**Associated ilium and femur from Koobi Fora, Kenya, and**

**postcranial diversity in early *Homo***

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**Abstract**

During the evolution of hominins, it is generally accepted that there was a shift in postcranial morphology between *Australopithecus* and the genus *Homo*. Given the scarcity of associated remains of early *Homo*, however, relatively few fossil data are available on early *Homo* postcranial morphology. There are hints of postcranial diversity among species, but our knowledge of the nature and extent of potential differences is limited. Here we present a new associated partial ilium and femur from Koobi Fora, Kenya, dating to 1.9 Ma that is clearly attributable to the genus *Homo* but documents a pattern of morphology not seen in East African early *Homo erectus*. The ilium and proximal femur share distinctive anatomy found only in *Homo*. However, the geometry of the femoral midshaft and contour of the pelvic inlet does not resemble that of any specimens attributed to *Homo* *erectus* from East Africa. This new fossil confirms the presence of at least two postcranial morphotypes within early *Homo*, and documents diversity in postcranial morphology among early *Homo* species that may reflect underlying body form and/or adaptive differences.

**Keywords**: ilium, femur, *Homo*, Koobi Fora

**Introduction**

Because postcranial anatomy may reflect locomotion, manipulatory behaviors, reproductive biology, and more, understanding the morphology of the early *Homo* skeleton is key to understanding the initial evolution of the genus. Within the evolution of hominins, it is generally recognized that there was a shift in postcranial morphology between *Australopithecus* and *Homo* (e.g.Wood and Collard, 1999; Bramble and Lieberman, 2004). However, given the scarcity of associated remains of early *Homo* (Brown et al., 1985; Johanson et al., 1987; Leakey et al., 1989; Lordkipanidze et al., 2007), there has been limited evidence of postcranial diversity among species.

East African *Homo erectus* postcranial anatomy is known from only three specimens with associated craniodental material: KNM-WT 15000 (Brown et al., 1985; Walker and Leakey, 1993), KNM-ER 1808 (Walker et al., 1982; Leakey and Walker, 1985) and KNM-ER 803 (Leakey and Wood, 1974). To date, no postcranial elements have been confidently attributed to *Homo rudolfensis*. Just a few postcranial elements have been referred to *Homo habilis*. The type specimen, OH 7, includes the type mandible and a partial hand skeleton (Leakey et al., 1964), although some authors have questioned the association between these elements based on aspects of its anatomy compared with those of other early hominins (Tuttle, 1967; Robinson, 1972; Tocheri et al., 2003; Moyà Solà et al., 2008; Almécija et al., 2010). The partial foot OH 8 was also attributed to *H. habilis* as it was from the same locality as OH 7 (Leakey et al., 1964), but is not itself definitively associated with the type specimen or with other cranial or dental remains. Two partial skeletons have been referred to *H. habilis* based on associated cranial fragments: OH 62 (Johanson et al., 1987) and KNM-ER 3735 (Leakey et al., 1989). Both partial skeletons, however, are highly fragmentary. KNM-ER 3735 preserves only a few postcranial elements, and OH 62 lacks the ends of its long bones, leading to ambiguity about limb proportions in both skeletons. OH 62 is interpreted as having relatively longer and/or stronger upper limbs than found in *H. erectus* (Johanson et al., 1987; Hartwig Scherer and Martin, 1991; Leakey et al., 1989; Ruff, 2009) with a pattern of femoral diaphyseal cross-sectional geometry unlike that of *H. erectus* (Ruff, 2009). KNM-ER 3735 is too poorly preserved to evaluate limb proportions accurately, but comparison of all of its preserved elements suggest relatively larger upper vs. lower limbs (Leakey et al., 1989), as seen in OH 62. However, given the fragmentary nature of the OH 62 and KNM-ER 3735 skeletal elements on which these interpretations are based, reliability any estimate of limb proportions can be questioned (Korey, 1990; Richmond et al., 2002; Haeusler and McHenry, 2004; Reno et al., 2005).

Other isolated postcranial elements have been attributed to *Homo* (KNM-ER 737, KNM-ER 1472, KNM-ER 1481, OH 28, KNM-ER 3228, BSN 49/P27 (Day, 1971; Day and Leakey, 1973; Day et al., 1975; Leakey, 1976; Rose, 1984; Brown et al., 1985; McHenry, 1994; Ruff, 1995; Simpson et al., 2008). Because they are unassociated with craniodental remains, their actual taxonomic attribution is unknown. Given the probability that species of early *Homo* were synchronic with each other and with *Australopithecus boisei*, the uncertainty about the extent of differences in postcranial anatomy among species of African early *Homo* confounds our ability to identify which species is represented by these isolated postcranial fossils.

Here we present a new associated partial pelvis and femur from Koobi Fora, Kenya, dating to 1.9 Ma that is clearly attributable to the genus *Homo,* but which displays a pattern of postcranial morphology not seen in early *H. erectus*.

**Recovery of fossils**

In 1980, a femoral midshaft fragment, KNM-ER 5881, was recovered from Koobi Fora, Kenya (Leakey and Walker, 1985). In July 2009, the Koobi Fora Research Project field expedition returned to the site, which was still marked by a numbered metal tag. There, Hillary Sale discovered the proximal end of the same right femur, and Matthew Skinner found a partial left ilium from the same individual. Subsequent seiving at the site yielded a fragment which conjoins the ilium, and a larger proximal diaphyseal fragment which conjoins the original 1980 midshaft gragment, leaving no doubt that they are parts of the same bone. The proximal end of the bone does not quite meet the proximal shaft fragment, but preserved contours show that they very nearly meet. The ilium was found in close proximity to the femoral fragments (Fig. 1), and the preservation of the bones is comparable. The size of the acetabulum corresponds to that of the estimated femoral head size, confirming attribution to the same individual (see below).

*Figure 1 here*

**Geologic Context**

The KNM-ER 5881 hominin fossils were recovered from the surface of a gravelly sandstone in collecting Area 105 of the Koobi Fora region (Table 1).  The fossils exhibit adhering sandstone matrix, and in the local outcrop there are no comparable strata immediately above the site (the nearest stratigraphically higher sandstone is exposed >100 m away). The circumstances of discovery, with the original specimen found in 1980, and additional material recovered from the same locality in 2009, after a period of nearly 30 years, suggests the latter material was not yet exposed in 1980, and that these fossils were all found very close to the point of burial. The sandstone lies stratigraphically below the KBS Tuff (1.88 Ma; McDougall and Brown, 2006; Joordens et al., 2013) and above the base of the Olduvai Subchron (1.94 Ma; Horng et al., 2002; Joordens et al., 2013), yielding a depositional age for the fossils of approximately 1.9 Ma.

*Table 1 here*

Within Area 105, the KNM-ER 5881 locality lies in exposures attributed to the Upper Burgi and KBS members of the Koobi Fora Formation (Brown and Feibel, 1986). The stratigraphy of the area was investigated in detail by H. J. White and D. R. Burggraf in the 1970s (Burggraf, 1976; White, 1976; Burggraf et al., 1981; White et al., 1981). Field workers in the 1960s and 1970s considered all of the fluvial channels near the stratigraphic level of the KBS Tuff to relate to a “Post-KBS Erosion Surface” (Findlater, 1976, 1978, 1997), a single disconformity within this interval, and thus deposits above this ‘surface’ were correlated as a single stratigraphic level (Leakey and Leakey, 1978). KNM-ER 5881 was first reported by Leakey and Walker (1985) as derived from a level above the KBS Tuff based upon this understanding. Subsequent work (Feibel, 1988; Brown and Feibel, 1991) demonstrated that there are multiple erosional surfaces through this interval, and that many of the associated sandstone bodies predate the KBS Tuff. This observation is explained by base-level response behavior in the Turkana Basin system, which has been demonstrated to link closely to monsoonal variability at the frequency of orbital precession (20,000 years) (McDougall and Brown, 2006; Joordens et al., 2011; Joordens et al., 2013). Close investigation of the strata exposed around the KNM-ER 5881 locality (Fig. 2) shows a minimum of three disconformity surfaces below the KBS Tuff, and a further four or more above, all of which were once considered correlative. The sandstone body from which the KNM-ER 5881 fossils were recovered can be demonstrated to be stratigraphically below the KBS Tuff. The archaeological site FxJj 1, the type KBS locality, lies 375 m to the northeast, and additional tuff lenses geochemically demonstrated to be the KBS Tuff are found in outcrops 110 m to the northeast, and 450 m to the south of the fossil locality.

*Figure 2 here*

There are two styles of fluvial sand bodies in these exposures. One consists of the fairly typical upward-fining sand, overlain by a pedogenically-modified mudstone, forming a distinctive couplet. This represents channel aggradation via lateral accretion of the sand followed by vertical accretion of mudstone on the exposed floodplain. The second style is a channel-form sand body, with no associated fine sands. This is interpreted to represent a cut-and-fill event associated with a minor disconformity. At least some of these are likely paced by precessionally-driven (20,000 year) variation in monsoonal intensity. In this model, lowering of local base-levels occurs as a response to monsoonal minima (and drop in lake-level) cutting an erosional surface, and subsequent base-level rise results in the channel fill part of the cycle. Between these extremes, more normal fluvial processes result in the typical sand-mud couplets, such as the package from which KNM-ER 5881 derives.

**Description of KNM-ER 5881**

*KNM-ER 5881a: Right midshaft femoral diaphyseal fragment* (Fig. 3)

Preservation: KNM-ER 5881a consists of two parts of the femoral diaphysis. The initial portion was discovered in 1980 (Leakey and Walker, 1985). This fragment extends from roughly midshaft to a point 72.5 mm proximally, and preserves all sides of the diaphysis. The second portion of KNM-ER 5881a was recovered in 2009 and joins well with the initial fragment (Fig. 3), leaving no doubt that they are parts of the same bone. The new fragment consists of a segment of proximal shaft that includes only the anterior half of the diaphysis. It extends proximally from the proximal midshaft end of the original fragment for a length of 67.8 mm. With both fragments together, KNM-ER 5881a is 130 mm long.

The original KNM-ER 5881a fragment was described as a left femur preserved from midshaft distally. However, with the recovery of the new part of this bone, it is clear that it actually represents the right side extending from midshaft proximally. Because the distal end is clearly at or near midshaft, this new interpretation does not affect descriptions of the midshaft cross-sectional diaphyseal size or shape in this specimen (e.g. Ruff, 1995). The exact location of midshaft cannot be determined accurately, so a reasonable estimate of original bone length cannot be made. However, midshaft diaphyseal geometry can be estimated using the distal end of this fragment and compared with femora of other individuals, as femoral midshaft contours do not change appreciably from about 40% to 60% of bone length (see Ruff and Hayes, 1983; Sladek et al., 2010).

*Figure 3 here*

Morphology: At midshaft (the distal break), the diaphysis measures 22.8 mm anteroposteriorly by 21.0 mm mediolaterally. At the proximal end of the distal fragment, the bone is about 21.5 mm anteroposteriorly by 22.8 mm mediolaterally. There is a pronounced linea aspera and strong pilaster measuring roughly 5.5 mm across that begins to widen towards the distal end of the fragment. Towards the proximal end of the bone, the medial shaft begins to flare medially towards the neck to become 25 mm wide mediolaterally at the break as preserved. No portion of the gluteus maximus attachment is preserved. Cortical thicknesses at the distal break are 5.1 mm anteriorly, 5.8 mm medially, 8.0 mm posteriorly and 6.3 mm laterally. Where the two parts of this specimen articulate (proximal end of the original fragment) cortical thicknesses are 5.3, 6.1, 7.3 and 8.0 mm, respectively.

*KNM-ER 5881b: Proximal femur* (Fig. 3)

Preservation: KNM-ER 5881b consists of most of the femoral head and neck, and is 74 mm in maximum dimension as preserved. It does not quite join with KNM-ER 5881a, but we estimate that only a small amount of bone is missing between the fragments. The greater trochanter is missing, but the bone surfaces flare towards it at the tubercle along the proximal portion of the intertrochanteric line, and along its posterior, superior and anterior margins. No portion of the lesser trochanter is preserved. The intertrochanteric line is prominent and visible for most of its length, and the distal break is located at its distalmost extent. The only preserved surface of the head is along the proximoanterior portion, with another small peninsula of subchondral bone projecting laterally, so that the maximum preserved original surface of the femoral head is no larger than 20 x 20 mm.

A tomographic section taken through the femoral neck reveals that the preserved external contours of KNM-ER 5881b are largely unaffected by any apparent postmortem shape or size changes (Fig. 6). There is one crack that traverses the inferior portion of the neck that is up to 1 mm wide. Reconstruction of the neck to remove this crack alters the anteroposterior breadth of the bone here by only 0.3 mm, so we have used this lower value in our analyses to be conservative.

*Figure 4 here*

Morphology: The femoral neck flares out towards the head on all sides, even dorsally where very little of the trabecular bone of the head remains. Vascular grooves and foramina are visible along its superior margin. At its narrowest point, the neck measures 20.4 mm anteroposteriorly by 24.0 mm superoinferiorly. The head can be estimated to have been 37 mm in diameter (see below). KNM-ER 5881a and 5881b are clearly part of the same bone. Although a precise join between these specimens is not possible, they can be oriented relative to one another based on preserved contours (Fig. 3) to form roughly the proximal half of a single bone.

*KNM-ER 5881c: Partial left ilium* (Fig. 5)

Preservation: KNM-ER 5881c is a fragment of left ilium preserving the cranial third of the acetabulum, extending posteriorly to a point just where the auricular surface would have been, and superiorly to a point 72 mm from the acetabular margin. The anterior inferior iliac spine is preserved at its most proximal extent, but the anterior iliac border is missing superior to this point, and patches of surface bone are missing between it and the acetabulum, although the contours of the bone are preserved here. None of the iliac crest is preserved. The surface bone immediately internal to the acetabulum is somewhat crushed. Only part of the lunate surface is preserved for a maximum length of 34.5 mm. The margins of the lunate surface are not well preserved and its width cannot be measured due to damage to the bone along the acetabular floor, but the bone is preserved to what would have been the center of the floor.

*Figure 5 here*

Along some of the cracks in the ilium, mild displacement has occurred. Although most have a minimal effect on its overall morphology the superior fragment is visibly offset from the rest of the bone, so that it is inclined further medially than it would have been originally (Fig. 6). CT-based digital realignment of this fragment produces a more natural contour of the bone (Fig. 6). Other than along this fracture line, there is no other notable deformation apparent on the KNM-ER 5881 fossils. Comparative observations were made using both the reconstructed and unreconstructed versions of the specimen.

*Figure 6 here*

Morphology: The iliac blade as a whole is laterally convex in the transvers plane, but only very slightly so in a coronal plane. Its minimum thickness is 2.9 mm, which is immediately anterior to where the bone begins to swell towards the sacroiliac joint; the maximum thickness, 8.3 mm, is located at the iliac pillar. The linea terminalis is gently rounded with no discernable crest. Along the iliac body, between the sacroiliac and hip joints, the bone is 16.0 mm thick. At the posterior break, which we estimate is just anterior to where the auricular surface would have been, the bone is up to 21.5 mm at its thickest.

A shallow depression with no distinct edges flanks the margin of the auricular surface area. The margin of the auricular surface itself is broken away, but the contour of the bone indicates that the bone is broken just along this edge. The flanking depression is shallow and smooth and has no sharp crests or contours typical of a preauricular sulcus, and the sulcus qualifies as “absent” using the systems described by either Novak and colleagues (2012) or Buikstra and Ubelaker (1994).

Anteriorly, the preserved portion of anterior inferior iliac spine is up to 5.2 mm thick, which is at the inflection point superior to which it is flexed laterally. Any visible scarring for the reflected head of the rectus femoris muscle is obscured by mild surface damage, but a distinct gutter flanks the superolateral margin of the acetabulum extending to a point immediately superior to the anterior inferior iliac spine, with its posterior margin along the iliac pillar, forming the “shelf” for the reflected head of the rectus femoris muscle referred to by Simpson and colleagues (2008). There is also a gentle concavity on the lateral side of the iliac blade along the region opposite where the sacroiliac joint would have been. The acetabulum can be estimated to have inscribed a sphere 41.5 mm in diameter (see below). Actual rim-to-rim diameter of the acetabular margin cannot be estimated accurately.

**Materials and Methods**

*CT scanning*

To document the external and internal morphology of KNM-ER 5881 the specimen was CT scanned with the Siemens Somatom Sensation 16 of the Muthithi Clinic, Aga Khan University Hospital, Nairobi. The slice collimation was 0.75 mm, and images were reconstructed with a voxel size of 0.14 x 0.14 x 0.30 mm (KNM-ER 5881a) or 0.18 x 0.18 x 0.30 mm (KNM-ER 5881b,c), using an extended CT scale and both a H60s and H70h kernel.

*Comparative sample*

KNM-ER 5881 was compared with 274 nonhuman anthropoids and 89 modern humans (Table 2). Access to comparative specimens was graciously granted by the following institutions and curatorial staff: United States National Museum (Darrin Lunde, David Hunt), Museum of Comparative Zoology at Harvard (Judith Chupasko), Cleveland Museum of Natural History (Lyman Jellema), American Museum of Natural History (Eileen Westwig), Naturalis Leiden (Steven van der Mije), Bavarian State Zoological Collections (Michael Hiermeier), Field Museum of Natural History (Bill Stanley), National Museums of Kenya (Ogeto Mwebi), Royal Museum for Central Africa (Emmanuel Gilissen), University of Zurich (Carel van Schaik), and Powell Cotton Museum (Malcolm Harman).

*Table 2 here*

Laser scan data were collected using either a Konica-Minolta Vivid 9i (Konica-Minolta, Tokyo, Japan) or a Next Engine Desktop 3D Scanner (NextEngine, Malibu, CA). All scan data were imported into PolyWorks software (InnovMetric, Québec, Canada) for post-processing, final model creation and analysis. Models created from scan data derived from Next Engine and Konica-Minolta (Vivid 910, a lower-accuracy version of the Vivid 9i) scanners has been demonstrate to be nearly equivalent (Aguilar et al., 2009; Sholts et al., 2011). Superimposition in polyworks of 3D-models of the same bones scanned with both machines revealed minimal differences in surfaces, and nearly identical measurements of surface areas and volumes. All scan data were imported into PolyWorks software (InnovMetric, Québec, Canada) for post-processing, final model creation and analysis.

For all nonhuman primates and 20 of the humans, both hipbone and femur were scanned. Femoral scans were not available for 61 of the human specimens. Dr. Dave Hunt (USNM) kindly measured femoral head size with calipers on these specimens. Linear measures of femoral head size (superoinferior) taken on original specimens are highly correlated with estimates of femoral head sphere diameter derived from scan data (r = 0.930, n = 50), so combining data sets is reasonable. Repeating analyses using only data derived from the subset of 3D models yields equivalent results to those derived from the larger data set. Hipbones and femora of all published comparative fossil specimens from Pliocene and Pleistocene hominins were also scanned (Table 3).

*Table 3 here*

*Hip joint size estimates*

Polygonal models of both hipbone and femur were used to reconstruct joint diameters. Acetabular size was quantified by selecting the lunate surface manually for each individual using Polyworks and using least squares best-fit approach to fit a sphere to the surface using the procedure described by Hammond and colleagues (Hammond et al., 2013) (Fig. 7). Data points lying more than 2.5 standard deviations from the average used to compute the sphere were rejected, and the sphere was recomputed without outlier points. This method of fitting spheres has less than 1% error within and among observers (Hammond et al., 2013).

*Figure 7 here*

The KNM-ER 5881c ilium does not preserve the entire lunate surface. It does preserve regions of the acetabulum that correspond to lunate regions 4-5 described by Hammond and colleagues (2013). Using only this portion of the lunate surface to fit a sphere in human acetabulae is associated with up to 5% prediction error compared to a sphere diameter generated from the entire lunate surface (Hammond et al., 2013). Spheres were fit three times by ASH to the preserved portion of KNM-ER 5881c lunate surface, avoiding abraded or cracked surfaces. The three values were averaged to generate a “best estimate” acetabular sphere diameter of 41.5 mm (Hammond et al., 2013) with a minimum estimate of 39.0 mm and maximum of 44.0 mm (Table 4).

*Table 4 here*

Femoral head size was quantified in two ways to ensure the best estimate possible given the abraded nature of the KNM-ER 5881b femoral head. First, for extant specimens, a least-squares best-fit sphere was fit to the entire femoral head subchondral surface, not including the fovea capitis (Fig. 7). As for the acetabulum, points more than 2.5 standard deviations from the average for the femoral head sphere used to compute the sphere were rejected, and the sphere was recomputed without outlier points. Fitting least squares spheres to the femoral head has a less than 1.5% error rate (Plavcan et al., 2012), comparable to that observed for the acetabulum.

Three observers (CVW, ASH, JMP) independently fit spheres to the preserved portion of KNM-ER 5881b femoral head articular surface, avoiding uneven or abraded cracked surfaces. Because of the limited surface preserved for KNM-ER 5881b, the observers each independently fit 5 spheres to the 3D model. Averages of the estimates for each observer were within 0.3 mm of each other. The average estimated sphere diameter for all three observers was 36.8 mm (Table 4).

To provide a second estimate of femoral head size, femoral head diameter was also estimated from the acetabular sphere diameter following Plavcan and colleagues (2014). For all extant specimens, the natural log-transformed femoral head diameter was regressed on log-transformed acetabular sphere diameter using ordinary least squares (Table 5). Regressions were run for (1) the entire sample, (2) all apes and humans combined, (3) just humans, and (4) a sample of great apes and humans. This latter sample was chosen because of the influence of hylobatids on the ape-human regression (Plavcan et al., 2014). Whereas the human data overlap that of great apes almost perfectly, and the regression line through the entire hominoid sample passes through the monkey sample, hylobatids appear to have either a relatively large acetabulum or small femoral head for their size. Given the small body size of hylobatids, they have large leverage on the regression, and generate a larger estimate of femoral head size for KNM-ER 5881 than all other regressions. As predicted, there is a significant correlation between femoral head and acetabulum sphere diameter across all individuals (r = 0.997, p ≤ 0.001, n = 365) as well as for a subset comprised of just *Homo sapiens* (r = 0.996, p < 0.001, n = 91).

*Table 5 here*

Estimates were back-transformed from log data space and corrected using the “smearing estimate” correction factor (Smith, 1999), as reported in Plavcan et al (2014). The estimates of femoral head size derived from the three regressions are almost identical to the best estimate derived from fitting spheres directly to the surface, 37 mm (Tables 4 and 5, see also Fig. 11). This finding (a) suggests a low level of error in the KNM-ER 5881 sphere diameter estimate and (b) provides strong evidence that the two halves of the fossilized joint belonged to the same individual. We therefore feel comfortable that the estimate of 37 mm represents a reasonably accurate femoral head diameter for KNM-ER 5881.

*Femoral neck and diaphysis dimensions*

Femoral neck shape was quantified using maximum superoinferior diameter and minimum anteroposterior diameter at the narrowest point of the neck, following Harmon (2006). Traditional measures of femoral neck length cannot be taken because the head of KNM-ER 5881 is incomplete, its greater trochanter is missing, and the diaphyseal fragment does not join securely to the proximal femur. For this reason, a proxy measure was taken from the margin of the femoral head anteriorly to the anteromedial margin of the greater trochanter at its midpoint (Fig. 8). Although less precisely replicable than traditional measures, reflects femoral neck length fairly well. Also, it is a metric that can be taken on the fossil itself with reasonable accuracy, and we were able to repeat this measurement five times with less than 3% error among trials. Traditional neck lengths require either a complete greater trochanter, or an articulated diaphysis, neither of which are present in KNM-ER 5881 and would have to be estimated. The proxy neck length value for KNM-ER 5881 may be a very slight underestimate of its original dimension given the abrasion of the femoral head margin and that the trochanter is missing. However, given the preserved contours of the head, and the fact that the anterior surface of the femur begins to flare out towards the lateral margin of the fragment at the margin of the greater trochanter, this value is close to what it would have been originally.

Femoral midshaft diaphyseal cross-section dimensions were taken from Ruff (1995) who calculated second moments of area from photographs of the broken end of the original KNM-ER 5881a fragment.

*Figure 8 here*

*Iliac morphology*

The position and orientation of the iliac pillar were quantified following Kibii and colleagues (2011). Location of the iliac pillar was quantified as the minimum distance between the most prominent (thickest) point on the pillar to the anterior border of the ilium at the level of superior margin of the anterior inferior iliac spine (Fig. 9). so as to provide a metric that could be quantified on the fragmentary KNM-ER 5881c specimen, with a measurement error of less than 2 mm among five trials. Iliac pillar orientation was quantified by computing the angle formed between a line through the anterior inferior and posterior inferior iliac spines and the long axis of the iliac pillar (Kibii et al., 2011) (Fig. 9), which can be estimated for KNM-ER 5881 with reasonable accuracy, and with variation in estimates less than 3° total among five measurement trials. Dimensions of the iliac body, defined here as the region between sacroiliac and hip joints, were also quantified. Iliac body length (also referred to as lower iliac height (Ward, 1993) is defined as the minimum distance between auricular surface and centerpoint on of the floor (sensu Ward, 1993) of the bony acetabulum. Breadth was calculated as the minimum transverse distance across this area.

*Figure 9 here*

*Sciatic notch*

Sciatic notch shape was quantified on the polygonal models using Polyworks software. Landmarks were selected that were preserved in KNM-ER 5881c. First, sciatic notch length was defined as a straight vector line (A) drawn from the point at the posterior break, which is along the posterior border of the ilium adjacent to the point where the convexity of the anteroinferior corner of the auricular surface margin straightens out to where the posterior margin of the bone is broken inferiorly, which is immediately adjacent to the acetabulum (near the ilio-ischial junction) (Fig. 10). A second vector, sciatic notch depth (B) was then created as the maximum depth of the notch perpendicular to vector 1. Vector 2 also divided breadth of the notch into anterior (A1) and posterior (A2) portions (Fig. 10). Three ratios were created to summarize the shape of the sciatic notch: 1) Depth to width of sciatic notch (B ÷ A); 2) Breadth of anterior to posterior portions of the sciatic notch (A1 ÷ A2); and 3) Posterior sciatic notch breadth to depth of the notch (A2 ÷ B). Repeated trials demonstrate that each measurement can be made with 5.5% or less error. Mean values of all three measures were calculated for males and females in extant taxa.  Discriminant function analysis was performed on the extant comparative sample to determine the utility of each individual sciatic notch ratio to estimate sex, as well as for the utility of all three ratios to determine sex when used in conjunction with each other.

*Figure 10 here*

*Pelvic inlet*

Because of the fragmentary nature of KNM-ER 5881, pelvic inlet dimensions cannot be quantified directly using standard anteroposterior and mediolateral dimensions (e.g. following Tague, 2005). Instead, curvature of the linea terminalis of the pelvic inlet was quantified on individual hipbones following Ruff (1995) (Fig. 11). A line was first drawn between a point along the linea terminalis adjacent to the inferior surface of the anterior inferior iliac spine and the dorsal-most point along linea terminalis adjacent to the auricular surface margin, defined as “length” of the linea terminalis. Linea terminalis “depth” was calculated perpendicular to this line to the furthest point along the brim. The ratio of linea terminalis depth to linea terminalis length represents the pelvic inlet curvature of the linea terminalis (Fig. 11) (Ruff, 1995).

*Figure 11 here*

Because of the way that the KNM-ER 5881c pelvis is fractured, assessing relative pelvic inlet breadth using Ruff’s method was not possible, so we modified Ruff’s method (Fig. 11). Based on careful comparison of the preserved morphology of KNM-ER 5881c with other fossil hominin and modern human pelves it was determined that 80% of the original linea terminalis length was preserved on the KNM-ER 5881 specimen, with roughly the same amount missing from anterior and posterior ends of linea terminalis length. Thus, the endpoints for measurement of the original linea terminalis length on all specimens were taken in such that the new linea terminalis length, which we call ‘modified linea terminalis length,’ was 80% of the length of the original linea terminalis length and parallel to the original linea terminalis length (Fig. 11). A modified linea terminalis depth was taken between the modified linea terminalis length and the deepest point along linea terminalis. The ratio of the modified linea terminalis depth to modified linea terminalis length represents what we term the modified pelvic inlet curvature of the linea terminalis. Repeated trial

Regression of modified pelvic inlet curvature on Ruff’s original pelvic inlet curvature measurement in the human sample used for this study (n=89) yields a high correlation (r = .966), demonstrating that the modified pelvic inlet curvature metric used here is nearly as effective as Ruff’s (1995) original metric to capture pelvic inlet shape.

*Assessment of significance of size difference between KNM-ER 5881 and KNM-ER 3228*

KNM-ER 5881 is similar in geological age to KNM-ER 3228, another hipbone from Koobi Fora (Rose, 1984), but it is notably smaller. Given that the two specimens are roughly contemporaneous, this raises the question of whether they are a male and female of the same species, large and small specimens of the same sex, or too variable to be accommodated in a single species.

To assess size, a ratio of KNM-ER 3228 to KNM-ER 5881, as well as the absolute difference between the two specimens, was calculated for both the estimated femoral head diameter and estimated acetabular diameter. Analyses were carried out on ln-transformed data to assist in visual comparison of variation across the interspecific size range, but results of the sampling experiment do not differ using transformed or untransformed data. A program was written in Matlab (v. 13) that randomly sampled pairs of individuals and calculated both the ratio and difference between the two specimens. This was done sampling one male and one female, and separately sampling two individuals of the same sex. For each measure and each composition (both sexes, only males, only females), 1000 pairs were sampled and the number of times that the fossil pair’s value exceeded that of the reference sample was tabulated. This was done using 10 extant reference samples from which femoral head and acetabular sphere diameters were calculated.

**Comparative Analysis**

*Proximal femur*

The proximal femur of KNM-ER 5881b resembles those of fossils attributed to early *Homo* (Fig. 12). The estimated femoral head diameter of KNM-ER 5881b (36.8 mm) falls within the absolute size ranges of both *Australopithecus* and of fossils generally attributed to early *Homo* (Fig. 13; Table 6). There are five *Australopithecus* fossils that exceed it in absolute size. It is smaller than those of all fossil *Homo* except for BSN49/P27 (Simpson et al., 2008). Femoral head size alone does not distinguish *Australopithecus* from *Homo*.

*Figures 12 and 13 and Table 6 here*

The KNM-ER 5881b femoral head is large relative to the size of the femoral neck (Fig. 14; Table 6). There is some overlap between *Homo* and non-*Homo* specimens, but KNM-ER 5881b falls above the range of all known *Australopithecus* specimens, and well within the range of *Homo* (Fig. 14; see also Simpson et al., 2008) It is exceeded in its proportions only by the juvenile KNM-WT 15000 (Fig. 14).

*Figure 14 here*

Femoral neck shape (anteroposterior relative to superoinferior diameter) also aligns KNM-ER 5881 exclusively with early *Homo* (Fig. 14; Table 6). In this index, there is no overlap between the available samples of *Homo* and *Australopithecus* from East Africa. The only Homo specimen to fall within the range of *Australopithecus* values is the d4167 femur from Dmanisi (Fig. 14). The KNM-ER 5881b femoral neck is expanded anteroposteriorly, unlike the compressed necks of *Australopithecus*  and the Dmanisi *Homo* specimen (Figs. 12 and 14) (Day, 1969, 1976, 1978; Lovejoy and Heiple, 1972; Lovejoy et al., 1973; Walker, 1973; Lovejoy, 1975; Wood, 1976; Corruccini and McHenry, 1978; McHenry and Corruccini, 1978; Stern and Susman, 1983; Jungers, 1990; Maclatchy, 1996; Ruff, 1998; Ruff et al., 1999; Lovejoy et al., 2002; Richmond and Jungers, 2008; Ruff, 2008; Harmon, 2009). The large femoral head relative to neck size and anteroposteriorly expanded femoral neck ally KNM-ER 5881b exclusively with East African *Homo* specimens among early hominins.

The femoral neck in KNM-ER 5881b is proportionally long compared with modern humans, as is the case for all *Australopithecus* and early Pleistocene *Homo* (Napier, 1964; Day, 1969; Robinson, 1972; Lovejoy et al., 1973; Walker, 1973; Lordkipanidze et al., 2007; Lovejoy, 1975; McHenry and Corruccini, 1976, 1978; Wolpoff, 1976; Kennedy, 1983; Wood, 1978; Ruff, 1995; Lovejoy et al., 2002; Richmond and Jungers, 2008) (Figs. 4, 12 and 15, Table 7). In addition to the “proxy” femoral neck length metric, qualitatively it is apparent that the KNM-ER 5881b neck was long. A large, flat area extends between the intertrochanteric line and the trochanteric margin, as seen in all other early hominins, and distinctly different from the modern human condition (Figs. 4 and 12). Metric and nonmetric evidence demonstrates that KNM-ER 5881b retains what is apparently the primitive hominin condition of having a relatively long femoral neck.

*Figure 15 and Table 7 here*

*Femoral diaphysis*

While the morphology of the ilium and proximal femur clearly support the attribution of KNM-ER 5881 to the genus *Homo*, the morphology of the femoral diaphysis is distinct from those of all definitive early *Homo* from East Africa, except OH 62 (Johanson et al., 1987) (Fig. 16) The midshaft diaphyseal contours of all known or hypothesized early *Homo* differ from those of humans and *Australopithecus* in two ways. They have a weakly defined pilaster (as defined by Hrdlicka, 1934), and have an expanded mediolateral dimension compared with anteroposterior diameter (Ruff, 1995) (Fig, 16) . The KNM-ER 5881a femoral diaphysis displays a pronounced linea aspera with strong pilaster (Hrdlicka, 1934), rather than the weakly developed pilaster seen on most other early *Homo*, except for OH 62 (Fig. 16) (Johanson et al., 1987; Ruff, 1995, 2009) and possibly KNM-ER 3735 (Leakey et al., 1989), both of which are attributed to *H. habilis*.

*Figure 16 here*

Perhaps partly related to development of the pilaster (see Ruff, 1995), the femoral diaphysis is mediolaterally narrow relative to its anteroposterior diameter at midshaft (23.0 mm anteroposteriorly and 21.0 mm mediolaterally) (Fig. 16 and 17, Table 8). This ratio, or pilasteric index, is well below one for all three East African *Homo erectus* fossils, which have mediolaterally broad femoral midshafts. The other East African femora that have been provisionally attributed to *Homo* (see Ruff, 1995) also have ratios above one. KNM-ER 5881, like *H. habilis* and the Dmanisi *H. erectus* femora, falls well above the line with a high index. Thus, KNM-ER 5881 is distinct from *H. erectus* in East Africa, more closely resembling the one *H. habilis* specimen OH 62, as it does in pilaster morphology.

*Figure 17 and Table 8 here*

KNM-ER 5881 is, however, similar in pilasteric index to the Dmanisi *H. erectus* femora. The exact significance of this is unclear, as these fossils have not been formally described or figured in print in posterior or cross-sectional views (see Lordkipanidze et al., 2007). At present, is not known whether they resemble other *Homo erectus* in pilaster morphology. There are several possible hypotheses that could explain the discrepancy between East African and Georgian *Homo erectus* femoral diaphyseal diameters. It is possible that pilasteric index varies among individuals, although the consistency within geographic regions suggests that this is not likely. Ruff’s (1995) argument that femoral diaphyseal morphology is related to overall body proportions would also predict that this much variation within or among conspecific populations is unlikely. It may be that midshaft cross-sections are variable among populations of *H. erectus* in different geographic regions. Or, since Dmanisi predates the East African specimens (Lordkipanidze et al., 2007; Joordens et al., 2013), it could be that there was change in this morphology over time within early *Homo erectus*. These hypotheses remain to be tested.

The relative bending strength of the KNM-ER 5881 femur at midshaft is lower mediolaterally relative to anteroposterior breadth than all other East African early *Homo*, putative early *Homo*, and later *H. erectus* fossils (Figs. 16 and 18; also Ruff, 1995, 1998, 2009). The midshaft section modulus of KNM-ER 5881a, an indicator of bending strength, falls well below the distribution for that of other early *Homo*, lacking the mediolateral bending strength of these other early *Homo* specimens. It falls further from the early *Homo* line (compared with a line calculated through fossil *Homo* data [Ruff, 1995], KNM-ER 5881 has a reduced major axis residual [calculated orthogonal to the RMA line] of .325 compared with a range of -.015 to .182 for other early *Homo* femora, and from a line calculated through human data points has a residual of .096 as compared with a range of -1.085 to -.226 for the other early *Homo* specimens, see Fig. 18). Overall, the KNM-ER 5881a femoral diaphysis more closely resembles those of later *Homo* and *H. habilis* (OH 62; Ruff, 2009) (Fig. 18), and is clearly distinct from those of East African *H. erectus.*

*Figure 18 here*

*Ilium*

Few standard linear metrics can be taken on KNM-ER 5881c as it is too fragmentary. Nonetheless it displays morphologies aligning it with other specimens attributed to early *Homo* (KNM-ER 3228, KNM-ER 1808, KNM-WT 15000, OH 28, BSN 49/P27; Day, 1971; Leakey, 1971; Walker et al., 1982; Rose, 1984; Brown et al., 1985; Leakey and Walker, 1985; Walker and Leakey, 1993; Simpson et al., 2008) (Fig. 19). The iliac pillar is not as thick as in other *Homo* pelves, perhaps related to the fact that KNM-ER 5881c is smaller than most *Homo* fossils, although it does display characteristic *Homo* morphology.

*Figure 19 here*

The anterior border of the ilium is flexed laterally, with an inflection point around the anterior inferior iliac spine conforming in parts preserved to a sigmoidal pattern, as seen in modern human pelves, and contrasting with the straight anterior border of the *Australopithecus* ilium (Figs. 19 and 20) (Simpson et al., 2008; Berger et al., 2010; Kibii et al., 2011). In anterior view, KNM-ER 5881c displays an inflection along the anterior border of the ilium superior to the anterior inferior iliac spine. Even though there is some variation within the *Australopithecus* ilia, with slightly more curved anterior borders seen in StW 431 and MH 2 (Fig. 20), the KNM-ER 5881c morphology is clearly more closely aligned with that of *Homo*.

*Figure 20 here*

KNM-ER 5881 has a distinct iliac pillar, although less thick than found in the much larger KNM-ER 3228 (Rose, 1984) and OH 28 (Day, 1971) hipbones and as described for BNS 49/S27 (Simpson et al., 2008), is nevertheless more pronounced than the weak or indistinct ones of *Australopithecus* (Zihlman, 1971; Robinson, 1972; Lovejoy et al., 1973; McHenry, 1975; Arsuaga, 1981; Simpson et al., 2008; Berger et al., 2010; Kibii et al., 2011). The iliac pillar does not run along the anterior border of the bone, but instead is positioned well posterior to it (Fig. 21 and 22). Even though broken, enough morphology is preserved to show clearly that there was more distance between the pillar and anterior margin of the bone than in any australopith specimen (Table 9) At the superior margin of the anterior inferior iliac spine, the pillar is at least 25 mm from the anterior iliac border, farther than of any *Australopithecus* specimen (Table 9, Figs. 21 and 22). KNM-ER 5881c falls within the morphological range of early *Homo* specimens, which is especially notable given that KNM-ER 5881c is smaller in size than the other early *Homo* fossils to which it is compared metrically here, although is similar to KNM-ER 1808.

*Figures 21 and 22 and Table 9 here*

The iliac pillar of KNM-ER 5881c is also more craniocaudally directed than typical for *Australopithecus*, and instead resembles that of *Homo* (Table 10; Figs. 19 and 22) (Kibii et al., 2011). Estimated iliac pillar orientation in KNM-ER 5881c is between 62-67°. The highest estimate (67°) was computed by drawing a line through the center of the anterior inferior iliac spine to the most inferiorly preserved point near where the posterior inferior iliac spine would have been, and the lowest estimate was made using an estimate of the highest position the posterior inferior iliac spine may have been. Values below 62° are unlikely given the preserved contours of the bone. KNM-ER 5881c has an iliac pillar orientation within the range of early *Homo* specimens, and higher than that of *Australopithecus*.

*Table 10 here*

A distinct sulcus is present along the posterosuperior margin of the acetabulum extending to the cranial end of the anterior inferior iliac spine as seen in anterior view (Figs. 19 and 22). This sulcus runs just along the anterior margin of the pillar, and flanks a large area for attachment of the reflected head of the rectus femoris muscle. This morphology is not seen in most *Australopithecus* pelves, which have either an indistinct gutter or one that extends only to the center or inferior portion of the anterior inferior iliac spine along a more anteriorly positioned iliac pillar. StW 431 has a visible sulcus, but in this fossil the sulcus is continuous with the center of the anterior inferior iliac spine, not with its cranial margin as in the early *Homo* specimens and KNM-ER 5881c. The distinctive nature of the shape of this gutter is less clear-cut than some of the other morphologies described here, but it also generally allies KNM-ER 5881c somewhat more closely with *Homo* than *Australopithecus.*

*Pelvic inlet*

Early hominins have relatively wide (platypelloid) pelvic inlets compared with modern humans (Tague and Lovejoy, 1986; Ruff, 1995, 1998; but see Haüsler and Schmid, 1995), except for BSN49/P27 (Simpson et al., 2008). Although inlet dimensions can only be quantified indirectly for KNM-ER 5881c, and using a metric not published for BSN49/P27, it appears that KNM-ER 5881 had a less platypelloid pelvic inlet than seen in *Australopithecus* (A.L. 288-1 and Sts 14) or known early *Homo* fossils to which it can be compared (KNM-ER 3228 and OH 28) (Figs. 19 and 23; Table 11). This morphology does not seem to be a reflection of sex, as KNM-ER 3228 was likely a male individual and OH 28 a female based on sciatic notch shape (see below). KNM-ER 5881 was a smaller individual than either of these, so size cannot be ruled out as a factor affecting inlet dimensions in early *Homo*. However, within humans, pelvic inlet shape is not correlated with size (e.g. Tague, 2005), so size is unlikely to be a factor shaping inlet dimensions in early hominins either. Instead, KNM-ER 5881 falls within the range of Pleistocene and modern humans with a more anteroposteriorly expanded inlet shape. Samples available for this analysis are very small, so these results should be interpreted with caution. Still, based on the model of Ruff (1995), the platypelloid shape is consistent with the lack of mediolateral expansion at the midshaft femur. If indeed BSN49/P27 (Simpson et al., 2008) is reported to have a more human-like rounder inlet shape than the two other specimens (KNM-ER 3228 and OH 28), it may be either that inlet shape is individually variable within species of early *Homo*, or that more than one species is represented by these four fossils. Only with additional fossils will be possible to test these hypotheses.

*Figure 23 and Table 11 here*

*Sex of KNM-ER 5881*

Whether KNM-ER 5881 represents a female or male is significant for potential taxonomic attribution and functional interpretation of its morphology. KNM-ER 5881 is considerably smaller than KNM-ER 3228. If the two fossil specimens represent male and female of the same species, the magnitude of femoral head and acetabular dimorphism would be most consistent with that seen in *Gorilla*, *Pongo*, and *Nasalis*, which are among the most size dimorphic living primates (Table 12). However, “dimorphism” of both variables would not significantly differ from that of the extant *Homo* sample used here (Table 12). Results from the resampling of single sexes suggest that it would be unlikely to draw two individuals of the same sex from most species. Only *Nasalis larvatus* and *Colobus guereza* show within-sex variation in one or both measures compatible with a single-species/single-sex model. Thus, if KNM-ER 5881 was a male individual, the implied degree of within-sex size variation is inconsistent with that typically seen in samples of extant primates. If it was female, however, KNM-ER 5881 could either represent a female of the same species as KNM-ER 3228, or simply belong to a different species than KNM-ER 3228. If KNM-ER 5881 was indeed a female from the same species as the male KNM-ER 3228, dimorphism levels in this species would probably exceed that seen in humans, and instead resemble that *Pongo* and *Gorilla*. For this reason, determining the sex of KNM-ER 5881 is of significant interest.

*Table 12 here*

The only sex indicator preserved in this fragmentary fossil is the sciatic notch, which tends to be broader and less symmetric in modern human females than males. Unfortunately, using each individual measurement of sciatic notch shape, or combining them all in a discriminant function analysis, modern human males and females are not completely separate in their distributions and KNM-ER 5881 falls within the area of overlap for all measures (Table 13). KNM-ER 3228 is exclusively aligned with males, consistent with its very large size, suggesting that this individual was almost certainly male. Statistically, there is a 65% chance that KNM-ER 5881 was female, but because of the extensive overlap between sexes seen in humans there is no way to confidently determine whether KNM-ER 5881 was either male or female, so we conclude that its sex is indeterminate. The apparent absence of a distinct preauricular surface also does not provide any information about sex, as this groove has been found to be absent in 94.8% of males, but also 36.6% of modern human females (n=129, Bruzak, 2002;Matt Novak et al., 2012).

*Table 13 here*

**Discussion**

Because it is unassociated with craniodental remains, the taxonomic attribution of KNM-ER 5881 must remain tentative. However, some observations can be made. Because the iliac and proximal femoral morphology of KNM-ER 5881 is clearly similar to *Homo* and distinct from that seen in *Australopithecus,* the most appropriate taxonomic attribution of KNM-ER 5881 is to the genus *Homo*. The KNM-ER 5881 femoral diaphysis is not consistent with a taxonomic attribution to East African *H. erectus*, however (Ruff, 1995). The combination of femoral and iliac morphology found in KNM-ER 5881 is not seen in any early *H. erectus* fossil from East Africa. The pilasteric index of the midshaft femur does, however, resemble those of the two femora from Dmanisi which have been attributed to *H. erectus* (Lordkipanidze et al., 2007). However, without further information on these specimens with which to evaluate proximal femoral or posterior diaphyseal morphology, and without an associated pelvis, the significance of this similarity is difficult to interpret at present.

Currently, two broadly contemporaneous species of non-*erectus* early *Homo* are recognized below the KBS Tuff at Koobi Fora, *H. habilis* and *H. rudolfensis* (Wood, 1991, 1992; Joordens et al., 2013), and KNM-ER 5881 could represent either of these species. The only femur attributed to *H. habilis* is that of OH 62. Its midshaft cross-sectional shape is similar to that of KNM-ER 5881. It has a partial femoral neck, but this is too incompletely preserved to retain diagnostic morphology. So at present, there is nothing specific to align KNM-ER 5881 exclusively with, or to exclude it from, *H. habilis*. No postcranial morphology for *H. rudolfensis* is currently documented in the fossil record. Therefore, it is not possible to determine which of these species is represented by KNM-ER 5881. The most appropriate and precise attribution of this fossil that can be made at present is to the genus *Homo*, but not *H. erectus*.

At a minimum, though, KNM-ER 5881 provides evidence of a second postcranial morphotype within early East African *Homo* distinct from that of early *H. erectus*. Preliminary evidence that there were different postcranial morphotypes within the genus *Homo* come from analyses of the two partial skeletons attributed to *H. habilis*, OH 62 and KNM-ER 3735 (Johanson et al., 1987; Leakey et al., 1989; Haeusler and McHenry, 2004, 2007; Ruff, 2009) (Fig. 24). Both appear to have had longer intermembral indices than later *Homo* and at least OH 62 appears to have different femoral diaphyseal geometric proportions from *H. erectus* as well (Ruff, 1995; Fig. 21). The OH 62 femoral diaphyseal midshaft cross section is virtually identical to that of KNM-ER 5881 in shape with a narrow mediolateral dimension and strong pilaster (Figs. 16, 17 and 18), although the latter is slightly larger (Figs. 17 and 18; Table 8). KNM-ER 5881 provides new and more complete evidence for postcranial variability among species of early *Homo*. Observed differences between KNM-ER 5881 and *H. erectus* do not support the hypothesis that all of early *Homo* should be subsumed into a single species, *H. erectus* (*contra* Lordkipanidze et al., 2013).

*Figure 24 here*

The combination of morphological features seen in KNM-ER 5881 is unlike that of any early hominin fossil yet described, suggesting a pattern of functional morphology that differs as well. A long femoral neck and mediolaterally expanded midshaft relative to its anteroposterior diameter is associated with a mediolaterally broad pelvic inlet in previously known early *Homo* fossils (Ruff, 1995, 1998). Ruff (1995) proposed that the broad pelvic inlet and long femoral neck of early *H. erectus* would result in high mediolateral bending moments about the femoral diaphysis, leading to the mediolaterally broad femoral diaphyseal cross-sectional shape and weak pilaster characteristic of this species. According to this model, *Australopithecus* would not have experienced such high mediolateral bending along the femoral diaphysis, because of their long femoral necks but smaller pelvic inlets, thus explaining their less mediolaterally expanded femoral diaphyseal midshaft cross-sections. Modern humans have broader pelvic inlets than early hominins given their large bony birth canals, but shorter femoral necks, also mitigating femoral mediolateral bending moments about the femoral diaphysis, and yielding a femoral mid-diaphyseal structure similar to that of australopiths. Thus, *Australopithecus* and modern humans have less mediolaterally expanded femoral diaphyseal midshaft cross-sections than seen in early *H. erectus*.

Based on Ruff’s (1995) model, the presence of a long femoral neck but mediolaterally narrower femoral midshaft of KNM-ER 5881 suggests that this individual would have had a relatively smaller, or at least less platypelloid, pelvic inlet than early *H. erectus*. Indeed, preserved contours of the linea terminalis in KNM-ER 5881 suggest a less platypelloid shape of the pelvic inlet in KNM-ER 5881 than in the other early *Homo* specimens and *Australopithecus* (Figure 26; Table 11). This difference could reflect either a more modern pelvic inlet geometry, and/or an absolutely smaller pelvic inlet than in early *H. erectus*. The *H. erectus* pelvis BSN29/P47 (Simpson et al., 2008; but see Ruff (2010) for an alternate taxonomic attribution for this specimen) has an anteroposteriorly expanded (gynecoid) inlet, but one that is also capacious and so also is mediolaterally broad. Because of this, Ruff’s (1995) model predicts that BSN29/P47 was probably unlike KNM-ER 5881 given the mediolaterally narrow femoral midshaft of the KNM-ER 5881 femur, which would imply a narrower pelvic inlet in this fossil than in BSN29/P47.

**Summary and Conclusions**

KNM-ER 5881 adds to the growing picture of morphological diversity in East African hominin evolution (e.g. Leakey et al., 2012). It supports the hypothesis that not all early *Homo* species had similar postcranial skeletons (Johanson et al., 1987; Leakey et al., 1989; Haeusler and McHenry, 2004, 2007; Ruff, 2009). The extent of postcranial variation, and its implications for understanding the morphological diversification and pattern of evolution that led to later *Homo*, remain unknown. KNM-ER 5881 provides a further basis for assessing taxonomy of the many isolated postcranial fossils known from East Africa. More fossil discoveries and more detailed comparisons of KNM-ER 5881 with other early hominin fossils will undoubtedly continue to shed light on this diversity and on the biology of the origins and early evolution of the genus *Homo*.

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**Figure Captions**

Figure 1. Photograph of the locality where KNM-ER 5881 was recovered (showing Hillary Sale and Matt Skinner). Approximate positions of original fragment found in 1980 and the other two found in 2009 indicated. The third femoral fragment and a piece of the ilium were recovered from sieving at the site.

Figure 2. Graphic sections of strata in Area 105, Koobi Fora, showing the context of the KNM-ER 5881 fossils.  Vertical scale in meters.  Local chronostratigraphic control based on isotopic age of the KBS Tuff (1.88 Ma; McDougall and Brown 2006) and magnetic polarity boundary at base of the Olduvai Subchron (bC2N, 1.94 Ma; Horng et al., 2002) as determined by Joordens and colleagues (2013).

Figure 3. KNM-ER 5881 femur. Top row: superior and inferior views. Bottom row: KNM-ER 5881a and b shown in approximate articulation in anterior (right side) and posterior (left side) views, with lateral view of the diaphysis only in between. The distal portion of the diaphysis, KNM-ER 5881a, originally found in 1980 is indicated. KNM-ER 5881b consists of the proximal diaphysis and proximal end of the bone, both of which were recovered in 2009. The two diaphyseal fragments join well, but the proximal end of the bone does not quite articulate with the diaphysis.

Figure 4. CT scan images of KNM-ER 5881b. Top row shows original scan on the left, and on the right a scan with cracks digitally removed. Bottom image depicts plane of section through the nexk. No expansion distortion is present, but the large crack is up to 1 mm in diameter. Note that even when the pieces are replaced, it does not alter the anteroposterior dimension of the bone by more than 0.3 mm.

Figure 5. KNM-ER 5881c in external (left) and internal (right) views.

Figure 6. Virtual reconstruction of KNM-ER 5881c. Top row shows the *in silico* polygonal model of the fossil in external, internal and anterolateral views with arrows indicating the crack along which the superior portion of the fragment is displaced to angle further medially than it would have been originally. Bottom row shows the fragment returned to its original position, determined by matching contours of the adjacent fragments in anterior view, and the reconstructed ilium in anterolateral and external views.

Figure 7. Methods of reconstructing acetabular and femoral head spheres. For both acetabulum (A) and femoral head (B), preserved subchondral surface was manually selected on the polygonal model in Polyworks. A best-fit sphere was fit to the surface ignoring outliers. (C) The close and appropriate correspondence in size between these two spheres matches the metric analyses, supporting the interpretation that both of these spheres represent reasonable estimates of the sizes of the opposing hip joint surfaces.

Figure 8. “Proxy” femoral neck length used to compare KNM-ER 5881 to other fossils. Distance extends from margin of the femoral head subchondral surface to the midpoint of the anteromedial margin of the greater trochanter

Figure 9. Metrics taken to capture iliac pillar position and morphology. (A) Distance of iliac pillar to anterior border of the ilium. (B) orientation of pillar, following Kibii and colleagues (2011).

Figure 10. External view of KNM-ER 5881c showing vectors constructed to quantify and compare sciatic notch size and shape.

Figure 11. Measurement of pelvic inlet contours shown on *Homo sapiens* hipbone (USNM 2057). (A) Original measurement taken by Ruff (1995), and (B) modified method used in this study.

Figure 12. *In silico* polygonal models of fossil and *Homo sapiens* femora in anterior (above) and superior (below) views. All scaled to similar neck length except for *Homo sapiens*, which has a comparatively shorter neck than early hominins. KNM-ER 5881 shown as preserved, and with superimposed femoral head sphere reconstructed from preserved contours. It is compared with early *Homo* specimens KNM-ER 1472, KNM-ER 1481 (left side reversed for comparison) and KNM-WT 15000 (reversed), *Australopithecus afarensis* A.L. 288-1 (reversed), A.L. 333-3, A.L. 827-1 (reversed), and specimens considered to be *Australopithecus* SK 97, SK 82, KNM-ER 1503 and KNM-ER 738 (reversed). All scans of original fossils except A.L. 288-1 and A.L. 333-3, which are scans of casts.

Figure 13. Femoral head diameters of fossil hominins. Dark grey bars indicate specimens generally attributed to *Homo*, light grey to *Australopithecus*, and white are those with less certain attribution. KNM-ER 5881 bar shown in black. All measures are in mm. Data in Table 6.

Figure 14. Proximal femoral morphology. Above, superoinferior diameter of head divided by superoinferior diameter of neck with fossils compared by taxonomic assignment, and by a combination of site and taxon. Below, femoral neck index (neck anteroposterior ÷ mediolateral diameter) also by taxon and by site/taxon. In both comparisons, KNM-ER 5881 overlaps only the early *Homo* distributions. Data in Table 6.

Figure 15. Proxy femoral neck length in modern *Homo sapiens* and fossil hominins. (A) Even in absolutely neck length, early hominins tend to have longer necks than modern humans. The one value that falls at the low end of the human distribution is A.L. 288-1, which is the smallest individual in the sample. (B) When scaled to femoral head size, the difference between the early hominins and modern humans is even more apparent. In all cases, KNM-ER 5881 has a relatively long femoral neck. Data in Table 7.

Figure 16. Midshaft femoral cross-sections of (Top row) KNM-ER 5881 (actual photo) compared with that of *Homo habilis* OH 62 (gray) and *Homo erectus* KNM-ER 803, KNM-ER 1808 (reconstruction without external pathological bone courtesy of A. Walker), KNM-WT 15000. (Bottom row) Midshaft femoral cross-sections of of probable early *Homo* that have diaphyses resembling those of *Homo erectus* KNM-ER 736, KNM-ER 737, KNM-ER 1472, KNM-ER 1481 and OH 28. The mediolaterally broad shape relative to anteroposterior diameter and weak pilasters of *Homo erectus* and probably early *Homo* contrast with that of KNM-ER 5881, which more closely resembles that of *Homo habilis*, Directional arrows are 1 cm long. KNM-ER 5881 is a photo of the original fossil. All other cross-sectional outlines modified from sections kindly provided by C. B. Ruff.

Figure 17. Pilasteric index (femoral midshaft anteroposterior ÷ mediolateral diameter) in early *Homo* specimens. East African *Homo erectus* KNM-ER 803, KNM-ER 1808 (reconstruction without external pathological bone courtesy of A. Walker), KNM-WT 15000; East African probable *Homo* KNM-ER 736, KNM-ER 737, KNM\_ER 1472, KNM-ER 1481, OH 28; Dmanisi d3160 and d4167 (data kindly provided by G. P. Rightmire); *Homo habilis* OH 62; and KNM-ER 5881. Dashed line represents equal anteroposterior and mediolateral diameters. All three East African *Homo erectus* fall below the line with midshaft cross-sections wider mediolaterally than they are deep anteroposteriorly. *Homo habilis*, the Dmanisi femora and KNM-ER 5881 fall above the line with femoral midshaft cross-sections that are deeper anteroposteriorly than they are wide mediolaterally. Data in Table 8.

Figure 18. Figure modified from Ruff (1995). Mediolateral (M-L) against anteroposterior (A-P) section moduli of the femoral 50% section for modern humans, early *Homo*, possible early *Homo*, later *H. erectus*, *Australopithecus*, and taxonomically indeterminate fossil femora. All data natural log-transformed. Least squares regression lines plotted through modern (solid) and early *Homo* (dashed) samples. Mean deviation of early *Homo* mediolateral bending strength values from those predicted for the modern sample is 41% (transformed to real units). Key to fossils noted individually by number: Early *H. erectus*: 1) KNM-ER 1808m,n, 2) KNM-ER 803a; probable early *Homo*: 3) OH 28, 4) KNM-ER 1472, 5) KNM-ER 737, 6) KNM-ER 1481a; 7) KNM-ER 1475b, 8) KNM-ER 736; possible *Australopithecus*: 9) KNM-ER 1463, 10) KNM-ER 1822, 11) KNM-ER 993, 12) KNM-ER 3728; unidentified: 13) KNM-ER 5882, 14) KNM-ER 1809, 15) KNM-ER 1807. Definitive attribution to early *H. erectus* is based on association with craniodental remains. Assignment to ‘probable early *Homo*’ and ‘possible *Australopithecus*’ is used for specimens that lack associated diagnostic craniodental remains, and so is based on morphology and follows Ruff (1995). Later *H. erectus* specimens include Aîn Maarouf 1, Geher Benot Ya’acov 1, Zhoukoudian 2, Zhoukoudian 5, Zhoukoudian 4, Zhoukoudian 6, Zhoukoudian1, Castel de Guido 1. All data from Ruff (1995) except for OH 62 which is from Ruff (2008).

Figure 19. *In silico* polygonal models of the ilia of *Australopithecus afarensis* A.L. 288-1 (scan taken from cast), KNM-ER 5881 (scan taken on original fossil), and early *Homo* KNM-ER 3228 (scan taken on original fossil), and demonstrating relevant comparative morphology. First row: Anterolateral views of ilia showing the anterior border of the ilium in KNM-ER 5881 and *Homo* are flexed at the anterior inferior iliac spine, whereas that of *Australopithecus* is relatively straight. Second row: External views of ilia showing the relatively posterior position and vertical inclination of the distinct iliac pillar in KNM-ER 5881 and *Homo* as compared with *Australopithecus*, which has an indistinct pillar running anteriorly along the anterior border of the ilium. Third row: Inferior views of ilia showing the short, thick iliac body in KNM-ER 5881 and *Homo*, as compared to the longer, thinner morphology characteristic of *Australopithecus*. Curvature of the linea terminalis mirrored by curved black lines.

Figure 20. *In silico* polygonal models of fossil hominin adult hipbones in anterolateral view. All scaled to similar iliac size and aligned to the cranial acetabular margin. KNM-ER 5881 is compared with: A.L. 288-1, *Australopithecus afarensis*, Hadar; Sts 14, Sts 65 (left side reversed for comparison), StW 431 (reversed), *A. africanus*, Sterkfontein; SK 50 (reversed), SK 3155b (reversed), *A. (P.) robustus*, Swartkrans; MH 2(reversed), *A. sediba*, Malapa (reversed); KNM-ER 3228 (reversed), *Homo* sp.*,* Koobi Fora; OH 28 *Homo* sp.*,* Olduvai. All scans of original fossils except A.L. 288-1 and MH 2, which are scans of casts.

Figure 21. Iliac cross-sections of *Australopithecus* and early *Homo*. Sections taken transversely at the level of the superior portion of anterior inferior iliac spine parallel to the inferior border of ilium immediately anterior to the auricular surface. All iliac cross-sections depicted as if they were from the left side, and scaled to the same length between anterior iliac margin and anterior margin of the auricular surface. Arrows indicate position of the iliac pillar. KNM-ER 5881c resembles the two *Homo* specimens with a pillar positioned relatively further posteriorly than in the *Australopithecus* ilia.

Figure 22. *In silico* polygonal models of fossil hominin hipbones in external view. All scaled to similar iliac size and aligned to the cranial acetabular margin. KNM-ER 5881 compared with: A.L. 288-1, *Australopithecus afarensis*, Hadar; Sts 14, Sts 65 (reversed), StW 431 (reversed) *A. africanus*, Sterkfontein; SK 50 (reversed), SK 3155b (reversed) *A. (Paranthropus) robustus*, Swartkrans; MH 2(reversed) *A. sediba*, Malapa; KNM-ER 3228 (reversed), *Homo* sp.*,* Koobi Fora; OH 28, *Homo* sp.*,* Olduvai. All scans of original fossils except A.L. 288-1 and MH 2, which are scans of casts.

Figure 23. Inlet curvature in KNM-ER 5881, extant and fossil ilia. Modified inlet curvature plotted here. Note that KNM-ER 5881 falls below observed ranges for *Australopithecus* and early *Homo*, but well within the range of extant *Homo sapiens*. This measure does not reflect inlet size, only curvature as represented by the portion of the iliac brim preserved in KNM-ER 5881. Although conclusions must remain fairly tentative given the incomplete nature of KNM-ER 5881, they suggest that the pelvic inlet in this individual may have been less platypelloid than typical of other contemporaneous and earlier hominins. A relatively small inlet that is not as platypelloid as *Australopithecus* is consisted with the mechanical model presented by Ruff (1995). SW *Homo sapiens* represent Zuni and Puye collections, B/W Terry and Hamann Todd specimens. F = female, M = male. Data in Table 11.

Figure 24. OH 62 and KNM-ER 3735 partial *Homo habilis* skeletons. OH 62 photo courtesy of D.C. Johanson.

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