

## Fossil *Homo* Femur From Berg Aukas, Northern Namibia

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**ABSTRACT** The proximal half of a hominid femur was recovered from deep within a paleokarst feature at the Berg Aukas mine, northern Namibia. The femur is fully mineralized, but it is not possible to place it in geochronological context. It has a very large head, an exceptionally thick diaphyseal cortex, and a very low collodiaphyseal angle, which serve to differentiate it from Holocene homologues. The femur is not attributable to *Australopithecus*, *Paranthropus*, or early *Homo* (i.e., *H. habilis* sensu lato). *Homo erectus* femora have a relatively longer and AP flatter neck, and a shaft that exhibits less pilaster than the Berg Aukas specimen. Berg Aukas also differs from early modern femora in several features, including diaphyseal cortical thickness and the degree of subtrochanteric AP flattening.

The massive diaphyseal cortex of Berg Aukas finds its closest similarity within archaic *H. sapiens* (e.g., Castel di Guido) and *H. erectus* (e.g., KNM-ER 736) samples. It has more cortical bone at midshaft than any other specimen, although relative cortical thickness and the asymmetry of its cross-sectional disposition at this level are comparable with those of other Pleistocene femora. The closest morphological comparisons with Berg Aukas are in archaic (i.e., Middle Pleistocene) *H. sapiens* and Neandertal samples.

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We here report a heavily mineralized proximal half of a right femur attributable to the genus *Homo*. The specimen was recovered during vanadium mining operations at Berg Aukas, northern Namibia.

The Berg Aukas locality has become widely known following the discovery in 1991 by Martin Pickford of a Miocene hominoid mandible in rubble from the mine (Conroy et al., 1992). Berg Aukas is but one of a number of fossiliferous paleokarst features that dot the landscape of northern Namibia, southern Angola, and western Botswana (Beetz, 1933; Dart, 1950; Arambourg and Mouta, 1954; Robinson, 1959; Antunes, 1965; Pickford and Mein, 1988; Pickford, 1990; Pickford et al., 1990, 1993; Grine, 1991; Jablonski, 1994) (Fig. 1).

Primate fossils that have been recovered from these localities include, in addition to

the specimens of *Otavipithecus* from Berg Aukas, cercopithecoids from Leba, Malola, and Cangalongue in southern Angola, from Jaqersquell in the Otavi mountains, and from Kaonaka, Botswana (Minkoff, 1972; Pickford et al., 1992). A galagine is known from Harasib 3a in the Otavi Mountains (Senut et al., 1992; Conroy et al., 1993a,b).

The only other hominid fossil that has been reported from this region was found on the farm Otjiseva, near Windhoek, Namibia. This specimen comprises a partial calotte, a mandible, and fragmentary postcranial bones. It is almost certainly Holocene in age,

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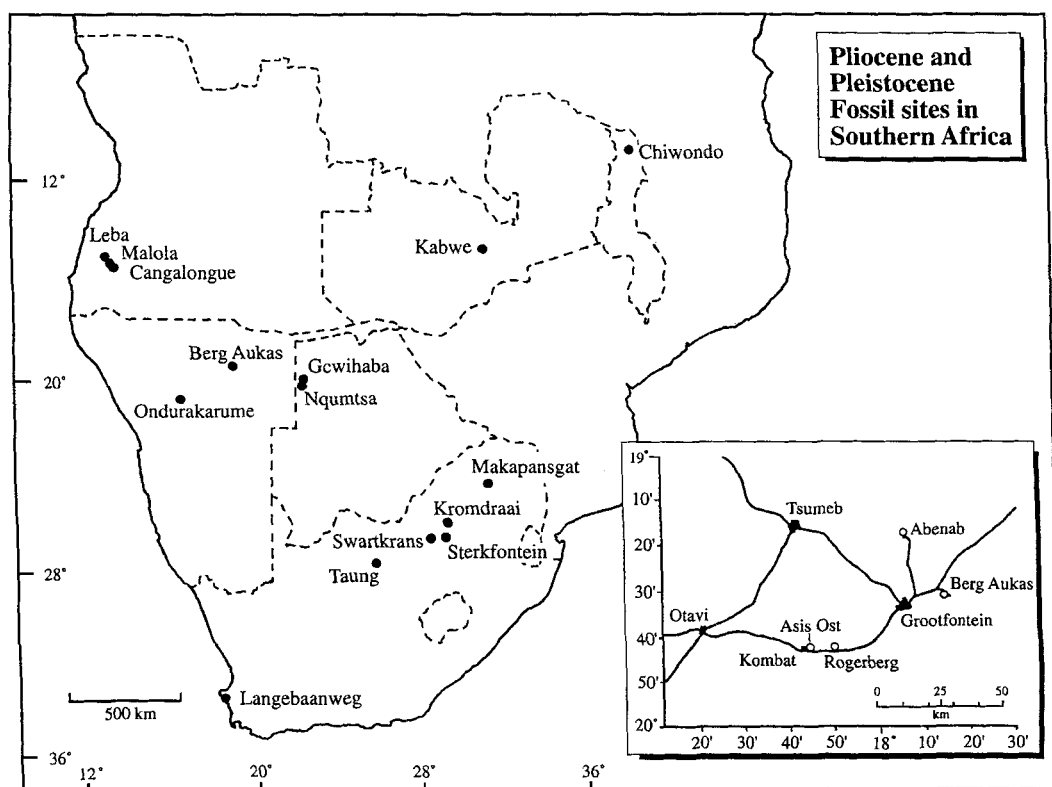


Fig. 1. Principal Plio-Pleistocene fossil sites in Malawi, Zambia, Angola, Botswana, South Africa, and Namibia. Inset: Berg Aukas mine in relation to other karst mines, and to the towns of Grootfontein, Kombat, Otavi, and Tsumeb.

however, and likely dates to around only 4 kyr BP or less (Sydow, 1969; De Villiers, 1972; Tobias, 1973).

The Berg Aukas mine ( $10^{\circ}30'58''\text{S}$ ;  $18^{\circ}15'10''\text{E}$ ) is located some 20 km east of the town of Grootfontein, in the vicinity of a number of other mines, in the Otavi Mountains (Fig. 1). This region is composed of Damara Sequence (late Precambrian) limestones and dolomites. The Berg Aukas Formation forms the base of the Otavi Group within the Damara Sequence; it consists of black limestone and dolomite with interbedded arkose, graywacke and shales (Schneiderhöhn 1920; Stahl, 1926; Söhnge, 1957). The Otavi Group rocks contain numerous paleokarst features, ranging from caves to fissures, and a number of these possess rich ore deposits (e.g., the mines at Tsumeb, Abenab, Asis Ost, Rogerberg, and Berg Aukas).

The femur was recovered during vanadium mining operations at level 5, which was 177.4 m below the collar of shaft number 1 (Fig. 2). According to C. Begley and A. Palfi (pers. comms.), the femur was found in 1965 together with other loose bone fragments in a semiconsolidated mud and ore breccia. Unfortunately, due to the high ore grade of the breccia, almost all of the material was put through the crusher. The circumstances surrounding the discovery of the femur are rather cloudy, and it is admitted that it was not necessarily found *in situ*. There are reports that other parts of the skeleton were present (D. de Jager and J. Horn, pers. comm.), but this cannot be confirmed. The location from which the bone fragments are reported to have come was destroyed by subsequent mining operations.

The femur and reportedly several other bones that were removed by the miners be-

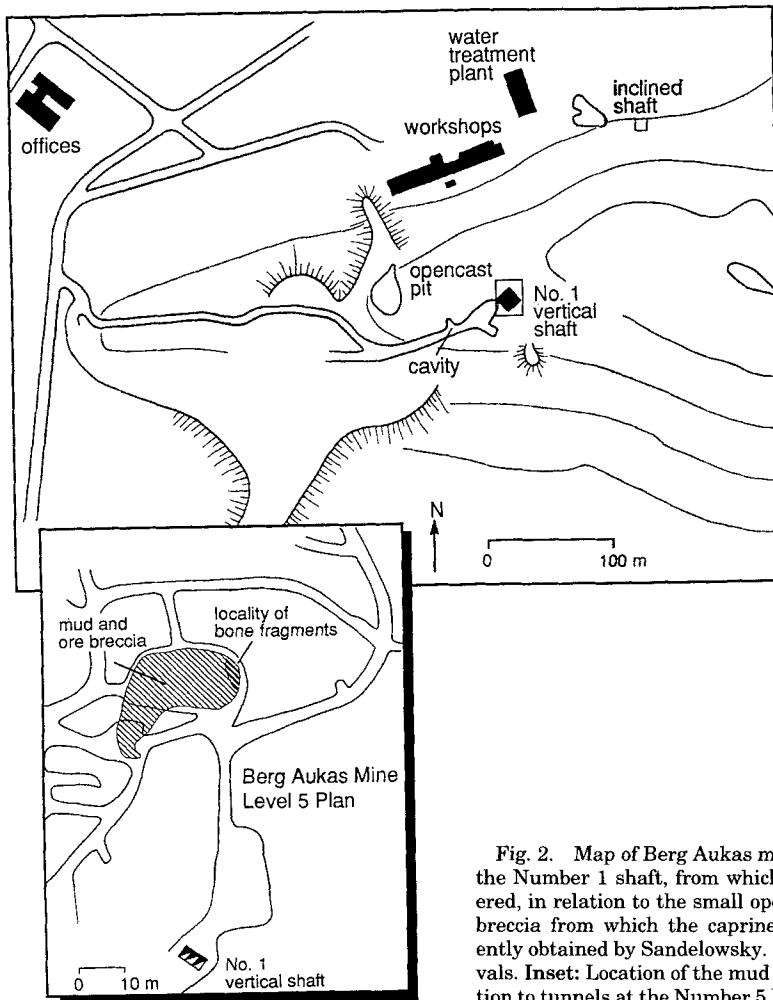


Fig. 2. Map of Berg Aukas mine showing position of the Number 1 shaft, from which the femur was recovered, in relation to the small open cavity with calcified breccia from which the caprine mandible was apparently obtained by Sandelowsky. Contours = 20 m intervals. Inset: Location of the mud and ore breccia in relation to tunnels at the Number 5 level.

came part of the personal collections of individuals in the Grootfontein area. In particular, the femur became part of Mr. E. Chatterton's collection. In 1968, Mr. C. Begley acquired it from him and took it to the Museum of Man and Science in Johannesburg, South Africa. Some time later, the femur was handed over to one of us (P.V.T.) for study. Similarities between the Berg Aukas specimen and later Pleistocene (e.g., Neanderthal) homologues were apparent, and enquiries were made in an attempt to establish more information regarding its provenance.

Sandelowsky (1983) drew attention to the existence of the femur, and noted that other

bones were found in association with it. According to her:

One identifiable piece studied by a paleontologist was a tooth, not readily comparable with extant African species of antelope but with caprine affinities (E.S. Vrba, pers. comm.).

Unfortunately, the tooth cannot now be located, and in any event it does not appear that it was derived from level 5 of the mine. The site was visited by Sandelowsky in 1975, who reported (letter to P.V.T. dated May 3, 1975) that she had located bone breccia in a small cave and that a caprine tooth with jaw fragment obtained on that visit had

been examined by E.S. Vrba. Thus, the specimen appears to have come from a small breccia cavity near shaft No. 1 rather than from the mine from which the femur was recovered (Fig. 2).

Three bones in the collection of the Rehoboth Museum, Namibia, are purported to have been found together with the femur (apparently they were also part of the private collection of Mr. Chatterton). However, these elements (a proximal humerus of *Giraffa camelopardalis*, a distal radius of a juvenile *G. camelopardalis*, and a proximal tibia of a rhinocerotid), which have been examined and identified by one of us (F.E.G.), exhibit little if any secondary mineralization or discoloration. The femur, on the other hand, is heavily mineralized with a dark brown patina. It is, therefore, doubtful that these three ungulate bones were associated with the femur in any meaningful context.

With the cessation of mining activity, level 5 of shaft No. 1 is currently under at least 100 m of water. It is, therefore, unlikely that we shall ever gain any contextual information pertaining to the provenance or age of the hominid femur. To date, no attempt has been made to obtain a direct radiometric date for the specimen.

In comparison to modern femora, the Berg Aukas specimen has a large head, a low colodiaphyseal angle, and extremely thick cortical bone, as revealed by the fractured shaft. Notwithstanding its lack of geochronological context, the femur is significant because it is the only human fossil from Namibia that possesses any archaic features.

The Berg Aukas femur is described here. It is compared with modern human femora and, because of its uncertain geochronological age, with homologues from a number of fossil hominid taxa that span several million years.

## MATERIALS AND METHODS

The Berg Aukas femur was radiographed in standard AP alignment using a Siemens 715-65209 at 73 kV and a distance of 115 cm in order to record the trabecular network of the head, neck, and proximal diaphysis. The specimen was laid flat on its anterior sur-

face, which approximates the coronal plane of the body, for radiographic purposes. Because the distal half of the bone is missing it is not possible to determine the degree of anteversion (if any) that this femur may have exhibited. It was examined also by computed tomography (CT) in order to obtain information concerning cortical bone thickness and cross-sectional geometry of the diaphysis. For this purpose, a series of 18 cross-sections of the shaft and three of the head and neck were obtained by F.E.G. from a GE 9800 scanner. Following the method employed by Daegling (1989) and Daegling and Grine (1991) for modern and fossil bone, each CT image was generated using a 1.5 mm thick slice with a 4 sec exposure at 170 MA and 120 kV; the bone reconstruction algorithm was used. No magnification factor was employed. The specimen was examined dry, with a window setting of 1,000 L and 4,000 W. Comparison of the most distal CT section with the fractured end of the fossil revealed an accurate match in several measurements.

Cross-sectional geometric variables were calculated from tracings of the CT hardcopies using a Summagraphics digitizing tablet interfaced to an IBM-compatible personal computer running a modified version of SLICE (Nagurka and Hayes, 1980; modifications by R. Chapman, Smithsonian Institution). Cortical bone area (CBA), total subperiosteal area (TSA), minimum and maximum second moments of area or moments of inertia ( $I_{\min}$ ,  $I_{\max}$ ), the polar moment of area ( $J = I_{\min} + I_{\max}$ ), as well as the maximum and minimum section moduli ( $Z_{\max}$ ,  $Z_{\min}$ ) were calculated for the most distal section (which closely approaches the estimated midpoint of the diaphysis) and a subtrochanteric section (located just distal to the fractured lesser trochanter).

Cortical area (CBA, in  $\text{mm}^2$ ) is roughly proportional to tensile and compressive strength. Although it contributes to bending and torsional rigidity, it is usually considered as being proportional to "axial" strength. The second moments of area quantify the resistance to bending about the maximally and minimally reinforced axes. These variables are expressed as  $\text{mm}^4$ , and measure how a given amount of material is dis-

tributed about the plane of reference. The polar moment of area ( $J$ ) is proportional to torsional rigidity and average bending rigidity (Wainwright et al., 1976). The ratio of  $I_{\max}$  to  $I_{\min}$  (i.e., a bending ratio,  $I_{\max}/I_{\min}$ ) describes the symmetry of a section; a perfectly cylindrical section would be characterized by a ratio of 1.0 (Trinkaus and Ruff, 1989). Similar information may be obtained by comparisons of the major and minor section moduli.  $Z_{\max}$  and  $Z_{\min}$  take into account distances from the neutral axis, and are proportional to bending strengths with respect to the principal axes (Demes and Jungers, 1993). The cortical index ( $CI = CBA/TSA \times 100$ ), which provides a measure of the relative amount of compact bone in the cross-section, also reflects the degree of medullary constriction or stenosis (Ruff et al., 1993). No attempt has been made here to standardize any of these values for overall body size. Rather, we are interested simply in the absolute values for the Berg Aukas femur and selected comparative samples.

Standard anteroposterior (AP) radiographs of the proximal half of the femur, together with CT images of the subtrochanteric and midshaft sections of the diaphysis, were recorded for three modern subSaharan African samples, and a sample of African Americans. It seemed reasonable to compare Berg Aukas to modern populations of African origin for several reasons, not the least of which is geographical propinquity. Additionally, not only are the African American femora the most robust of the recent samples, but American blacks possess, on average, higher bone mineral density and larger amounts of bone in cross-section than do Native Americans and Americans of European extraction (Pollitzer and Anderson, 1989). The CT images of the femora comprising these four samples were obtained with the same parameters as for the Berg Aukas fossil. The "midshaft" cross-section recorded for the recent human femora is the midpoint of maximum interarticular length. As such, it will depart slightly (in the proximal direction) from the "50%" level used by Ruff and Hayes (1983) and Ruff et al. (1993), but this difference in location is of minor consequence for the questions addressed here. The AP radiographs were obtained with a

fine gray detail cassette using 5 MAS and 52 kV at a distance of 115 cm. The AP radiographs were used to record the neck-shaft angle (NSA) of each specimen.

The smallest of our three recent African samples ( $N = 12$  males and 2 females) is geographically diffuse. It comprises skeletal remains available in the American Museum of Natural History and the United States National Museum American from Kenya and Tanzania (6), Liberia (1), Nigeria (1), Namibia (1), and South Africa (5). The second African sample comprises 50 Zulu individuals of known age and sex (25 males and 25 females) from South Africa. The third sample comprises 47 Khoisan individuals from radio-carbon dated archaeological sites along the Cape coastal region of South Africa that predate European contact. It is made up of 28 males and 19 females; individual sex was determined independently from associated skeletal elements (most commonly pelvic remains) by two of us (F.E.G. and O.M.P.). The African American sample derives from New York City; only eight of the 53 are female.

All linear measurements are in millimeters. The following abbreviations are used: AP, anteroposterior; ML, mediolateral.

## DESCRIPTION

### Preservation

The specimen consists of a 244 long proximal segment of an adult right femur (Fig. 3). Surface bone has been lost from the lateral quarter of the head along its superior and posterior aspects, so that the articular rim is discernible only anteriorly, inferiorly, and inferoposteriorly. A few small patches of the articular surface of the head are missing from its anteromedial aspect, and on its posteromedial aspect adjacent to the fovea capitis. Surface bone has been lost also from the medial part of the superior surface of the neck, and the greater trochanter has been broken off along an inclined plane that slopes inferoposteriorly. Thus, the superior aspect of the neck is represented by a narrow (15–18 wide) strip of surface bone. The lesser trochanter is missing. A 13 by 28 flake has been lost from the anterior aspect of the shaft about 29 below the greater tro-

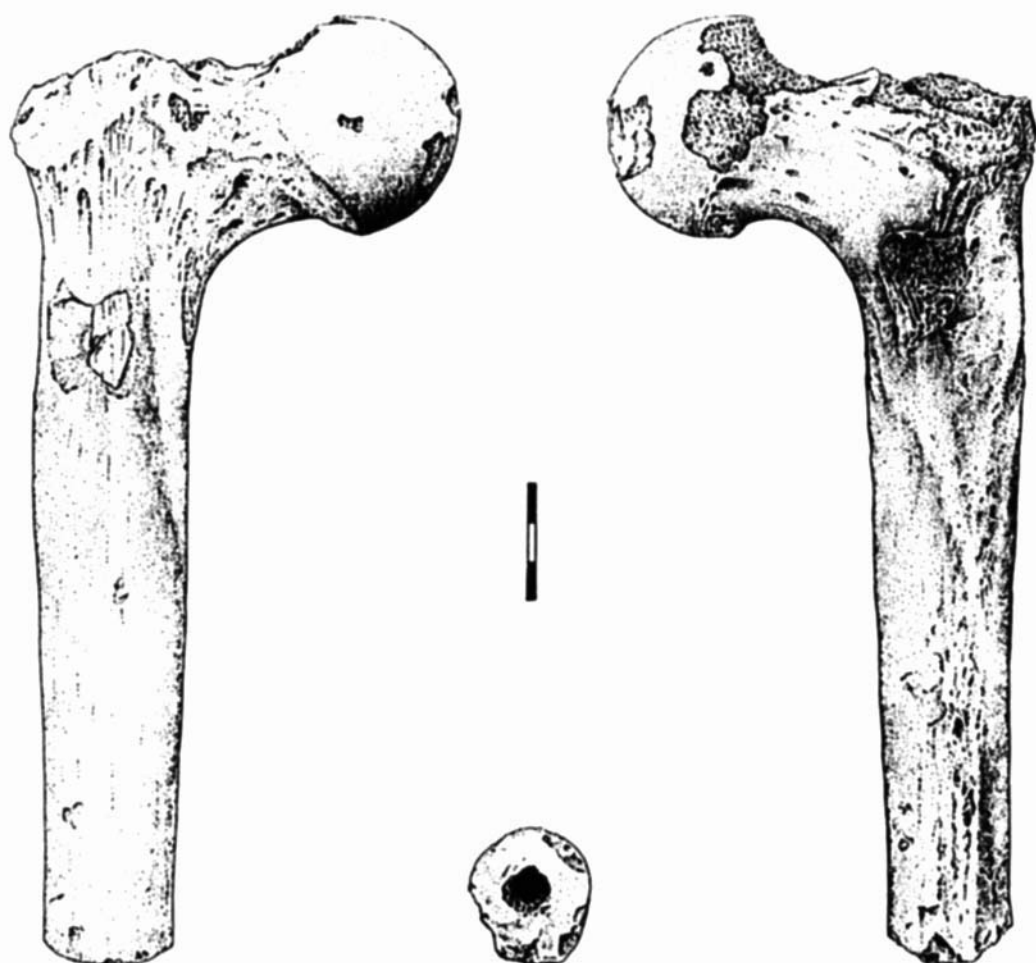


Fig. 3. Anterior (left), posterior (right), and inferior (center) views of the Berg Aukas femur. Scale in cm.

chanter, and two small flakes are missing from the posterior surface of the shaft adjacent and distal to the nutrient foramen. These represent postfossilization damage. Similarly, slivers of cortical bone are missing along the fractured distal margin.

The shaft is fractured about 188 below the neck. Anteriorly, the fractured surface is flat and horizontally disposed, thus forming a right angle with the diaphyseal surface. This surface extends to a level almost coincident with the posterior margin of the medullary canal. Posteriorly, the fracture surface is somewhat more irregular, and has a slight postero-inferior bevel.

Right-angled fractures are reported to be preferentially associated with dry bone breakage (Morlan, 1984; Johnson, 1985), and this pattern of damage has been found to predominate at archaeological sites where bones have been broken either by sediment pressure or by the shovels of excavators (Villa and Mahieu, 1991). A smooth fracture surface, such as that on the Berg Aukas femur, has been claimed to be characteristic of green bone breakage (Morlan, 1984; Johnson, 1985), although Villa and Mahieu (1991) reported that this type of damage predominates at the French site of Bezouze, where dry bones had been broken

in the course of excavation. It would appear, therefore, that the Berg Aukas shaft was fractured when the bone was dry, and the smooth nature of the surface suggests post-fossilization damage. It is not possible to ascertain whether the fracture was induced by sediment pressure or by the miners who removed it.

There are a number of irregularly disposed scratches and cut-marks near the distal fracture; all of them appear fresh and to have been created after fossilization.

### MORPHOLOGY

The head is very large. It measures 56.4 vertically (Martin, 1923, No. 18), c. 57.6 sagittally, and has a maximum diameter of 58.0, with a circumference of approximately 175. The fovea opens posteromedially; it has a maximum diameter of about 17. Antero-inferiorly, there is a rugose band of bone along the lateral border of the articular margin.

The neck is short and stocky. Its minimum vertical (Martin, 1923, No. 15) and horizontal (Martin, 1923, No. 16) diameters are 40.8 and 36.6, respectively, with a minimum circumference of some 130. It has a length of 42.5, measured from the medial edge of the broken base of the lesser trochanter to the articular margin of the head. The specimen measures 109.6 from the lateral edge of the greater trochanter to the medial surface of the head. The biomechanical neck length, calculated according to the technique of Reed et al. (1993), is 80.9. The neck intersects the long axis of the shaft at just over a right angle, namely, 106° (Martin, No. 29; Bräuer, 1988). There is no obvious groove for the tendon of obturator externus on the posterior surface of the neck. Inferiorly, posteriorly, and especially superiorly there are a number of large nutrient foramina for branches of the lateral and medial circumflex femoral arteries.

The base of the greater trochanter, measured from the medial edge of the anterior lip of the trochanteric fossa to the lateral edge of the trochanter, is approximately 50 ML. Anteriorly, a moderate, sigmoidal ridge is raised between the attachment areas of the gluteus minimus and vastus lateralis, and along the superior margin of the attach-

ment of the iliofemoral ligament. This ridge becomes indistinct as it runs posteriorly on the lateral aspect of the greater trochanter. On the posterolateral surface of the shaft a prominent gluteal line is raised along the border between the attachments of gluteus maximus and vastus lateralis. The base of the lesser trochanter is preserved; it measures approximately 22 ML, and projects posteromedially. The intertrochanteric ridge is about 12 broad.

The shaft is straight in AP view, although it narrows somewhat from a ML diameter of 40.8 below the level of the lesser trochanter to 31.5 at the distal end. Seen from the lateral aspect, the posterior surface of the shaft is slightly concave; the anterior surface is very slightly concave over the proximal 90 of its length, and slightly convex over its distal portion. The shaft is AP deeper distally than proximally. Proximally, the shaft, which measures 30 AP (Martin, 1923, No. 9) and 40.8 ML (Martin, 1923, No. 10) below the lesser trochanter, is platymeric (index value of 73.5%) with a transversely expanded ellipsoid outline. It has a circumference of 112 at this level. At the fractured distal end, which probably approximates the midshaft position (see below), it measures 35.9 AP (Martin, 1923, No. 6) and 31.5 ML (Martin, 1923, No. 7), with a pilastric index value of 114.0%. At this level, it has a circumference of some 106, and presents an irregular cross-sectional outline with a prominent, broad *linea aspera* (Fig. 3). Lateral, posterolateral, and posteromedial borders separate rather flat lateral and posterior surfaces from a convex anterolateral surface. The latter surface is highly curved anteriorly, while in its medial part it is very gently curved (Fig. 3).

Anteriorly, the proximal part of the shaft has an 8 broad, nearly vertical ridge of bone that runs obliquely for about 50 from a level coincident with the lower margin of the head to the medial surface of the shaft. This ridge separates the attachment areas of vastus medialis and vastus intermedius. The intertrochanteric line has a rugose tubercle above and laterally, but the rest of the line is ill-defined. It terminates medial to the aforementioned ridge. There is a modest spiral line along the medial surface of the shaft. Posteriorly, the prominent gluteal tuberos-

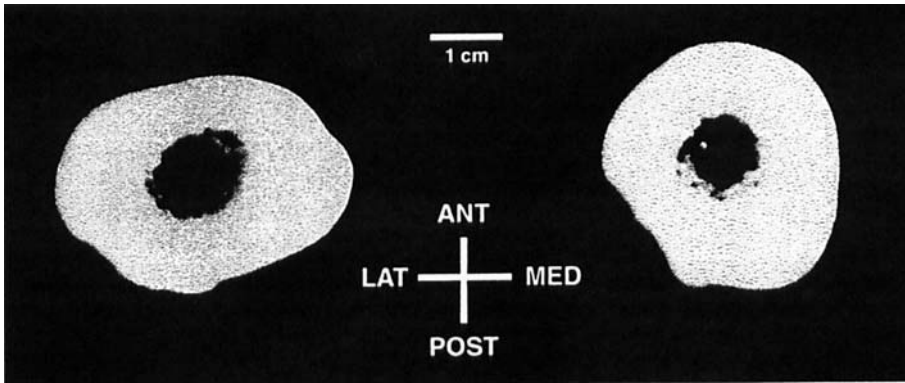


Fig. 4. CT sections at the subtrochanteric (left) and midshaft (right) levels of the Berg Aukas femur.

ity and moderate gluteal ridge form the medial margin of a shallow, vertically elongate (c. 62) hypotrochanteric fossa. The lateral border of the hypotrochanteric fossa is formed by a low, broad crista lateralis that creates a slight lateral swelling of the proximal part of the shaft. The crista lateralis is separated from the gluteal tuberosity such that the hypotrochanteric fossa opens proximally onto the lateral surface of the shaft. The gluteal ridge courses distally and somewhat medially for about 67, where it meets the pectineal line to form the linea aspera some 40 distal to the lesser trochanter. The linea aspera is about 11 broad, and rather low at this point; it remains poorly elevated but with distinct lips for some 50, to a point immediately below the nutrient foramen. Here it forms a high, steeply inclined medial wall and a very steep, high lateral wall. The nutrient foramen is located 100 below the lesser trochanter, and 165 below the upper surface of the neck.

The fractured distal end of the diaphysis reveals thick cortical bone with moderate constriction of the medullary canal. At this level, the cortical bone is 9.5 thick anteriorly, c. 12.7 posteriorly, 9.3 laterally, and 10.5 medially. The medullary canal measures 11.6 AP and 11.6 ML at this level.

The subtrochanteric and "midshaft" CT sections are illustrated in Figure 4. The latter was recorded approximately 5 proximal to the level of the break on the anterior surface. This section misses the flake scars at

TABLE 1. Cross-sectional geometric properties of the Berg Aukas femur<sup>1</sup>

Variable	Section	
	Subtrochanteric	"Midshaft"
Cortical area (mm <sup>2</sup> )		
CBA	794	750
Area moments (mm <sup>4</sup> )		
$I_{\max}$	84,677	67,149
$I_{\min}$	47,362	49,112
J	132,038	116,261
Section moduli (mm <sup>3</sup> )		
$Z_{\max}$	4,285	3,791
$Z_{\min}$	3,156	3,329
Cortical index	88.40	87.90
$I_{\max}/I_{\min}$	1.79	1.37
$Z_{\max}/Z_{\min}$	1.36	1.14

<sup>1</sup>All values based on an average of five tracings. Cortical index = (cortical area [CBA]/total subperiosteal area [TSA])  $\times$  100.

the distal end except for a 6.1 broad scar along the posterolateral aspect that has a maximum depth of only 0.5. Thus, cortical thickness and other sectional properties are not compromised at this level. The subtrochanteric CT section was taken some 20 below the level of the lesser trochanter, i.e., distal to the large flake scar on the anterior surface of the bone. The cross-sectional properties obtained for the proximal and distal CT slices through the Berg Aukas femur are recorded in Table 1. The cortical index and polar moment of area are notably large.

The proximal CT sections reveal a well-defined calcar femorale (Harty, 1957; Griffin, 1982) extending anteromedially into the neck from the posteromedial aspect of the diaphysis at the level of the lesser trochanter.



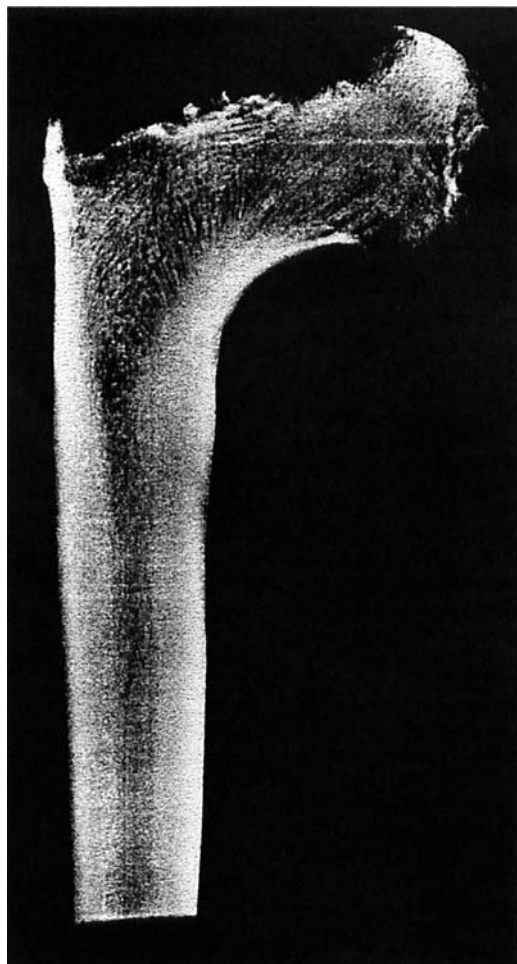


Fig. 5. AP radiograph of the Berg Aukas femur.

The AP radiograph of the Berg Aukas femur is reproduced in Figure 5. The trabecular network of the head and neck is well-developed, presenting a rather dense meshwork of lamellae. The medial trabecular bundle (Koch, 1917) is broad, extending superomedially from the thick cortical bone along the inferior aspect of the neck. It forms an angle of  $135^\circ$  with the diaphyseal axis, as measured according to the technique employed by Heller (1989) and Trinkaus et al. (1991). The arcuate bundle comprises a broad, gently curved band of trabecular lamellae that courses from the inferomedial aspect of the head to the inferolateral margin of the greater trochanter. The lateral

trabecular bundle (= trochanteric bundle of Kapandji, 1987) is composed of a diffuse network of lamellae that radiate superolaterally from the inferomedial part of the neck. As a result of this rather dense meshwork of trabeculae, Ward's triangle is not clearly defined, whereas the nucleus of the head is readily discernible as a large (c.  $26 \times 26$ ) opaque square.

The thick medial and lateral walls of the diaphysis seen in the AP radiograph enclose a medullary canal that is slightly fusiform at its proximal end. Thus, at the level of the lesser trochanter, the lateral wall begins to taper markedly superiorly, whereas the medial wall thickens very slightly before turning at the neck. The inferior spur of the neck (= the vault of Adams) begins to taper rather rapidly approximately 29 from the head, although dense cortical bone extends to within about 13 of the inferior articular margin.

#### ESTIMATION OF ORIGINAL LENGTH

Measurements recorded for the proximal femur in our African American sample ( $N = 53$ ) were combined in a multiple regression analysis to predict the maximum interarticular length of the femur. We elected to use this sample because it is comprised of the most robust femora available to us. Six variables that could be recorded for the Berg Aukas femur were also used: vertical head diameter (vhd), horizontal head diameter (hhd), neck height (nh), neck breadth (nb), neck length (nl), and biomechanical neck length (bnl). The resulting predictive equation is based on raw (i.e., not logged) data:

$$\begin{aligned} \text{Length} = & 5.0975 \cdot \text{hhd} - 4.9306 \cdot \text{vhd} \\ & + 2.9036 \cdot \text{nh} - 0.7395 \cdot \text{nb} + 1.1854 \cdot \text{bnl} \\ & + 0.8697 \cdot \text{nl} + 240.73 \text{ [measurements} \\ & \text{in mm].} \end{aligned}$$

The multiple correlation coefficient for this relationship is 0.57. Relatively low correlations are not uncommon in intraspecific samples, and often do not accurately reflect the predictability of the equation (Smith, 1981). The mean absolute prediction error is just over 16 mm.

TABLE 2. Femoral head and neck dimensions for recent human samples and Berg Aukas

		N	$\bar{X}$	SD	Observed range	Reference
Vertical head diameter (M18)						
Romano-British	♂	57	48.9	2.6	42.1–53.0	Kennedy, 1983b
	♀	43	43.0	2.4	39.2–49.1	
Medieval English	♂	174	49.0		45.0–55.0	Parsons, 1914
	♀	103	42.5		36.0–48.0	
Modern English	♂	56	49.0		43.0–57.0	Holtby, 1918
	♀	44	41.7		37.0–46.0	
Australian Aborigine	♂	150	43.1	2.1	39.0–50.0	Davivongs, 1963
	♀	110	38.2	1.3	35.0–42.0	
Sub-Saharan African	♂	12	44.2	1.9	41.6–47.8	This study
	♀	2	41.9		40.1–43.7	
Zulu	♂	25	45.7	2.6	40.5–50.0	This study
	♀	25	40.7	1.6	38.0–45.0	
Khoisan	♂	25	40.9	2.2	37.0–46.0	This study
	♀	18	37.3	2.2	33.0–41.0	
American black	♂	45	47.5	2.9	40.6–54.7	This study
	♀	8	41.2	1.7	39.0–43.5	
Berg Aukas			56.4			
Sagittal head diameter						
Medieval Serbian	♂	40	48.3	2.6		Trinkaus, 1980
	♀	40	41.9	2.1		
Amerindian	♂	40	43.3	2.2		Trinkaus, 1980
	♀	40	37.8	1.6		
Sub-Saharan African	♂	12	44.0	2.1	40.8–47.4	This study
	♀	2	41.8		39.9–43.6	
Zulu	♂	25	45.5	2.5	41.0–49.0	This study
	♀	25	40.6	2.1	38.0–45.0	
Khoisan	♂	27	40.7	2.2	36.0–46.0	This study
	♀	18	37.5	1.9	33.0–40.0	
American black	♂	45	47.6	2.9	40.8–54.4	This study
	♀	8	41.5	2.3	38.0–43.8	
Berg Aukas			57.6			
Head size index (M18/M10 $\times$ 100)						
Sub-Saharan African	♂	12	150.4	10.5	132.4–165.3	This study
	♀	2	156.7		144.2–169.2	
American black	♂	45	149.4	14.3	121.5–192.9	This study
	♀	8	138.1	6.1	129.8–147.5	
Zulu	♂	25	142.6	10.5	123.1–162.1	This study
	♀	25	139.5	9.3	120.0–164.0	
Khoisan	♂	28	145.6	9.7	128.1–168.2	This study
	♀	19	138.3	8.8	121.1–160.9	
Berg Aukas			138.2			
Vertical neck diameter (M15)						
Sub-Saharan African	♂	12	30.5	2.3	26.5–35.5	This study
	♀	2	29.2		26.4–31.9	
American black	♂	45	33.3	2.8	27.6–40.2	This study
	♀	8	28.5	1.5	26.4–31.6	
Zulu	♂	25	31.6	2.2	28.0–36.0	This study
	♀	25	27.8	1.6	25.0–31.0	
Khoisan	♂	28	28.4	2.4	25.0–34.0	This study
	♀	19	25.7	2.3	21.0–29.5	
Berg Aukas			40.8			
Horizontal neck diameter (M16)						
Sub-Saharan African	♂	12	23.7	2.9	18.3–28.8	This study
	♀	2	23.6		23.4–23.8	
American black	♂	45	26.2	2.2	21.8–31.0	This study
	♀	8	22.7	1.6	20.3–24.7	
Zulu	♂	25	26.2	2.6	21.5–31.0	This study
	♀	25	23.8	2.4	20.0–28.0	
Khoisan	♂	28	24.5	2.1	20.0–27.5	This study
	♀	19	22.4	2.4	17.0–27.0	
Berg Aukas			36.6			

(continued)

TABLE 2. Femoral head and neck dimensions for recent human samples and Berg Aukas (continued)

		N	$\bar{X}$	SD	Observed range	Reference
Neck shape index (M16/M15 $\times$ 100)						
Sub-Saharan African	♂	12	78.0	8.7	62.0–94.4	This study
	♀	2	81.6		74.6–88.6	
American black	♂	45	79.2	6.4	58.9–90.1	This study
	♀	8	79.6	4.6	73.6–85.6	
Zulu	♂	25	83.0	5.7	74.1–96.9	This study
	♀	25	85.7	7.1	75.0–100.0	
Khoisan	♂	28	86.2	5.9	74.1–96.2	This study
	♀	19	87.2	6.1	79.3–100.0	
Berg Aukas						
Neck length index (length/M15 $\times$ 100)						
Sub-Saharan African	♂	12	134.6	21.9	108.0–186.0	This study
	♀	2	151.6		130.4–172.7	
American black	♂	45	118.8	23.3	88.9–172.4	This study
	♀	8	120.9	8.2	108.2–134.0	
Zulu	♂	25	118.0	13.8	90.1–164.5	This study
	♀	25	125.9	14.6	96.6–164.8	
Khoisan	♂	28	123.5	19.9	88.2–160.0	This study
	♀	19	127.1	13.2	103.9–144.4	
Berg Aukas						
			104.2			

A value of 518 mm is obtained for the interarticular length of the Berg Aukas femur using this regression formula. The distance from the top of the head to the most distal point preserved on the shaft is 244 mm, a value that is 47% of the estimated total length. It is appropriate, therefore, to compare the cross-sectional geometry of the distal diaphysial section of Berg Aukas to mid-shaft values recorded in our modern samples and in other studies.

## COMPARISONS

### The head

One of the most striking features of the Berg Aukas femur is its large head. Its vertical and sagittal diameters fall just within or above the respective upper limits recorded for recent human males of European and African heritage (Table 2). It is noticeably larger than the head of any femur attributed to *Australopithecus*, *Paranthropus*, *H. cf. habilis*, or *H. erectus*, and it is also larger than early modern *H. sapiens* homologues (Table 3).<sup>1</sup> Walker and Leakey (1993) have recorded a maximum diameter of 46 mm for the KNM-WT 15000 femoral head; if this individual had grown to adulthood, and his

femoral head diameter had followed a growth trend similar to that in bone length (Ruff et al., 1994), the resultant 17.5% to 23.5% increase in size (depending upon whether he had died at a skeletal age of 11 or 12 years—Ruff and Walker, 1993) would have resulted in a femoral head equivalent to that of the Berg Aukas specimen (i.e., between 54 and 57 mm). Archaic *H. sapiens* femora approximate Berg Aukas in the absolute size of the head, as do some of the Neandertals, especially Spy 2 and La Ferrassie 1.

The relative size of the Berg Aukas femoral head, as revealed by an index (Wood, 1976) that compares its vertical diameter to the subtrochanteric ML diameter of the diaphysis, is considerably greater than that of any australopithecine homologue, but it is comparable to the *H. cf. habilis* and *H. erectus* specimens with the relatively largest heads (i.e., KNM-ER 1481A and KNM-WT 15000). The value recorded here for KNM-WT 15000 pertains to a juvenile, whose femoral head to diaphysis ratio is likely influenced by ontogenetic age (Ruff et al., 1994). KNM-WT 15000 has femoral proportions that are not atypical for modern human juveniles of similar developmental age, and his femoral head is smaller relative to shaft dimensions than the majority (5 out of 7) of modern juveniles measured by Ruff et al. (1994). By our measure, Berg Aukas

<sup>1</sup>One of us (P.V.T.) prefers *Australopithecus*, whereas the others recognize *Paranthropus*; for the purposes of this paper we follow the senior author in the use of taxonomic names.

TABLE 3. Femoral head and neck dimensions for fossil hominid samples<sup>1</sup>

	N	$\bar{X}$	SD	Observed range
Vertical head diameter (M18)				
<i>A. afarensis</i>	2	34.0		28.6–39.4
<i>A. africanus</i>	2	34.2		31.2–37.1
<i>P. robustus</i>	3	34.0	3.3	30.5–37.1
<i>P. boisei</i>	2	32.7		32.2–33.2
<i>H. cf. habilis</i>	3	43.4	3.1	40.0–46.1
<i>H. erectus</i>	3	45.0	4.5	41.0–49.9
Archaic <i>H. sapiens</i>	3	51.4	1.2	50.0–52.2
Neandertals	14	48.8	4.1	40.0–54.3
Early modern	4	47.0	2.6	44.0–50.0
Berg Aukas		56.4		
Head size index (M18/M10 × 100)				
<i>A. afarensis</i>	1	105.9		
<i>A. africanus</i>	1	120.0		
<i>P. robustus</i>	2	109.2		105.1–113.2
<i>P. boisei</i>	2	114.3		103.2–125.3
<i>H. cf. habilis</i>	2	134.0		125.0–142.9
<i>H. erectus</i>	3	156.8	33.5	133.4–195.2
Archaic <i>H. sapiens</i>	3	150.6	5.2	145.0–155.2
Neandertals	10	148.5	7.4	139.0–159.0
Early modern	4	143.9	16.3	120.1–154.8
Berg Aukas		138.2		
Vertical neck diameter (M15)				
<i>A. afarensis</i>	2	27.2		23.0–31.4
<i>A. africanus</i>	2	24.7		22.0–27.3
<i>P. robustus</i>	2	26.3		26.2–26.3
<i>P. boisei</i>	5	27.3	3.5	24.0–33.0
<i>H. cf. habilis</i>	3	28.2	1.7	26.0–30.0
<i>H. erectus</i>	3	32.8	2.0	31.0–35.0
Archaic <i>H. sapiens</i>	2	36.5		35.0–38.0
Neandertals	9	33.9	4.0	27.0–38.0
Early modern	6	32.7	3.1	28.5–36.5
Berg Aukas		40.8		
Horizontal neck diameter (M16)				
<i>A. afarensis</i>	2	20.5		16.0–25.0
<i>A. africanus</i>	2	15.9		13.0–18.7
<i>P. robustus</i>	2	18.2		17.4–18.9
<i>P. boisei</i>	7	16.9	1.6	15.0–19.5
<i>H. cf. habilis</i>	4	20.5	3.9	15.0–24.0
<i>H. erectus</i>	3	23.2	1.0	22.0–23.8
Archaic <i>H. sapiens</i>	2	29.0		28.0–30.0
Neandertals	9	27.3	4.2	22.0–34.0
Early modern	6	28.9	3.0	25.0–33.0
Berg Aukas		36.6		
Neck shape index (M16/M15 × 100)				
<i>A. afarensis</i>	2	74.6		69.6–79.6
<i>A. africanus</i>	2	63.8		59.1–68.5
<i>P. robustus</i>	2	69.2		66.4–71.9
<i>P. boisei</i>	5	62.8	2.2	59.1–64.6
<i>H. cf. habilis</i>	3	79.5	0.8	78.6–80.0
<i>H. erectus</i>	3	70.7	2.6	68.0–73.2
Archaic <i>H. sapiens</i>	2	79.5		79.0–80.0
Neandertals	9	80.4	9.8	65.7–96.6
Early modern	6	90.7	5.5	83.3–96.1
Berg Aukas		89.7		
Neck length (L)				
<i>A. afarensis</i>	2	32.4		27.4–37.4
<i>A. africanus</i>	1	38.7		
<i>P. robustus</i>	2	44.3		41.7–46.8
<i>P. boisei</i>	2	36.0		35.0–37.0
<i>H. cf. habilis</i>	2	42.5		41.0–44.0
<i>H. erectus</i>	2	52.3		49.5–55.0
Berg Aukas		42.5		

(continued)

TABLE 3. Femoral head and neck dimensions for fossil hominid samples<sup>1</sup> (continued)

	N	$\bar{X}$	SD	Observed range
Neck length index ( $L/M15 \times 100$ )				
<i>A. afarensis</i>	2	119.1		119.1–119.1
<i>A. africanus</i>	1	141.8		
<i>P. robustus</i>	2	168.6		159.2–178.0
<i>P. boisei</i>	2	132.1		132.1–132.1
<i>H. cf. habilis</i>	2	151.1		136.7–165.4
<i>H. erectus</i>	1	177.4		
Berg Aukas		104.2		

<sup>1</sup>Information pertaining to the composition of the fossil hominid samples, and the derivation of the individual specimen values is contained in the Appendix.

falls comfortably within the observed ranges of recent human samples, and within the range of the early "modern" human sample from Skhul. The archaic *H. sapiens* specimens, as well as the majority of Neandertal femora, possess higher index values, presumably reflecting an absolutely large head atop a comparatively slender shaft.

### The neck

The Berg Aukas specimen differs from *Australopithecus*, *Paranthropus*, *Homo cf. habilis*, and *H. erectus* femora in having a relatively short neck (Table 3). The Berg Aukas neck length index value falls within the range for American black males, Zulu males and females, and Khoisan males (Table 2). The vertical and horizontal diameters of the Berg Aukas neck fall above the observed ranges for recent human and for all fossil hominid samples. The Berg Aukas neck shape index value places it within the upper limits of most of the recent human sample ranges (Table 2). This value falls within the upper portion of the observed Neandertal range and in the middle of the early modern human sample range (Table 3). Berg Aukas possesses a noticeably more symmetrical neck according to this ratio than *Australopithecus*, *Paranthropus*, *H. cf. habilis*, *H. erectus*, and archaic *H. sapiens* femoral (Table 3).

One of the most striking features of the Berg Aukas femur is its low neck-shaft angle. At 106° it is lower than that recorded for any nonpathological recent human (Table 4), or for any fossil femur (Table 5). Among the latter, Amud 1 (113°) and KNM-WT 15000 (110°) most closely approximate Berg

Aukas. Although the published angles of European Upper Paleolithic femora from Predmosti ( $P\ 4 = L109^\circ + R112^\circ$ ;  $P\ 14 = 112^\circ$ ) (Matiegka, 1938) and Dolní Věstonice ( $DV\ 13 = L107^\circ + R112^\circ$ ;  $DV\ 14 = 113^\circ$ ) (Vlček, 1991) are lower than or equal to that recorded for Amud 1, they are still higher than the Berg Aukas value. In recent humans, this angle is developmentally plastic and shows an ontogenetic decrease that is correlated with levels of normal physical activity (Houston and Zaleski, 1967). Adult neck-shaft angles, however, are attained during adolescence (Houston and Zaleski, 1967). Thus, although KNM-WT 15000 is an immature individual whose permanent canines were in the process of eruption at time of death, it is unlikely that its neck-shaft angle would have altered substantially. In addition, Trinkaus (1993a) has observed that among recent human populations, neck-shaft angle means show a distinct tendency to be higher with urbanization and lower with foraging lifestyles, regardless of the geographic distribution of the sample.

### The shaft

The inferior part of the greater trochanter on the Berg Aukas femur flares laterally from the shaft. Walker (1973) noted that the greater trochanter does not flare outward in *Australopithecus* and *Paranthropus*. This certainly holds for the three specimens of *P. boisei* that retain this part of the femur (i.e., KNM-ER 1463, KNM-ER 1503, OH 20), and for both *A. afarensis* specimens (AL 288-1, AL 333-3). Unfortunately, it cannot be confirmed for *A. africanus* because of damage to both Sts 14 and MLD 46. While SK 82 con-

TABLE 4. Femoral neck-shaft angles (M29) for recent human samples and Berg Aukas

		N	$\bar{X}$	SD	Observed range	Reference
Urban						
French	♂ + ♀	73	129.1	7.0	110–147	Trinkaus, 1993a
American white	♂ + ♀	55	129.6	5.5	119–146	Trinkaus, 1993a
American white	♂ + ♀	55	135.0	6.8	120–149	Trinkaus, 1993a
Belgian	♂ + ♀	186	133.1	5.6	114–153	Twisselmann, 1961
Japanese	♂ + ♀	50	130.5	4.9	118–143	Hirai and Tabata, 1928
Chinese	♂	122	131.0		120–147	Weidenreich, 1941
	♀	15	132.4		122–147	
Chinese	♂ + ♀	53	136.2	3.6	127–146	Trinkaus, 1993a
American black	♂	45	126.2	5.8	115–140	This study
	♀	8	126.4	4.1	119–131	
Agriculturist						
Amerindian	♂ + ♀	84	124.8	5.5	112–137	Trinkaus, 1993a
Amerindian	♂ + ♀	50	126.7	4.4	114–135	Trinkaus, 1993a
Amerindian	♂ + ♀	48	131.6	3.7	123–145	Trinkaus, 1993a
Amerindian	♂ + ♀	153	130.8	3.5	120–139	Trinkaus, 1993a
Polynesian	♂ + ♀	21	133.7	5.6	118–144	Murrill, 1968
Medieval Serbian	♂ + ♀	50	128.5	4.7	120–142	Trinkaus, 1993a
Medieval British	♂ + ♀	288	125.5	5.1	113–140	Parsons, 1914
Sub-Saharan African	♂	12	127.3	8.0	120–150	This study
	♀	2	132.5		130–135	
Zulu	♂	25	125.8	6.4	115–138	This study
	♀	25	127.6	6.2	116–140	
Hunter/gatherer/forager						
European Mesolithic	♂ + ♀	12	125.1	6.2	116–136	Trinkaus, 1993a
North African Mesolithic	♂ + ♀	14	126.4	8.1	114–140	Trinkaus, 1993a
Jomon	♂ + ♀	117	124.5	4.5	114–139	Ishisawa, 1931
Australian Aborigine	♂	150	127.8	4.3	117–142	Davivongs, 1963
	♀	110	127.3	5.0	114–139	
Khoisan	♂	28	121.4	4.5	114–129	This study
	♀	19	125.8	5.0	117–135	
Berg Aukas			106.0			

TABLE 5. Femoral neck-shaft angles (M29) for fossil hominid samples

	N	$\bar{X}$	SD	Observed range
<i>A. afarensis</i>	2	124.0		123–125
<i>A. africanus</i>	2	119.0		118–120
<i>P. robustus</i>	2	120.5		118–123
<i>P. boisei</i>	4	115.5	1.0	115–117
<i>H. cf. habilis</i>	4	124.0	1.2	123–125
<i>H. erectus</i>	4	120.3	7.6	110–127
Archaic <i>H. sapiens</i>	2	121.5		121–122
Neandertals	10	120.2	3.7	113–126
Early modern	6	132.9	5.5	122–137
Berg Aukas		106.0		

forms to this observation, the inferior margin of the anterolateral part of the greater trochanter of the other *P. robustus* proximal femur (SK 97) has a distinct lateral elevation. With reference to *Homo cf. habilis*, the greater trochanter is flush with the lateral margin of the shaft in KNM-ER 1472, as it appears to have been in OH 62, whereas it is slightly flared in KNM-ER 1481A. The greater trochanter of the juvenile *H. erectus* specimen (KNM-WT 15000) flares outward beyond the level of the diaphysis, and al-

though there is no abrupt change in level, the trochanteric epiphysis had not yet fused at time of death. The OH 28 femur preserves only the inferior margin of the greater trochanter, but this flares laterally. The only other *H. erectus* specimen that preserves this region (Zhoukoudian I) is also damaged, but here too the inferior margin of the greater trochanter flares laterally from the shaft. The fossil *H. sapiens* specimens are similar to modern human femora in the lateral flare of the greater trochanter.

Thus, in this feature, Berg Aukas differs from *A. afarensis* and *P. boisei*., *P. robustus*, and *H. cf. habilis* specimens vary in the degree to which the trochanter is laterally flared. Berg Aukas resembles *H. erectus*, archaic *H. sapiens*, Neandertal, and early modern femora in this regard.

The Berg Aukas femur possesses impressive, albeit not strikingly large, subtrochanteric diaphyseal dimensions, which fall at or below the upper ends of the observed ranges of some recent human samples (Table 6). Its AP diameter falls within the upper

TABLE 6. Subtrochanteric femoral dimensions for recent human samples and Berg Aukas

		N	$\bar{X}$	SD	Observed range	Reference
Subtrochanteric AP diameter (M9)						
Chinese	♂	135	24.5		21–28	Weidenreich, 1941
	♀	15	19.8		18–22	
Medieval English	♂	185	28.1		23–38	Parsons, 1914
	♀	105	25.5		21–29	
Romano-British	♂	57	27.0	2.1	23–32	Kennedy, 1983b
	♀	43	24.1	2.3	20–30	
Australian Aborigine	♂	150	22.9	1.9	18–29	Davivongs, 1963
	♀	110	20.4	1.9	16–25	
San	♀	8	20.5	1.5	18–23	Kennedy, 1983b
Sub-Saharan African	♂	12	23.8	1.4	22–26	This study
	♀	2	21.3		20–23	
Zulu	♂	25	26.2	1.9	23–31	This study
	♀	25	24.6	1.6	22–29	
Khoisan	♂	28	22.8	2.2	18–26	This study
	♀	19	21.2	1.9	17–25	
American black	♂	45	27.7	2.0	24–33	This study
	♀	8	26.8	1.5	25–29	
Berg Aukas			30.0			
Subtrochanteric ML diameter (M10)						
Chinese	♂	135	30.5		26–38	Weidenreich, 1941
	♀	15	26.1		23–29	
Medieval English	♂	185	35.6		30–45	Parsons, 1914
	♀	105	32.5		27–39	
Romano-British	♂	57	34.2	3.1	27–41	Kennedy, 1983b
	♀	43	30.9	2.8	25–39	
Australian Aborigine	♂	150	29.0	2.1	24–34	Davivongs, 1963
	♀	110	26.0	1.7	23–29	
San	♀	8	24.8	2.0	23–27	Kennedy, 1983b
Sub-Saharan African	♂	12	29.5	3.0	26–36	This study
	♀	2	27.0		24–30	
Zulu	♂	25	32.2	3.1	27–39	This study
	♀	25	29.3	2.3	25–35	
Khoisan	♂	28	28.1	2.4	22–32	This study
	♀	19	27.1	2.5	23–31	
American black	♂	45	32.0	3.0	26–40	This study
	♀	8	29.9	1.4	28–32	
Berg Aukas			40.8			
Platymeric index (M9/M10 × 100)						
Amerindian	♂ + ♀	117	71.5		52.5–93.2	Weidenreich, 1941
Chinese	♂	135	80.1		67.7–96.3	Weidenreich, 1941
Chinese	♀	200	81.3		64.7–103.8	Hasimoto, 1938
Medieval English	♂	185	79.3		59.0–100.0	Parsons, 1914
	♀	105	78.5		61.0–98.0	
Romano-British	♂	57	79.0	8.4	64.4–108.5	Kennedy, 1983b
	♀	43	77.9	8.6	62.6–107.3	
Australian Aborigine	♂	150	79.2	6.5	62.1–100.0	Davivongs, 1963
	♀	110	78.8	7.4	62.1–96.2	
San	♀	8	82.7	7.3	71.7–94.3	Kennedy, 1983b
Sub-Saharan African	♂	12	81.0	7.5	65.7–90.7	This study
	♀	2	79.1		75.9–82.3	
Zulu	♂	25	81.8	7.5	65.4–96.6	This study
	♀	25	84.1	5.6	73.3–96.2	
Khoisan	♂	28	81.2	5.8	69.6–90.9	This study
	♀	19	78.7	6.7	67.9–91.3	
American black	♂	45	87.3	10.1	70.4–119.2	This study
	♀	8	90.0	6.8	78.4–98.9	
Berg Aukas			73.5			

limits of the archaic *H. sapiens*, Neandertal, and early “modern” human sample ranges (Table 7). Its ML diameter falls just above the *H. erectus*, archaic *H. sapiens*, and Neandertal ranges, but within the early “modern” human sample range (Table 7). The Berg

Aukas platymeric index value falls just below the female sub-Saharan African, Zulu, and American black sample ranges, but within the corresponding male sample ranges, and it falls within all other recent human sample ranges (Table 6). It also falls

TABLE 7. Subtrochanteric femoral dimensions for fossil hominid samples

	N	$\bar{X}$	SD	Observed range
Subtrochanteric AP diameter (M9)				
<i>A. afarensis</i>	1	18.3		
<i>A. africanus</i>	0			
<i>P. robustus</i>	2	23.6		22.3–24.8
<i>P. boisei</i>	8	23.6	2.4	19.6–26.8
<i>H. cf. habilis</i>	3	22.0	1.0	21.0–23.0
<i>H. erectus</i>	8	24.5	2.9	21.8–30.0
Archaic <i>H. sapiens</i>	7	25.1	4.1	19.8–30.0
Neandertals	16	27.3	3.6	21.4–37.0
Early modern	6	29.4	3.9	25.0–34.8
Berg Aukas		30.0		
Subtrochanteric ML diameter (M10)				
<i>A. afarensis</i>	1	27.0		
<i>A. africanus</i>	1	26.0		
<i>P. robustus</i>	2	32.9		30.4–35.3
<i>P. boisei</i>	8	29.3	2.7	26.3–33.0
<i>H. cf. habilis</i>	3	27.9	6.0	21.0–32.0
<i>H. erectus</i>	8	33.4	5.8	23.6–40.0
Archaic <i>H. sapiens</i>	7	32.9	2.6	28.8–36.0
Neandertals	16	33.1	3.0	27.0–37.1
Early modern	6	33.3	5.1	27.3–40.7
Berg Aukas		40.8		
Platymetric index (M9/M10 $\times$ 100)				
<i>A. afarensis</i>	1	67.8		
<i>A. africanus</i>	0			
<i>P. robustus</i>	2	73.8		66.0–81.6
<i>P. boisei</i>	8	80.7	6.4	72.1–89.9
<i>H. cf. habilis</i>	3	81.2	16.6	68.8–100.0
<i>H. erectus</i>	8	74.9	14.5	62.3–108.1
Archaic <i>H. sapiens</i>	7	76.3	9.4	64.9–89.6
Neandertals	16	79.8	6.1	72.2–94.2
Early modern	6	83.6	4.7	76.5–90.4
Berg Aukas		73.5		

within, though near the lower end of the observed ranges for all fossil hominid samples except the early “modern” humans, whose values are somewhat larger (Table 7). Almost all Neandertal femora, however, are relatively deeper AP at the subtrochanteric level than Berg Aukas.

The medial border of the proximal end of the Berg Aukas diaphysis is very slightly convex, and this is owing at least in part to the development of the ridge that separates the attachment areas of vastus medialis and vastus intermedius, and partly to the spiral line. In this, Berg Aukas differs from *Australopithecus*, *Paranthropus*, *Homo habilis*, and *H. erectus* femora. On the other hand, a similar ridge is present on at least one archaic *H. sapiens* femur (Kabwe E689), and in some early modern homologues (e.g., Skhül 4, and remnants of a medially expanded ridge are palpable on KNM-ER 999).

The lateral surface of the proximal end of the Berg Aukas diaphysis is bowed outward very slightly due to the development of a

blunt crista lateralis that borders a shallow hypotrochanteric fossa. This anatomy is not present on *A. afarensis*, *P. robustus*, or *P. boisei* homologues. While it is lacking on two specimens that have been attributed to *H. habilis* (KNM-ER 1472, OH 62), it is present on a third (KNM-ER 1481A). This ridge and the consequent slight lateral bowing of the shaft are absent from KNM-ER 1809, and appear to have been lacking also from the Zhoukoudian IV femur, whilst they are present on five other specimens of *H. erectus* (KNM-ER 736, KNM-ER 737, KNM-WT 15000, OH 28, and Zhoukoudian I). Neither of the Kabwe proximal femora display this morphology, whereas Arago XLVII evinces a marked crista lateralis and a broad, deep hypotrochanteric fossa. Trinkaus (1976) reported that some 64% of Neandertal femora ( $N = 14$ ) have a hypotrochanteric fossa, although Kidder et al. (1991) noted that this pattern is not present in the Levantine Neandertals. This morphology is also absent from the early modern specimens from the



Levant, whereas KNM-ER 999 has both a broad hypotrochanteric fossa and a laterally bowed crista lateralis. Trinkaus (1976) has reported that some 58% of European Upper Paleolithic humans and 25% of recent Europeans display a hypotrochanteric fossa.

Thus, in the morphology of the posterolateral part of the proximal diaphysis, Berg Aukas differs from *Australopithecus* and *Paranthropus* specimens. It is similar in this regard to one of three *H. habilis* femora, five of six *H. erectus* specimens, one of three archaic *H. sapiens* fossils, the majority of European Neandertals, and at least one early "modern" homologue from Africa.

Although Berg Aukas appears to resemble some Neandertals in the presence of a distinct gluteal tuberosity, a hypotrochanteric fossa, and a laterally bowed proximal shaft, European Neandertal femora tend to be characterized by gluteal ridges that flank a deep, broad hypotrochanteric fossa (Trinkaus 1976, 1983a). According to Trinkaus, the fossae in Neandertals are "not merely sulci between a gluteal ridge and a lateral proximal shaft swelling . . . They are distinct depressions within the tuberosities (1976, p. 308)." On the Berg Aukas femur, however, the shallow hypotrochanteric fossa is bounded medially by the gluteal ridge and tuberosity, but laterally by a weak crista lateralis that is separated along its entire length from the gluteal ridge. This is the condition described by Hrdlička (1934) for recent human thigh bones. In this detail, Berg Aukas differs from European Neandertal homologues, and it appears to differ also from the Arago XLVII femur, in which a distinct hypotrochanteric fossa is bounded by a markedly prominent lateral crest that is confluent proximally with the gluteal tuberosity.

The gluteal tuberosity on Berg Aukas is notably better developed than on any *Australopithecus*, *Paranthropus*, or *Homo cf. habilis* homologue. It is somewhat more prominent than on the juvenile KNM-WT 15000 *H. erectus* femur, and it appears comparable to that on Zhoukoudian I and IV. The tuberosity on Berg Aukas is stronger than on either of the Kabwe homologues, but similar to that on the Arago XLVII femur. In addition to being matched on several Nean-

dertal specimens, Skhül 4 possesses a gluteal tuberosity that is similar in development to that on the Berg Aukas femur. Thus, the degree of development of the gluteal tuberosity, which is quite variable among both fossil and recent *H. sapiens* samples, appears to differentiate Berg Aukas from only australopithecines and *H. habilis*.

The midshaft AP and ML diameters of Berg Aukas are equally impressive, but not unusual among recent and fossil *H. sapiens* samples. Thus, the Berg Aukas diameters are within the upper limits of several recent human male samples, and just above the ranges of corresponding female samples (Table 8). Similarly, they are within the archaic *H. sapiens*, Neandertal and early "modern" human sample ranges. On the other hand, the Berg Aukas values are considerably larger than those recorded for specimens comprising the other fossil samples (Table 9). The resultant pilastric index value of the Berg Aukas femur falls within the observed ranges for recent human samples (Table 8), but well above *Australopithecus*, *Paranthropus*, and *H. cf. habilis* values (Table 9). Similarly, all *H. erectus* femora exhibit less pilastering than Berg Aukas. The archaic *H. sapiens* and Neandertal sample ranges fall just short of the Berg Aukas index value, while the early modern human sample range encompasses this value (Table 9). Thus, while *H. erectus*, archaic *H. sapiens*, and Neandertal femora tend to have less developed lineae asperae, early modern femora tend to be marked by a better developed pilaster than Berg Aukas.

The relative AP depth of the Berg Aukas femur is achieved through the expansion of the entire posterior aspect of the diaphysis without a sharp, crest-like linea aspera. In this regard it is unlike the early modern specimens from the Levant and Europe.

### Radiological features

As noted above, the AP radiograph of Berg Aukas (Fig. 5) reveals a dense and diffuse lateral trabecular bundle, which precludes the identification of Ward's triangle. Weidenreich (1941) described a similar pattern for Zhoukoudian I, in which Ward's triangle is missing because the medial and lateral

TABLE 8. *Midshaft femoral dimensions for recent human samples and Berg Aukas*

		N	$\bar{X}$	SD	Observed range	Reference
Midshaft AP diameter (M6)						
Chinese	♂	133	27.9		24–32	Weidenreich, 1941
	♀	15	22.8		20–25	
Medieval English	♂	184	31.6		26–40	Parsons, 1914
	♀	108	28.0		23–33	
Romano-British	♂	57	28.8	2.1	25–34	Kennedy, 1983b
	♀	43	25.5	2.0	22–29	
Australian Aborigine	♂	149	27.6	2.6	21–37	Davivongs, 1963
	♀	109	23.9	2.6	18–30	
San	♀	8	22.9	3.5	21–28	Kennedy, 1983b
Sub-Saharan African	♂	12	29.3	2.5	25–35	This study
	♀	2	26.1		24–28	
Zulu	♂	25	29.9	2.6	26–36	This study
	♀	25	27.8	2.3	25–34	
Khoisan	♂	28	29.1	2.8	24–34	This study
	♀	19	25.2	2.1	21–28	
American black	♂	45	29.3	2.7	24–36	This study
	♀	8	28.2	0.8	27–29	
Berg Aukas			35.9			
Midshaft ML diameter (M7)						
Chinese	♂	133	26.5		22–33	Weidenreich, 1941
	♀	15	22.3		19–27	
Medieval English	♂	184	29.6		24–35	Parsons, 1914
	♀	108	26.5		21–31	
Romano-British	♂	57	28.1	1.5	26–31	Kennedy, 1983b
	♀	43	25.6	1.8	23–30	
Australian Aborigine	♂	149	24.7	1.7	21–29	Davivongs, 1963
	♀	109	22.4	1.3	19–26	
San	♀	8	21.8	1.0	21–24	Kennedy, 1983b
Sub-Saharan African	♂	12	24.8	1.7	22–27	This study
	♀	2	23.3		21–26	
Zulu	♂	25	26.9	2.1	23–30	This study
	♀	25	24.3	1.6	22–27	
Khoisan	♂	28	22.9	1.8	19–27	This study
	♀	19	22.0	1.8	18–25	
American black	♂	45	28.4	2.7	23–35	This study
	♀	8	25.3	2.5	22–29	
Berg Aukas			31.5			
Pilastric index (M6/M7 × 100)						
Chinese	♂ + ♀	48	102.3		85.0–125.0	Black, 1925
Chinese	♂	131	105.6		83.9–131.6	Weidenreich, 1941
Jomon	♂ + ♀	149	111.0	8.7		Ishisawa, 1931
Amerindian	♂ + ♀	129	108.6	10.4		Trinkaus, 1993b
Medieval Serbian	♂ + ♀	81	106.3	9.3		Trinkaus, 1993b
Belgian	♂ + ♀	208	102.2	8.6		Twisselmann, 1961
Medieval English	♂	184	108.0		85.7–148.0	Parsons, 1914
	♀	108	104.1		80.0–125.0	
English	♂	56	108.4		93.3–125.8	Holtby, 1918
	♀	44	108.2		87.5–128.0	
Romano-British	♂	57	102.3	7.3	88.9–123.5	Kennedy, 1983b
	♀	43	99.7	15.4	90.9–117.5	
Australian Aborigine	♂	149	112.0	10.0	84.6–134.6	Davivongs, 1963
	♀	109	106.6	9.8	86.4–131.6	
San	♀	8	105.0	11.7	99.5–135.5	Kennedy, 1983b
Sub-Saharan African	♂	12	118.4	9.8	105.5–132.8	This study
	♀	2	112.4		107.3–117.6	
Zulu	♂	25	111.3	8.6	96.3–125.9	This study
	♀	25	114.7	10.4	100.0–136.4	
Khoisan	♂	28	127.0	9.8	106.8–145.7	This study
	♀	19	115.1	8.9	100.0–131.7	
American black	♂	45	104.3	14.2	79.2–135.0	This study
	♀	8	112.1	11.6	100.0–132.3	
Berg Aukas			114.0			

bundles (his “System I” and “System II” trabeculae) diverge diffusely from the end of the shaft. The Berg Aukas and Zhoukoudian

I radiographs also compare favorably in the appearance of the trabeculae in the infero-lateral part of the metaphysis.

TABLE 9. Midshaft femoral dimensions for fossil hominid samples

	N	$\bar{X}$	SD	Observed range
Midshaft AP diameter (M6)				
<i>A. afarensis</i>	2	23.4		20.5–26.2
<i>A. africanus</i>	0			
<i>P. robustus</i>	0			
<i>P. boisei</i>	3	25.0	2.1	23.0–24.8
<i>H. cf. habilis</i>	2	20.8		19.0–22.5
<i>H. erectus</i>	10	25.3	1.8	22.8–28.2
Archaic <i>H. sapiens</i>	8	27.6	4.7	22.1–35.0
Neandertals	17	29.5	3.6	22.2–36.5
Early modern	10	34.6	4.4	28.0–41.3
Berg Aukas		35.9		
Midshaft ML diameter (M7)				
<i>A. afarensis</i>	2	24.9		21.1–28.6
<i>A. africanus</i>	0			
<i>P. robustus</i>	0			
<i>P. boisei</i>	3	26.0	2.4	23.4–28.2
<i>H. cf. habilis</i>	2	22.2		19.0–25.3
<i>H. erectus</i>	10	28.8	3.5	23.2–32.7
Archaic <i>H. sapiens</i>	8	28.3	2.5	24.6–32.0
Neandertals	17	29.7	2.4	24.1–34.3
Early modern	10	28.5	2.8	25.7–34.4
Berg Aukas		31.5		
Pilastric index (M6/M7 $\times$ 100)				
<i>A. afarensis</i>	2	94.4		91.6–97.2
<i>A. africanus</i>	0			
<i>P. robustus</i>	0			
<i>P. boisei</i>	3	96.1	2.2	93.9–98.3
<i>H. cf. habilis</i>	2	94.5		88.9–100.0
<i>H. erectus</i>	10	88.6	8.8	75.5–105.6
Archaic <i>H. sapiens</i>	8	97.7	14.2	80.0–116.3
Neandertals	17	100.2	8.1	86.7–114.1
Early modern	10	121.5	12.6	100.0–140.5
Berg Aukas		114.0		

Weidenreich (1941) considered the proximal trabecular pattern of the Zhoukoudian femur to represent a major departure from the modern human condition, and Kennedy (1983b) has noted that only 6% of Romano-British femora examined by her lacked diminished radiographic density in the region of Ward's triangle. The few published AP radiographs of Neandertal proximal femora that we have been able to examine reveal a pattern essentially similar to that described in most anatomy textbooks as being typically human. Thus, although the range of normal human variation in proximal trabecular patterns has yet to be established adequately, the diffuse network displayed by Berg Aukas may distinguish it from Neandertals and more modern human femora. Proximal trabecular networks are known to degenerate with age (Bergot and Bocquet, 1976; Walker and Lovejoy, 1985), which may suggest that the Berg Aukas individual was a comparatively young adult at time of death. Nevertheless, the dense trabecular

infilling that it possesses appears to be unusual for modern humans.

Trinkaus et al. (1991) have compared the angle assumed by the medial trabecular bundle (MTA) and the neck-shaft angle (NSA) in a sample of recent humans and a fossil *Homo* sample composed of Neandertals and the Kabwe proximal femora. They observed that the fossils tend to have a lower MTA than most modern humans in relation to the NSA. The Berg Aukas MTA of 135°, when compared to its NSA of 106°, falls just below the downward extension of the recent human regression line determined by them (Fig. 6). While Berg Aukas has a somewhat lower MTA than the lowest recorded by Trinkaus et al. (1991) for recent human femora, two of the eight fossils measured by them possess an even lower MTA. The low MTA of Berg Aukas is not surprising in light of its noticeably low NSA.

The AP radiograph of Berg Aukas (Fig. 5) reveals that the lateral diaphyseal cortical bone begins to taper at a more distal level

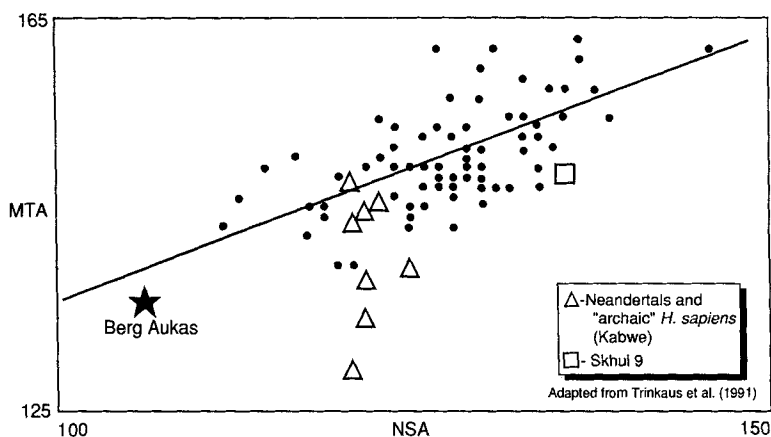


Fig. 6. Relationship between the medial trabecular angle (MTA) and neck-shaft angle (NSA) in a sample of recent human (American whites and Amerindians) (circles) and fossil human femora. Triangles = European and Levantine Neandertals and the Kabwe femora.

than described by Weidenreich (1941) for Zhoukoudian I and IV. In this regard, Berg Aukas resembles the few Neandertal femora whose published radiographs we have examined, and it appears also to represent the recent human condition, although this has yet to be quantified. The medial diaphyseal cortical bone, on the other hand, retains its thickness well into the inferior border of the neck, and in this regard Berg Aukas resembles the condition described by Weidenreich (1941) for the Zhoukoudian *H. erectus* femora. However, this feature also has yet to be documented quantitatively for recent humans or for fossil hominid femora, although Day (1971) and Kennedy (1983a) have noted that the cortex on the inferior aspect of the neck remains very thick in OH 28 and KNM-ER 737. Kennedy (1983a) has observed, moreover, that the inferior region of the neck of KNM-ER 737 shows "the same proximal extension seen in the Zhoukoudian specimens."

Modern human values pertaining to the geometry of cortical bone at the subtrochanteric level are recorded in Table 10. The Berg Aukas subtrochanteric cortical area and polar moment of area are nearly double the corresponding means recorded for the human samples. We have observed no recent human remur with values this great. The Berg Aukas cortical index value falls

just within the observed upper limit of the modern subSaharan male sample. The  $I_{\max}/I_{\min}$  value for Berg Aukas reflects greater asymmetry in the distribution of cortical bone than tends to be the case for modern Africans and American blacks, although the ranges include even larger values than that seen in Berg Aukas. Native American femora tend to display a greater discrepancy between major and minor axes than does Berg Aukas. Unfortunately, comparable values for fossil hominid femora have not yet been published, with the exception of Spy 2 with a  $I_{\max}/I_{\min}$  value of 1.25 (Trinkaus and Ruff, 1989).

Data recorded by Dr. Chris Ruff for the subtrochanteric section of the KNM-ER 736 *H. erectus* shaft reveal a cortical area of 656 mm<sup>2</sup>; J is 114,129 mm<sup>4</sup> for this specimen. The cortical area for KNM-ER 736 is smaller than that of Berg Aukas, although it exceeds the largest modern human value. The value of J for KNM-ER 736 is also smaller than that of Berg Aukas, but it falls just within the observed upper limit of the black American male sample.

Table 11 records the cortical area and polar moment of area at the femoral midshaft for a variety of modern human and fossil hominid samples. The cortical area of Berg Aukas is significantly larger than the corresponding mean recorded for any modern hu-

TABLE 10. Subtrochanteric cortical geometry in modern humans and the Berg Aukas femur<sup>1</sup>

		N	$\bar{X}$	SD	Observed range
Cortical area (CBA)					
Sub-Saharan African	♂	12	432	70	328–560
	♀	2	374		317–432
Zulu	♂	25	428	68	333–563
	♀	25	326	53	259–503
Khoisan	♂	27	333	58	205–447
	♀	20	262	54	204–399
American black	♂	45	463	59	327–585
	♀	8	375	56	271–427
Native American	♂ + ♀	119	316	51	286–602
Berg Aukas			794		
Polar moment of area (J)					
Sub-Saharan African	♂	12	52,293	16,218	34,874–80,026
	♀	2	38,320		25,705–50,936
Zulu	♂	25	65,774	16,868	43,817–94,128
	♀	25	43,405	8,972	26,487–65,800
Khoisan	♂	27	38,893	11,247	21,495–63,472
	♀	20	27,791	7,680	13,500–47,453
American black	♂	45	71,735	15,904	39,199–124,865
	♀	8	53,272	8,630	38,413–68,751
Native American	♂ + ♀	119	39,194	11,138	12,865–54,574
Berg Aukas			132,038		
Cortical index (CBA/TSA × 100)					
Sub-Saharan African	♂	12	74.9	6.3	66.6–89.2
	♀	2	77.1		75.1–79.0
Zulu	♂	25	63.1	6.5	50.1–73.4
	♀	25	57.3	9.2	41.2–77.7
Khoisan	♂	27	64.6	8.4	45.9–82.6
	♀	20	58.5	11.3	20.0–76.8
American black	♂	45	66.5	6.8	54.3–81.4
	♀	8	59.6	9.3	46.6–72.2
Native American	♂ + ♀	119	60.5	6.8	26.3–74.5
Berg Aukas			88.4		
$I_{\max}/I_{\min}$					
Sub-Saharan African	♂	12	1.55	0.31	1.16–2.31
	♀	2	1.16		1.60–1.92
Zulu	♂	25	1.55	0.31	1.05–2.28
	♀	25	1.52	0.23	1.20–2.05
Khoisan	♂	27	1.71	0.34	1.14–2.51
	♀	20	1.73	0.27	1.45–2.47
American black	♂	45	1.55	0.33	1.06–2.31
	♀	8	1.34	0.21	1.03–1.58
Native American	♂ + ♀	119	1.91	0.22	1.42–2.63
Berg Aukas			1.79		

<sup>1</sup> Data for Native American samples from Ruff and Hayes (1983).

man sample; indeed, it is almost 5 standard deviation units above the American black male mean, which has the largest dimensions of any published modern group. The contrast between most recent humans and Berg Aukas is even more remarkable with reference to the midshaft J value.

The midshaft cortical area of Berg Aukas is noticeably larger than that of any *H. cf. habilis*, *H. erectus*, or fossil *H. sapiens* homologue. The closest approximations to the Berg Aukas value are exhibited by the archaic *H. sapiens* shaft from Castel di Guido (CA = 675 mm<sup>2</sup>) and the KNM-ER 736 *H. erectus* diaphysis (CA = 659 mm<sup>2</sup>). The great cortical area of Berg Aukas can be

readily appreciated (Fig. 11) if this value is plotted against femoral head diameter, using the latter as a body size surrogate following Ruff et al. (1993). Extrapolation of the modern human regression line is necessary, and Berg Aukas is much larger than predicted despite its notably large femoral head, not unlike some "pre-recent" *Homo* (Ruff et al., 1993: Fig. 12). The same results obtain with reference to the value of J. Here, the closest approximation to Berg Aukas is KNM-ER 736, at a value of 116,628 mm<sup>4</sup>, although the specimen from Castel di Guido has a J of 103,870 mm<sup>4</sup>.

The midshaft cortical index value of Berg Aukas is notably larger than the corre-

TABLE 11. Cross-sectional geometric properties of the femoral midshaft in modern humans and fossil *Homo*<sup>1</sup>

		N	$\bar{X}$	SD	Observed range
Cortical area (CBA)					
Sub-Saharan African	♂	12	419	53	335–511
	♀	2	369		319–415
Zulu	♂	25	428	64	334–520
	♀	25	330	42	278–429
Khoisan	♂	27	345	58	214–470
	♀	20	270	47	202–355
American black	♂	45	457	60	312–559
	♀	8	368	63	263–444
Native American	♂ + ♀	119	325	52	162–445
Autopsy sample	♂ + ♀	36	378	75	242–500
Japanese	♂	22	293	44	
	♀	20	179	45	
<i>Homo cf. habilis</i>		2	366		332–400
<i>Homo erectus</i>		7	464	84	410–659
Archaic <i>Homo sapiens</i>		4	477	152	321–675
Neandertals		9	530	87	362–648
Upper Paleolithic		6	475	103	394–599
Berg Aukas			750		
Polar moment of area (J)					
Sub-Saharan African	♂	12	46,956	12,247	30,870–30,545
	♀	2	34,111		24,373–43,850
Zulu	♂	25	52,802	14,303	31,613–81,547
	♀	25	34,667	8,229	22,504–55,144
Khoisan	♂	27	35,495	10,879	15,037–57,618
	♀	20	23,247	6,069	10,282–34,165
American black	♂	45	60,367	12,714	31,802–88,041
	♀	8	42,565	7,428	33,204–57,192
Native American	♂ + ♀	119	31,768	8,891	12,865–54,574
Autopsy sample	♂ + ♀	36	45,049	15,348	23,463–76,660
Japanese	♂	22	30,860	7,160	
	♀	20	15,570	4,670	
<i>Homo cf. habilis</i>		2	29,381		24,583–34,178
<i>Homo erectus</i>		8	52,941	26,808	33,412–116,628
Archaic <i>Homo sapiens</i>		4	50,196	36,514	22,919–103,870
Neandertals		9	69,426	17,565	36,830–90,179
Upper Paleolithic		6	60,027	24,235	29,138–95,262
Berg Aukas			116,261		

<sup>1</sup> Data for the Sub-Saharan African, Zulu, Khoisan, and American black samples have not been published elsewhere. The Native American and autopsy sample data are from Ruff (1984). Japanese sample values derive from Kimura and Takahashi (1984); ranges were not included in the summary statistics. C.B. Ruff and E. Trinkaus kindly provided the data for all but one of the fossil *Homo* specimens; we group these specimens in a slightly different manner than did Ruff et al. (1993). The *Homo cf. habilis* sample comprises KNM-ER 1472 and KNM-ER 1481; the *H. erectus* sample includes Zhoukoudian 1, 2, 4, 5, and 6, KNM-ER 736, KNM-ER 737, and OH 28; the archaic *H. sapiens* sample consists of Kabwe E690, Geshen Benot Ya'acov 1, Castel de Guido 1, and Ain Maarouf. The Neandertal sample included St. Cesaire 1, Fond-de-Forêt 1, La Chapelle-aux-Saints 1, La Ferrassie 1 and 2, Neandertal 1, Shanidar 4, Spy 2, and Tabun C1. Upper Paleolithic specimens include Cro-Magnon 4323b/4325 and 4322, Mladec 27, Obercassel 1 and 2, and Paviland 1.

sponding mean recorded for any modern human sample, being 2 standard deviation units from the means for all but the Khoisan sample (Table 12). This value for Berg Aukas falls at the upper limits of the observed recent human sample ranges. It also falls within the archaic *H. sapiens* and *H. erectus* sample ranges, and just above the Upper Paleolithic, Neandertal, and *H. cf. habilis* ranges (Table 12). The "bending ratio" ( $I_{\max}/I_{\min}$ ) value of the Berg Aukas femur is comparable to modern human sample averages. This indicates that the asymmetric distribution of cortical bone in the middle of the Berg Aukas shaft is similar to the asymmetry dis-

played by modern humans. The Berg Aukas midshaft "bending index" value is comparable to the different fossil *Homo* sample means (Table 12).

## DISCUSSION

Comparisons of over a dozen non-radio-graphic features (both metrical and non-metrical) indicate that the Berg Aukas femur is not attributable to *Australopithecus*, *Paranthropus*, or *Homo cf. habilis*.

Berg Aukas clearly differs from these Pliocene and early Pleistocene elements by its large size (especially its head, but also its neck and diaphyseal diameters), its rela-

TABLE 12. Cortical shape of the femoral midshaft in modern humans and fossil *Homo*<sup>1</sup>

		N	$\bar{X}$	SD	Observed range
Cortical index (CBA/TSA $\times$ 100)					
Sub-Saharan African	♂	12	77.3	5.3	68.5–84.5
	♀	2	80.2		78.5–82.0
Zulu	♂	25	73.1	6.2	60.8–84.0
	♀	25	68.9	6.8	56.4–83.3
Khoisan	♂	27	73.6	7.2	56.7–84.1
	♀	20	68.8	11.4	40.6–91.0
American black	♂	45	72.7	7.7	55.5–86.4
	♀	8	68.3	11.6	50.6–85.5
Native American	♂ + ♀	119	71.6	7.8	31.0–83.3
European American	♂ + ♀	40	69.1	6.3	
<i>Homo cf. habilis</i>		2	85.6		84.9–86.2
<i>Homo erectus</i>		7	83.5	7.5	71.2–91.2
Archaic <i>Homo sapiens</i>		4	85.1	3.4	81.8–89.7
Neandertals		9	79.3	4.0	73.1–86.6
Upper Paleolithic		6	78.4	4.9	73.0–85.4
Berg Aukas			87.9		
$I_{\max}/I_{\min}$					
Sub-Saharan African	♂	12	1.44	0.25	1.16–1.91
	♀	2	1.61		1.58–1.64
Zulu	♂	25	1.32	0.16	1.04–1.59
	♀	25	1.42	0.22	1.03–1.99
Khoisan	♂	27	1.68	0.30	1.03–2.25
	♀	20	1.38	0.27	1.02–2.00
American black	♂	45	1.43	0.24	1.06–2.16
	♀	8	1.50	0.24	1.22–1.86
Native American	♂ + ♀	119	1.38	0.22	1.03–1.98
European American	♂ + ♀	40	1.28	0.19	
<i>Homo erectus</i>		5	1.37	0.07	1.30–1.47
Archaic <i>Homo sapiens</i>		2	1.40		
Neandertals		9	1.36	0.02	
Berg Aukas			1.37		

<sup>1</sup> Samples are drawn from the same sources as in Table 11 except that the European American and Native American data, together with the  $I_{\max}/I_{\min}$  values for Neandertal specimens, are from Trinkaus and Ruff (1989). The  $I_{\max}/I_{\min}$  data for the two archaic *H. sapiens* specimens—Castel de Guido 1 and Ain Maarouf—are from Mallengi et al. (1983) and Hublin (1992), respectively. The five *H. erectus* values are based upon drawings in Weidenreich (1941).

tively large head, its relatively short and more robust neck, and in the greater pilaster exhibited by its shaft (Figs. 7 and 8). In addition, femora of *Australopithecus*, *Paranthropus*, and *H. cf. habilis* lack the slight medial swelling of the proximal part of the diaphysis, their gluteal tuberosity tends to be less well defined, and the lateral border of the proximal part of the diaphysis lacks the bowing caused by the marginal ridge of the hypotrachantric fossa (although *H. cf. habilis* femora are variable in this last respect). Finally, the lateral surface of the greater trochanter tends to be flush with the shaft on early hominid femora, although this feature is variable in both *P. robustus* and *H. cf. habilis* (Figs. 7 and 8).

The Berg Aukas femur is unlikely to represent *H. erectus*. Its head, neck, and shaft are larger than in most *H. erectus* homologues, although at least one specimen (KNM-ER 736), which equals Berg Aukas in its subtrochanteric diaphyseal diameters,

also approaches its midshaft CA and J values, and another (KNM-ER 737) equals Berg Aukas in its midshaft ML diameter. Moreover, the KNM-WT 15000 femur may have had an equally large head had this individual reached adulthood. However, *H. erectus* femora possess a neck that is both relatively longer and relatively flatter AP, and the shaft exhibits less pilaster than Berg Aukas (Figs. 9 and 10). Indeed, *H. erectus* femora do not display pilaster; rather, they possess only a prominent linea aspera. The medial border of the proximal part of the diaphysis appears to be somewhat more convex in Berg Aukas, and it also appears to differ from at least some *H. erectus* specimens in the level at which the lateral diaphyseal cortex begins to taper.

Berg Aukas resembles *H. erectus* homologues in the relative size of its head, its platymetric index, the lateral flare of the greater trochanter, the development of the gluteal tuberosity, and the development of

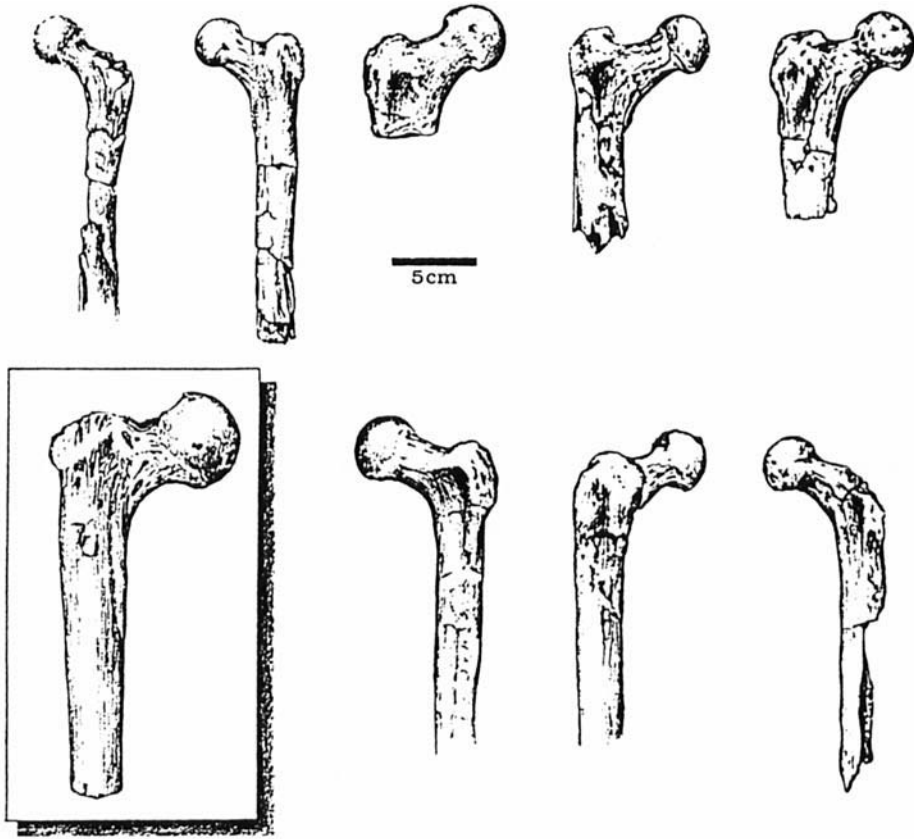


Fig. 7. Anterior views of the Berg Aukas femur (inset) compared with *Australopithecus*, *Paranthropus*, and *Homo cf. habilis* homologues. Top row, left to right: Sts 14 (*A. africanus*); AL 288-1, AL 333-3 (*A. afarensis*); SK 82, SK 97 (*P. robustus*). Bottom row, left to right: KNM-ER 1481A, KNM-ER 1472 (*H. cf. habilis*); KNM-ER 738 (*P. boisei*).

the hypotrochanteric fossa and crista lateralis. However, in these features Berg Aukas is similar also to some *H. sapiens* homologues. Berg Aukas also resembles *H. erectus* femora in the diffuse proximal trabecular network that precludes identification of Ward's triangle, an extension of the thick medial diaphyseal cortex well into the inferior aspect of the neck, and its thick diaphyseal cortex. However, while the first feature seems to differ in recent humans (Kennedy, 1983a) and in at least some Neandertals, these radiological characters have not been studied adequately in either recent or fossil *H. sapiens*.

The Berg Aukas femur is most likely attributable to *Homo sapiens*, insofar as the archaic, Neandertal, and early modern groups referred to here actually comprise a single species (Tattersall, 1986, 1992; Rightmire, 1990; Stringer, 1992, 1994). Berg Aukas resembles all fossil *H. sapiens* groups in the lateral flare of the greater trochanter, the convexity of the medial and lateral borders of the proximal part of the shaft, the subtrochanteric AP diameter of the shaft, and the AP and ML diameters at midshaft (Figs. 9 and 10).

Berg Aukas differs from the Middle Pleistocene archaic specimens in having an *abso*-



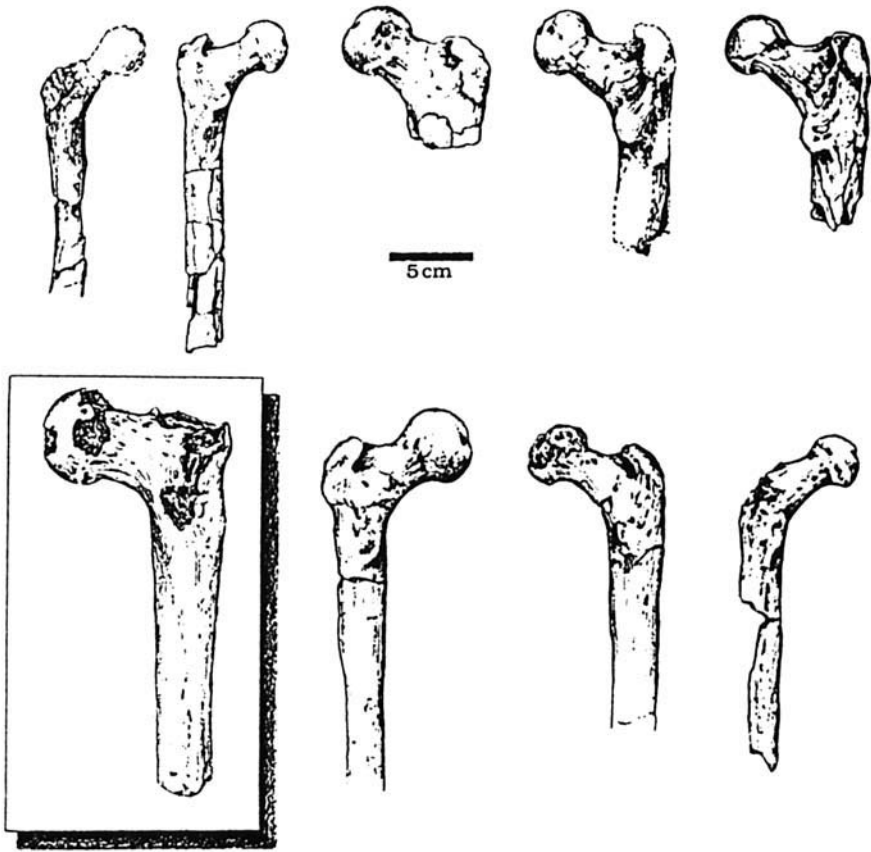


Fig. 8. Posterior views of the Berg Aukas femur compared with *Australopithecus*, *Paranthropus*, and *Homo cf. habilis* homologues. Legend as for Figure 7.

lutely larger but relatively smaller head, a more robust neck that is relatively thicker in its AP diameter, a larger subtrochanteric ML diameter, and a shaft that shows a greater degree of pilaster.

At the same time, Berg Aukas differs from Neandertal femora in possessing an *absolutely larger* head (although some Neandertal specimens approach it rather closely), but a head that is *relatively smaller*. It also has a larger subtrochanteric ML diameter. Its shaft is relatively flatter proximally, and relatively deeper in its middle compared to the majority of Neandertal homologues. Neandertal femora also tend to possess a deeper hypotrochanteric fossa that is flanked by strong gluteal ridges, and they also tend to show a greater degree of medial

convexity of the proximal end of the shaft than in Berg Aukas (Figs. 9 and 10).

Berg Aukas differs from Middle Pleistocene *H. sapiens* and Neandertals, and resembles early modern (and recent) humans in terms of the *relative* size of its head, its stronger pilaster, and in the absolute ML breadth of its shaft at the subtrochanteric level. It differs from early modern human femora by its absolutely larger head, and relatively flatter shaft at the subtrochanteric level.

The diaphyseal cross-sectional data further suggest that the Berg Aukas femur is not attributable to *H. cf. habilis* insofar as its absolute dimensions far exceed homologous values in femora currently attributed to that taxon. With the exception of the mid-

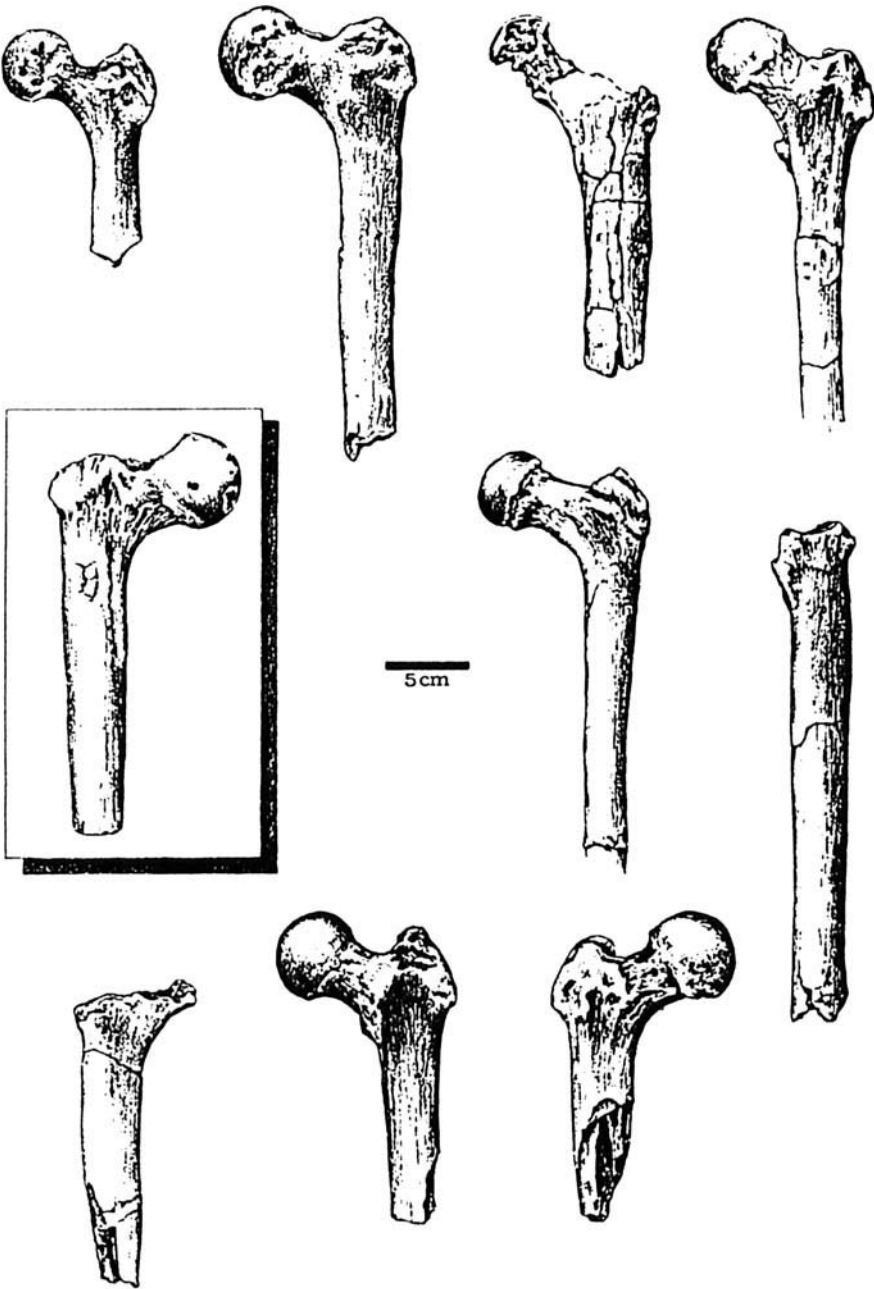


Fig. 9. Anterior views of the Berg Aukas femur (inset) compared with *Homo erectus*, archaic *H. sapiens*, Neandertal, and early modern homologues. Top row, left to right: Krapina 214, Spy 2 (Neandertals); KNM-ER 999, Skhul 4 (early modern humans). Middle row, left to right: KNM-WT 15000, OH 28 (*H. erectus*). Bottom row, left to right: Arago XLVIII, Kabwe E689, Kabwe E907 (archaic *H. sapiens*).

shaft J value of KNM-ER 736, the Berg Aukas cross-sectional values exceed those for femora attributed to *H. erectus*. Only the

very largest Neandertal and archaic *H. sapiens* (particularly Castel di Guido) specimens approach the Berg Aukas values.

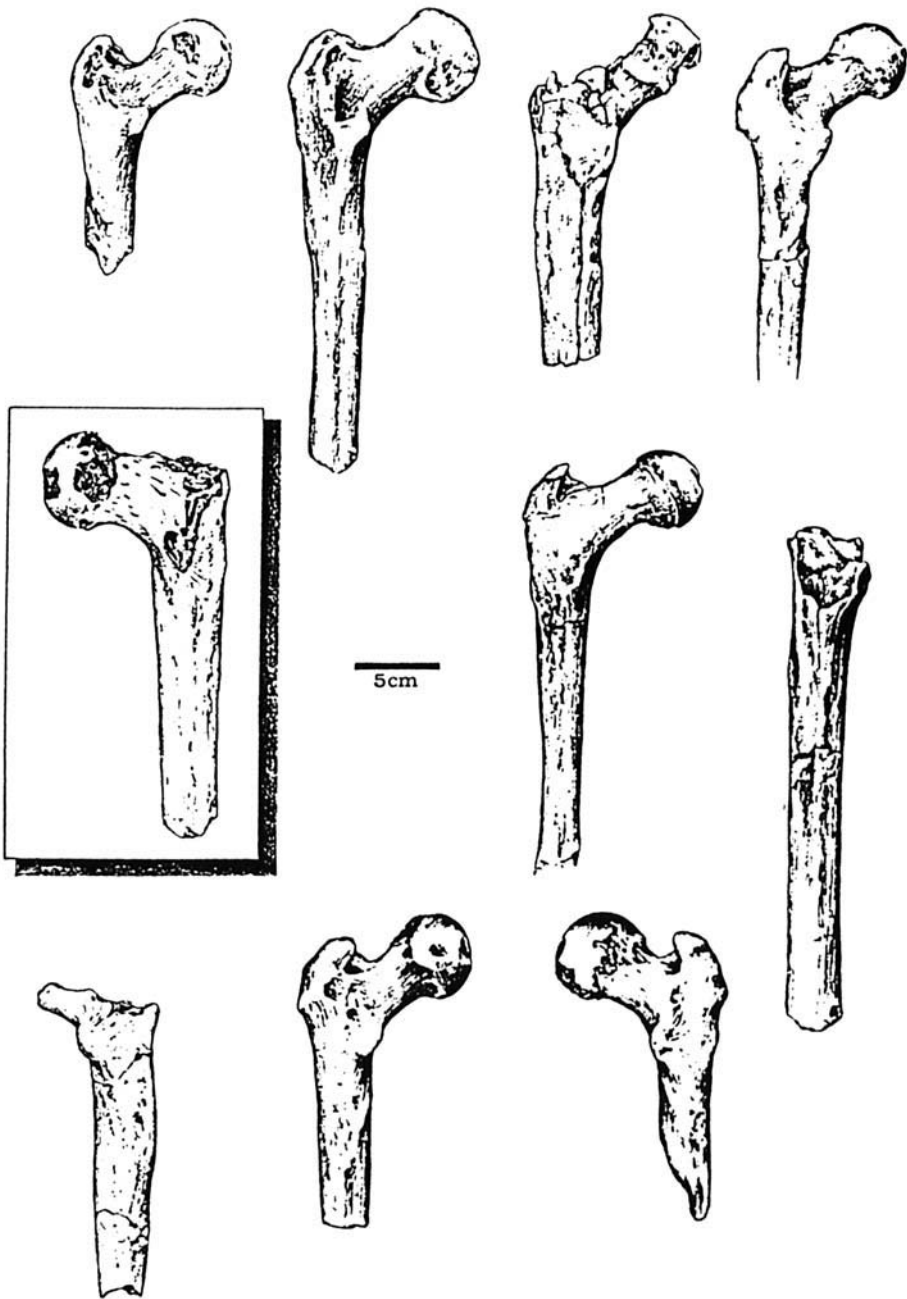


Fig. 10. Posterior views of the Berg Aukas femur compared with *Homo erectus*, archaic *H. sapiens*, Neandertal, and early modern human homologues. Legend as for Figure 9.

In terms of the absolute size of its femoral head and the geometric properties of its shaft, the Berg Aukas femur is the largest fossil hominid specimen on record (Fig. 11).

In an attempt to estimate the body size of the Berg Aukas individual, body mass (in kg) may be predicted from the size of the femoral head (fhd). Using a reference sam-

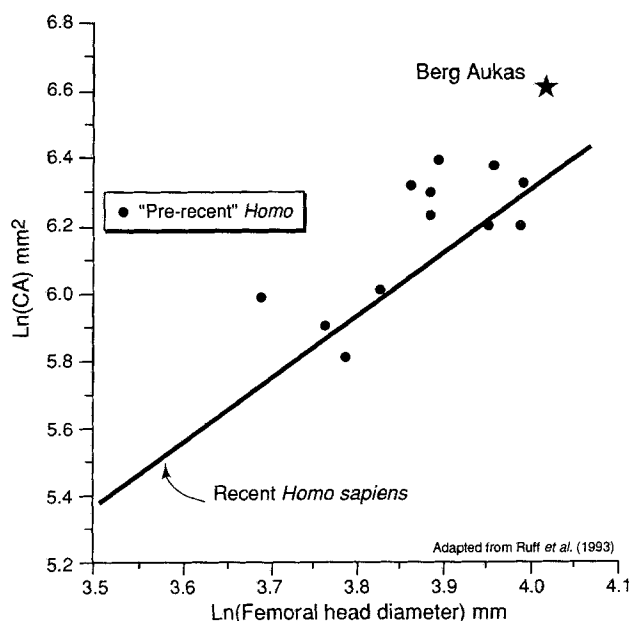


Fig. 11. Relationship between femoral head diameter and midshaft cortical area in logarithmic space. The regression for recent *Homo sapiens* from Ruff et al. (1993) has been plotted and extrapolated. The "pre-recent" *Homo* includes *H. erectus*, Neandertal, and Upper Paleolithic specimens. Note that Berg Aukas possesses a much larger cortical area than would be predicted by its large femoral head diameter.

ple of 10 sex-specific means for large-bodied modern human samples (including African Americans, European Americans, and Native Americans), the least squares predictive regression determined from data used by Jungers (1990) is

$$\text{body mass} = 2.268 \cdot \text{fhd} - 36.5.$$

The correlation between these two variables is 0.92, and the standard error of the estimate is 4.3 kg. The mean absolute percentage prediction error is approximately 5%. Logarithmic transformation does not improve upon these values. The diameter of the Berg Aukas femoral head results in a predicted body mass of almost 93 kg. Robust regression methods that give reduced weight to outliers yielded the same result. It seems reasonable to conclude that the Berg Aukas individual was relatively large bodied! Indeed, we are unaware of any individual in the fossil record of human evolution with a larger femoral head diameter or a greater estimated body mass.

## SUMMARY AND CONCLUSIONS

The Berg Aukas femur was recovered from deep within a paleokarst feature during vanadium mining operations near the town of Grootfontein, in the Otavi Mountains of northern Namibia. Details concerning its provenience are sketchy and there is no fauna that can be associated definitely with the specimen. It is not possible, therefore, to place it in a geochronological context. The femur is heavily mineralized; it has a remarkably thick diaphyseal cortex and a very low collodiaphyseal angle, which serve to differentiate it from Holocene homologues. Comparisons of over a dozen non-radiological features among fossil hominid femora reveal that Berg Aukas is not attributable to *Australopithecus* or *Paranthropus*. These features, together with aspects of diaphyseal geometry, preclude its attribution to early *Homo* (i.e., *H. habilis* sensu lato). The femoral neck is relatively longer and AP flatter, the shaft exhibits less pilaster, and absolute femoral dimensions tend to be smaller in *H. erectus* homologues. At the

same time, Berg Aukas differs from early modern femora in having a relatively flatter shaft at the subtrochanteric level, a larger head, and in the geometric properties of its diaphysis.

The closest comparisons with Berg Aukas appear to be with archaic (i.e., Middle Pleistocene) *H. sapiens* and Neandertal femora. It differs from these, however, in several features, including the larger subtrochanteric ML diameter of its diaphysis, and its stronger pilaster. Although some Neandertals approach Berg Aukas in absolute femoral head size, Berg Aukas differs from them because its head is *relatively smaller* (compared to the subtrochanteric ML diameter of the diaphysis). Among the archaic *H. sapiens* and Neandertal samples, the massive diaphyseal cortex of Berg Aukas finds its closest similarity within the former (cf. Castel di Guido 1).

Thus, notwithstanding the differences alluded to above, the femur from Berg Aukas would appear to be attributable to non-modern *H. sapiens*, insofar as the archaic and Neandertal groups that have been referred to here comprise a single species (but see Tattersall, 1986, 1992; Rightmire, 1990; Stringer, 1992, 1994). Furthermore, although it lacks several features that *tend* to characterize Neandertals, there are comparatively few complete proximal femora from the Middle Pleistocene of Europe and the Levant, and from the Middle and Late Pleistocene of Africa (our archaic *H. sapiens* sample) that we have been able to compare to Neandertals and to Berg Aukas. It is, therefore, difficult to establish at this point whether Neandertal proximal femora are actually characterized by any unique features that would serve to clearly differentiate them from other archaic humans. At any rate, there is no compelling reason to suppose Berg Aukas to be the only sub-Saharan Neandertal and, thus, it seems reasonable to consider this specimen as a representative of archaic *H. sapiens*. Although Berg Aukas differs from the Kabwe proximal femora, it is unclear whether these differences simply reflect individual variation, or a more profound biological distinction.

Howell (1978) noted that the archaic *H. sapiens* specimens from southern Africa

(e.g., Kabwe, Elandsfontein [Hopefield], Cave of Hearths) are customarily attributed to the subspecies, *H. sapiens rhodesiensis*. Although he posited that some (unspecified) evidence may suggest the presence of a separate late Middle Pleistocene subspecies in eastern Africa, he nevertheless included specimens from Kenya and Tanzania (e.g., from the Kapthurin Beds, Lake Ndutu, and Eyasi) in the hypodigm of *H. sapiens rhodesiensis* as defined by him (1978). Stringer et al. (1979) recognized the strong similarities among some of the more "primitive" African and European Middle Pleistocene specimens (e.g., those from Petralona and Kabwe), and proposed to allocate them to one of a series of grades of *H. sapiens* in order to distinguish them from Neandertals and more modern humans.

Rightmire (1990) concurred that there is no justification for separating the African and European fossils from sites such as Ndutu, Kabwe, Petralona, and Arago. He also noted that if the subspecies category, the use of which he had earlier advocated (e.g., Rightmire, 1983), were to be applied to this assemblage, it would carry the name *H. sapiens heidelbergensis*, but that this would result in the inappropriate inclusion of fossils from very distant geographical provinces. Rightmire (1990) concluded by accepting Tattersall's (1986) arguments that this material is best placed in a taxon of species-level rank, especially since the application of subspecies categories to denote time successive groups is highly debatable. Stringer (1992, 1994) has also advocated the recognition of *H. heidelbergensis* as the taxon to which this Middle Pleistocene fossil material should be allocated.

The attribution of the Berg Aukas femur to this taxonomic group seems reasonable in view of its similarities to Middle Pleistocene European and African homologues that might well be referable to *H. heidelbergensis*. If, on the other hand, the similarities between European and African Middle Pleistocene crania such as Kabwe and Petralona are only superficial, and the European and African specimens are viewed as representing two subspecies of *H. sapiens*, then the femur from Berg Aukas would be most reasonably attributed to *H. sapiens*

*rhodesiensis*. The latter attribution is preferred by one of us (P.V.T.).

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## APPENDIX

The *Australopithecus afarensis* sample comprises AL 288-1ap, AL 333-3, and an unpublished diaphyseal fragment (AL 333-131) that may be associated with the AL 333-3 proximal fragment (B. Latimer, pers. comm.). Values obtained from Johanson et al. (1982), Lovejoy et al. (1982), and B. Latimer (pers. comm.).

The *Australopithecus africanus* sample comprises Sts 14 and MLD 46. The Sts 14 vertical head diameter is estimated at 31.2 from the acetabular diameter recorded by Brain et al. (1974), whereas Robinson (1972) suggested an estimate of 33. Our estimate is calculated by a regression formula [ $0.943 \times \text{acet. ht.} - 5.77$ ] developed from a modern human sample by E. Trinkaus (pers. comm.). Values are from Robinson (1972) and Reed et al. (1993).

The *Paranthropus robustus* sample comprises SK 82, SK 97, and SK 3115b, the acetabular diameter of which was used to

calculate vertical head diameter. In the taxonomic attribution of the latter, we follow McHenry (1975) rather than Brain et al. (1974). Values are from Robinson (1972) and Brain et al. (1974).

The *Paranthropus boisei* sample comprises KNM-ER 738, KNM-ER 815, KNM-ER 993, KNM-ER 1463, KNM-ER 1465, KNM-ER 1500, and KNM-ER 1503. KNM-ER 738, KNM-ER 815, KNM-ER 993, KNM-ER 1463, and KNM-ER 1465 have been attributed to *Australopithecus* by Walker (1973) and Day (1976), and to *A. boisei* by Howell (1978). KNM-ER 1500 has been attributed to *Australopithecus* (Day, 1976), *A. africanus* (Howell, 1978), and *A. boisei* (Grausz et al., 1988); while Wood (1991) has referred it to Hominidae gen. et sp. indet. We follow Grausz et al. (1988) in the allocation of this specimen. KNM-ER 1503 (=1503 + 1505 + 1822) has been attributed to *Australopithecus* sp. indet. by Wood (1976) and Day (1976), and to *A. boisei* by Howell (1978). The attribution of the OH 20 fragment to *A. boisei* by Day (1969) has been accepted by both Walker (1973) and Howell (1978), while Wood (1976) referred it simply to *Australopithecus*. Values for *P. boisei* femora are from Day (1969), Leakey et al. (1972, 1978), Walker (1973), Leakey and Walker (1973), and Day et al. (1976).

The *Homo cf. habilis* sample comprises KNM-ER 1472, KNM-ER 1475, KNM-ER 1481A, OH 62, and the KNM-ER 3228 os coxae, the acetabular diameter of which was used to estimate vertical head diameter. KNM-ER 1472 and KNM-ER 1475 have been attributed to *Homo* sp. by Wood (1976) and Day (1976), and to *H. habilis* by Howell (1978). KNM-ER 1481A has been referred to *Homo* sp. by Wood (1976) and Day (1976) and to *H. habilis* by Howell (1978); although Kennedy (1983a) has attributed it to *H. erectus*, Trinkaus (1984) has argued that it is best referred to *H. habilis*. The KNM-ER 3228 os coxae has been attributed to *H. habilis* by Howell (1978), while Rose (1984) has compared it favorably with both *H. erectus* and archaic *H. sapiens*. OH 62 has been referred to *H. habilis* by Johanson et al. (1982). *H. cf. habilis* values are from Day et al. (1974), Leakey et al. (1978), Rose (1984), Johanson et al. (1987), W. Kimbel and D.C.

Johanson (pers. comm.), and B. Latimer (pers. comm.).

The *Homo erectus* sample comprises KNM-ER 736, KNM-ER 737, KNM-ER 1809, KNM-WT 15000, OH 28, OH 34, and femora I, II, IV, V, and VI from Zhoukoudian. KNM-ER 736 was attributed by Leakey et al. (1972) and Walker (1973) to *Australopithecus*, Day (1976) referred it to *Homo*; both Walker (pers. comm.) and Ruff (pers. comm.) currently consider that it represents *H. erectus*. KNM-ER 737 has been attributed to *Homo* sp. by Day (1976), and Howell (1978) has referred it and KNM-ER 1809 to *H. erectus*. KNM-WT 15000 has been attributed to early *H. erectus* by Brown et al. (1985); while Wood (1992) has argued that it is probably referable to *H. ergaster*, we follow Brown et al. (1985). KNM-ER 803 has been referred to *Homo* by Day and Leakey (1974), and to *H. erectus* by Day (1976) and Howell (1978), whereas Groves and Mazak (1975) included it in their hypodigm of *H. ergaster*. Wood (1991) has attributed it to Hominidae gen. et sp. indet. OH 28 has been referred to *H. erectus* by both Day (1971) and Howell (1978), and Howell (1978) and Sigmon (1982) attribute OH 34 to *H. erectus*. *H. erectus* values are from Weidenreich (1941), Day (1971), Day and Leakey (1973, 1974), Day and Molleson (1976), Day et al. (1976), Leakey et al. (1978), Sigmon (1982), Brown et al. (1985), and Walker and Leakey (1993). The OH 34 diaphyseal dimensions are abnormally small due to severe hydrological erosion; they are not used for comparative purposes.

The archaic *Homo sapiens* sample is composed of European and African specimens from the Middle Quaternary (i.e., between O-isotope stages 13 and 6). This includes Ain Maarouf 1; Gesher-Benot-Yaacov 1 and 2; Kabwe E689, E690, and E907; Castel di Guido 1 and 2; Venosa 1; Pont Mammolo 1; and Arago XLVIII, the acetabular diameter of which was used to calculate vertical head diameter. Archaic *H. sapiens* values are from Pycraft (1928), Clark et al. (1968), Lovejoy (1982), Sigmon (1982), Geraads and Tchernov (1983), Mallegni et al. (1983), Belli et al. (1991), Hublin (1992), Trinkaus (1993a), and casts of Kabwe E689 and E907. (The Venosa 1 subtrochanteric AP and ML

diameters published by Belli et al. [1991] are reversed.)

The Neandertal sample comprises Amud 1; Biscegli 1; La Chapelle 1; Ehringdorf 5; La Ferrassie 1 and 2; Fond-de-Forêt 1; Hortus 34; Krapina 208 and 209/212 (the acetabular diameters of which were used to compute vertical head diameter); Krapina 213 and 214; Neandertal 1; La Quina 5 and B2; Sedia-del-Diavolo 1; Shanidar 1, 4, 5 and 6; Spy 2; Tabun C1, C3, and E1; and the Kebara innominate, from which vertical head diameter was estimated. Values for Neandertal specimens are from Martin (1923), Weidenreich (1941), Rossi (1961), Stewart (1963), Endo and Kimura (1970), Trinkaus (1976, 1980, 1983b, 1993a,b), Smith (1976), Heim (1982), Mallegni (1986), and a cast of the Kebara os coxae.

With reference to the early modern human sample, we tentatively accept that the KNM-ER 999 femur, like the KNM-ER 3884 cranium (Bräuer et al., 1992) is derived from the Chari Formation, although they may come from the overlying Holocene Galana Boi Formation (Bräuer et al., 1992; Trinkaus, 1993b). Other specimens comprising this sample are Skhul 3, 4, 5, 6, and 9; Qafzeh 3, 8, and 9; and Omo 1. Data for these specimens are from McCown and Keith (1939), Day and Leakey (1974), Leakey et al. (1978), Vandermeersch (1981), Trinkaus (1983a), and Kennedy (1984).

Published neck-shaft angles for a number of specimens differ according to source; we have accepted those recorded by Trinkaus (1993a) where there are discrepancies.