimens that can be certainly assigned to *H. erectus* from Africa and Georgia yield adult stature estimates between about 145 and 185 cm and adult body mass estimates of between 40 and 65 kg (tables 5, 8; Graves et al. 2010; Lordkipanidze et al. 2007; McHenry 1992, 1994; Ruff and Walker 1993). The lower end of the range may decrease to as little as 120 cm and 30 kg if the Gona pelvis and Swartkrans postcrania are certainly assigned to *H. erectus*. The sparser evidence for early non-*erectus* *Homo* overlaps the lower end of this range (118–150 cm and 30–60 kg) but is about 15% smaller than the combined early *H. erectus* mean (Georgia + Africa) and 37% smaller than the early African *H. erectus* mean. Dimorphism as proxied by CVs seems no less than earlier *Australopithecus*, but the variables used and the scale of comparison seem to influence the results (table 5; and see Plavcan 2012).

Average differences in body size have implications for life

history and ranging that may be of particular importance to niche differentiation in Africa. The overall larger size of early *H. erectus* and their different patterns of postcranial strength if not length may indicate larger home range sizes and perhaps more open habitat for *H. erectus*, all of which may entail greater daily energy requirements (Aiello and Key 2002; Antón, Leonard, and Robertson 2002; Leonard and Robertson 1997; Ruff 2009; Steudel-Numbers 2006). Based on life history correlates in modern humans (Kuzawa and Bragg 2012), differences in average body size among and between taxa may also signal decreased extrinsic mortality rates and/or increased nutritional sufficiency in the larger-bodied morph, including some combination of decreased predator and parasite load or susceptibility and increased diet quality.

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