The Anomalous Archaic *Homo* Femur From Berg Aukas, Namibia: A Biomechanical Assessment

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ABSTRACT   The probably Middle Pleistocene human femur from Berg Aukas, Namibia, when oriented anatomically and analyzed biomechanically, presents an unusual combination of morphological features compared to other Pleistocene *Homo* femora. Its midshaft diaphyseal shape is similar to most other archaic *Homo*, but its subtrochanteric shape aligns it most closely with earlier equatorial *Homo* femora. It has an unusually low neck shaft angle. Its relative femoral head size is matched only by Neandertals with stocky hyperarctic body proportions. Its diaphyseal robusticity is modest for a Neandertal, but reasonable compared to equatorial archaic *Homo* femora. Its gluteal tuberosity is relatively small. Given its derivation from a warm climatic region, it is best interpreted as having had relatively linear body proportions (affecting proximal diaphyseal proportions, shaft robusticity, and gluteal tuberosity size) combined with an elevated level of lower limb loading during development (affecting femoral head size and neck shaft angle). Am J Phys Anthropol 110:379–391, 1999.   © 1999 Wiley-Liss, Inc.

In 1995, Grine, Jungers, Tobias and Pearson described the proximal half of a heavily mineralized human femur, which had been recovered 30 years earlier during vanadium mining operations at the Berg Aukas mine in northern Namibia (Conroy et al., 1993; Grine et al., 1995). The specimen is undated given its lack of stratigraphic association with any chronological indicators (biological or geological), but an assessment of its morphology relative to that of other hominid femora led Grine and colleagues to conclude that it is best attributed to Middle or Late Pleistocene archaic *Homo*, a conclusion with which we concur. In particular, the morphology of the proximal epiphyseal region distinguishes it from *Australopithecus* and some

early *Homo* femora and aligns it with members of *H. erectus* and later Pleistocene *Homo*. The absence of a pilaster distinguishes it from early and recent modern humans, whereas the strong development of a medial buttress places it closest to Middle and Late Pleistocene archaic *Homo* femora (Fig. 1).

In their assessment of the femur, Grine et al. (1995) emphasized the large size of the femoral head, its diaphyseal cross-sectional

Fig. 1. Anterior view of the Berg Aukas hominid femur, taken relative to the anteversion plane of the proximal femur. Scale in centimeters.

properties, its low neck shaft angle, and several details of the diaphyseal shape. However, their assessment did not include a biomechanical evaluation of the specimen. On-going assessments of Pleistocene and recent *Homo* femoral and tibial cross-sectional geometry (e.g., Ruff et al., 1993; Ruff, 1995; Trinkaus, 1997; Trinkaus et al., 1999) and proximal femoral proportions (Ruff et al., 1991; Trinkaus, 1993) have developed a framework within which we can now assess the biomechanical implications of the Berg Aukas femur. Given the dearth of Middle Pleistocene human postcrania, any insight which this, albeit undated, specimen might provide would add to our knowledge of genus *Homo* locomotor evolution.

MATERIALS AND METHODS
Comparative samples

The biomechanically relevant parameters of the Berg Aukas femur are compared primarily to those of three chronological (and by default partially geographical) samples of archaic *Homo* (see Tables 2 and 3 for specimens).

The first sample, designated "Early Archaic *Homo*," consists of mature femora which are distinct from those of *Australopithecus*, assigned to early *Homo* and *H. erectus*, and date from the terminal Pliocene (ca. 2.0 ma B.P.) to the early Middle Pleistocene (ca. 600 ka B.P.). Additional data are included for the Early Pleistocene early adolescent KNM-WT 15000 specimen. This sample and period represent a long stage of stasis in relative endocranial capacity and pelvic proportions (Ruff, 1995; Ruff et al., 1997); it also includes only specimens from warm climate zones. Since proximal femoral proportions are influenced by pelvic configurations, which in turn are affected by trends in encephalization and ecogeographical patterns in body shape (Ruff, 1995), this sample should encompass specimens whose femoral variation reflects primarily locomotor parameters and not separate effects from encephalization, pelvic aperture shape, and relative body breadth.

The second sample, the one to which the Berg Aukas femur may have close affinities, is designated "Middle Archaic *Homo*." It consists of specimens from the middle portion of the Middle Pleistocene, ca. 500 ka B.P. to ca. 200 ka B.P. Femoral variability in this group reflects both locomotor variation and the marked encephalization that occurred during the Middle Pleistocene (Ruff et al., 1997). It also includes specimens from across the Old World (Zambia to Germany to China), and some of its variation may reflect human geographical and ecogeographic variation.

The third sample, "Late Archaic *Homo*," includes the Neandertals sensu lato from the terminal Middle Pleistocene to the middle of oxygen isotope stage 3 (ca. 150 ka B.P. to ca. 35 ka B.P.). This sample, the only one of late archaic humans which preserves

femora, is notable for both its encephalization approaching that of recent humans (Ruff et al., 1997) and its hyperarctic body proportions (Holliday, 1997b).

In addition, a Eurasian sample of early modern humans ($\geq$ 18 ka B.P.) is used to provide a robust modern human baseline for the assessments of archaic *Homo* femora. These specimens derive from the sites of Arene Candide, Barma Grande, Caviglione, Cro-Magnon, Dolní Věstonice I and II, Grotte-des-Enfants, Minatogawa, Mladeč, Nahal Ein Gev, Ohalo II, Paglicci, Parabita, Paviland, Pavlov I, Předmostí, Qafzeh, La Rochette, Skhul, and Willendorf (N = 16 to 34 for various comparisons).

Methods

Six biomechanical parameters of interest are preserved on the Berg Aukas femur: head size reflecting hip joint reaction force levels and hence body mass (Jungers, 1988; McHenry, 1988; Ruff et al., 1991), femoral neck length influencing gluteal abductor muscle moment arms and load distributions through the proximal femur (Lovejoy et al., 1973; Ruff, 1995), gluteal tuberosity size related to hip muscle hypertrophy (Trinkaus, 1976), diaphyseal strength reflecting overall locomotor levels (Ruff et al., 1993), subtrochanteric diaphyseal shape reflecting hip region proportions and the resultant relative anteroposterior versus mediolateral load levels (Ruff, 1995), and midshaft diaphyseal shape reflecting in part hip proportions but mainly locomotor levels (Ruff, 1987, 1995, 1999; Trinkaus et al., 1998). The first four require the scaling of the relevant femoral measure to body mass or body mass times beam length. The second two involve comparisons of relevant perpendicular second moments of area.

The scaling of head size, neck length, gluteal tuberosity size, and midshaft diaphyseal rigidity require the estimation of femoral length, since it approximates the beam length for the femur and is the best estimator of stature (Feldesman et al., 1990). Body mass is dependent upon stature and relative body breadth (Ruff, 1994; Ruff et al., 1997), and both recent and Pleistocene *Homo* are known to have varied ecogeographically with

respect to their body proportions (Ruff, 1991, 1994; Holliday, 1997a,b). It is therefore necessary to know the body breadth of the individuals in question or to estimate it based on ecogeographical patterns, or to take known variation in relative body breadth into consideration in assessments of proximal and diaphyseal dimensions to femoral length. Given the incomplete state of the Berg Aukas femur, the latter approach is taken here.

The assessment of subtrochanteric (80%) diaphyseal shape was done using maximum to minimum second moments of area (I_{max} and I_{min}). Given variation in the orientation of the major axis at midshaft, from mediolateral in Early Archaic *Homo* to anteroposterior in early modern humans, the anatomically oriented I_x and I_y values are employed at that level. For I_x and I_y, the sagittal plane of the femur is defined as passing through the linea aspera and the mediolateral midpoint of the diaphysis near midshaft.

The cross-sectional geometric parameters (see Table 1 for a list) for the comparative samples were computed using versions of SLICE (Nagurka and Hayes, 1980). Most of the cross sections were obtained noninvasively by molding the subperiosteal contour, determining cortical thicknesses using multi- or biplanar radiography, and interpolating the endosteal contour within the boundaries set by the cortical thicknesses. A few were from scaled photographs of appropriate fossilization breaks, and several were taken from published cross-sections (e.g., Weidenreich, 1941; Mallegni et al., 1983).

Anteroposterior head diameter was measured directly or, for OH-28, Arago 44 and Amud 1, was estimated from acetabular height using a regression based on recent humans (r^2 = 0.896). Neck length was quantified using the biomechanical neck length of Lovejoy et al. (1973), the distance perpendicular to the diaphyseal axis from the most lateral point of the greater trochanter to its tangent to the proximal femoral head taken in the coronal plane of the femoral head and neck. Gluteal tuberosity size was quantified as the maximum breadth of the rugose area of the tuberosity proper (Trinkaus, 1976).

TABLE 1. Cross-sectional geometric properties of the midshaft (50% level)
and subtrochanteric level (80%) of the Berg Aukas femur[1]

	50% Grine et al. (1995)	50% CT scan	50% cast (adjusted)	80% Grine et al. (1995)	80% adjusted
TA	853	800	805	898	842
CA	750	708	697	794	744
I_x	—	51,599	50,365	—	—
I_y	—	51,050	52,720	—	—
I_{max}	67,149	61,019	59,889	84,677	75,604
I_{min}	49,112	41,631	43,917	47,362	42,288
J	116,261	102,649	103,085	132,038	117,892
Theta	—	134°	139°	—	—

[1] Areas in mm^2 and second moments of area in mm^4. TA, total area; CA, cortical area; I_x, anteroposterior second moment of area; I_y, mediolateral second moment of area; I_{max}, maximum second moment of area; I_{min}, second moment area perpendicular to I_{max}; J, polar moment of area; theta: orientation of I_{max}.

Assessments of the biomechanical affinities of the Berg Aukas femur relative to those of other archaic *Homo* specimens were done graphically for all but the neck length to bone length comparison (Figs. 3–6). Since all of these variables are, or may well be, related to each other in nonlinear ways (Ruff et al., 1993), the data were logged prior to graphing and analysis. In addition, a *z*-score from the early modern human reduced major axis regression line is provided for each archaic *Homo* femur.

Berg Aukas femur

This analysis is based on data derived for the Berg Aukas femur, combining the data presented by Grine et al. (1995) (head diameter, neck length, and neck shaft angle), data derived from computed tomographic (CT) scans of the specimen by GCC (taken using a Siemens Somatom DR3 scanner at 125 kV with a window width of 2050 and slice thickness of 1mm) (for cross-sections) and a high quality resin cast of the specimen (for 50% cross-sections and gluteal tuberosity breadth).

Grine et al. (1995, pp.159–160) estimated length using a multiple regression based on a recent human (African American) sample and six measurements of the head and neck. This provided an "interarticular" length of 518 ± 16 mm. To avoid any circularity in assessing proximal epiphyseal proportions in the present analysis, the midshaft of the Berg Aukas femur was determined by the relative position of the medial buttress, a swelling of bone along the medial proximal diaphysis which begins at the level of mid-

gluteal tuberosity on the medial diaphysis and gradually rotates posteriorly as it goes distally (Trinkaus, 1976, 1984). On femora where it is well developed, the medial buttress reaches the posteromedial aspect of the diaphysis near midshaft. On the Berg Aukas femur, this buttress is directly posteromedial at the distal break of the shaft. It was therefore assumed that the distal break is close to midshaft (see Grine et al., 1995).

The distance parallel to the diaphyseal axis, from the proximal neck to the distal break is ca. 235 mm, providing a biomechanical length (Ruff and Hayes, 1983) of ca. 470 mm. Given that the medial buttress had already reached the posteromedial aspect of the shaft 10 to 15 mm proximal of the distal break, this estimate is more likely to overestimate than underestimate the bone's original length. The addition of the 10 mm (the distance from the proximal neck to the proximal head measured parallel to the diaphyseal axis) provides a maximum length ca.480 mm, 38 mm below the previous mean prediction of 518 mm.

To obtain I_x and I_y as well as the other cross-sectional parameters, the bone was oriented using the linea aspera, the distal break of the cast was photographed (Fig. 2), the image was projected onto a Summagraphics digitizing tablet enlarged linearly 5.95 times, and the subperiosteal and endosteal contours were digitized (not including the trabeculae in the posterior medullary cavity) (Fig. 2). The same procedure was followed for the hardcopy print-out of our CT image taken just proximal of the distal break, linearly enlarged 3.84 times. Cross-
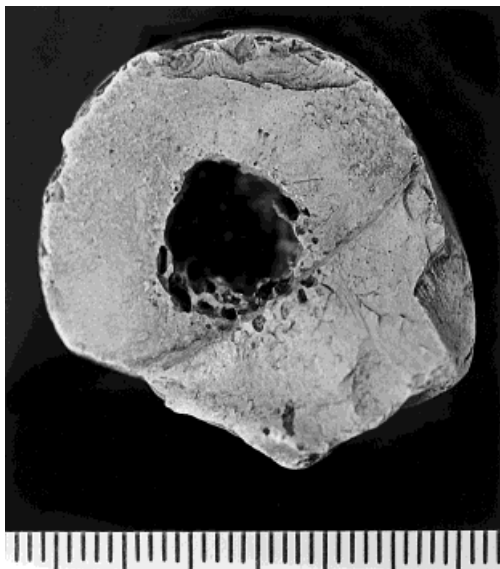
Fig. 2. Distal view of a cast of the Berg Aukas right hominid femur, showing the cross-sectional distribution of bone revealed by the transverse break of the diaphysis. Anterior is above and medial is to the right. The pencil mark indicates the position of the linea aspera. Scale in millimeters.

sectional parameters were computed using a PC-DOS version (Eschman, 1992) of SLICE (Nagurka and Hayes, 1980). Each image was digitized twice and the results averaged. The resultant values were then adjusted for linear shrinkage (ca.1.6%) of the cast (Table. 1). The final values are less than those calculated by Grine et al. (1995), but they remain consistent with the external diameters of the diaphysis.[1]

For comparable 80% measures, the values provided by Grine et al. (1995) were adjusted by the percentage differences found for the midshaft cross sections (6.7% and 12.0%) (Table 1). Since these are linear corrections and the only subtrochanteric values of interest here are I_{max} and I_{min}, this has a trivial effect on the comparisons.

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[1]To assess which values are more reasonable, total subperiosteal areas were regressed on the product of the midshaft diameters ("area") for archaic *Homo* femora (50% TA = 0.705 × "area" + 8.33, r^2 = 0.953, N = 31; Berg Aukas AP: 34.0 mm, ML: 33.5 mm), and z-scores for the different Berg Aukas total area residuals were computed. The Berg Aukas z-scores are 1.34 for the total area from Grine et al. (1995), −0.45 for the CT scan digitized here, and −0.27 for the shrinkage-adjusted cast values.

RESULTS
Overall size

The Berg Aukas femur is very large. Its femoral head diameter of 57.6mm is the largest known, although femoral head diameters between 50 and 55 mm are known for several Middle and Late Pleistocene humans, including Arago 44, Broken Hill E689 and E907, Krapina 213, La Chapelle-aux-Saints 1, La Ferrassie 1, Neandertal 1, and Spy 2 (only the largest male early modern humans have femoral head diameters exceeding 50 mm). Its midshaft cortical area of 697 mm^2 is the largest known for an archaic *Homo* femur, even though it is approached by those of KNM-ER 736 (659 mm^2), Ehringsdorf 5 (666 mm^2), and Amud 1 (659 mm^2). Its midshaft polar moment of area of 103,085 mm^4 is similarly among the largest known, being surpassed only by KNM-ER 736 (116,628 mm^4) and matched by those of Ehringsdorf 5 (102,449 mm^4), and Qafzeh 8 (102,428 mm^4).

These large femoral dimensions and the body mass estimate based on femoral head diameter of ca. 93 kg (Grine et al., 1995) are impressive. They also emphasize the need to scale these parameters to appropriate measures of body size.

Hip proportions

There are few archaic *Homo* specimens that provide biomechanical neck length and femoral length (or reasonable estimates of them), and it is inappropriate to scale femoral neck length against other proximal femoral dimensions since they are frequently highly correlated (Wolpoff, 1978; Ruff, 1995). All of the other archaic *Homo* femora fall above the regression line for the early modern human sample (Table 2), with KNM-ER 1481a and Spy 2 having relatively high values. In addition, the early *H. erectus* KNM-WT 15000 early adolescent provides a z-score of 2.93, in agreement with previous assessment of its femoral neck length (Ruff, 1995). Archaic *Homo* tend to have relatively long femoral necks (see also Wolpoff, 1978).

The Berg Aukas femur is in the middle of the early modern human sample and has the relatively shortest neck of the archaic *Homo*

TABLE 2. z-Scores for comparisons of femoral neck length, head diameter, and gluteal tuberosity breadth

	Neck length/ length	Head Diameter/ length	Gluteal tuberosity/ length	Gluteal tuberosity/ head
Berg Aukas	**0.06**	**2.48**	**−1.02**	**−4.88**
Early Archaic *Homo*				
KNM-ER 737	—	—	2.51	—
KNM-ER 1472	1.27	−0.36	—	—
KNM-ER 1481a	2.00	1.65	4.44	2.17
Gesher Benot Ya'aqov 1	—	—	4.27	—
OH 28	—	0.09	1.63	1.21
Middle Archaic *Homo*				
Broken Hill E689	—	—	—	−1.01
Broken Hill E690	—	—	0.82	—
Broken Hill E907	—	—	—	−1.85
Late Archaic *Homo*				
Amud 1	—	−0.26	0.79	0.89
La Chapelle 1	0.60	3.09	2.30	−2.02
La Ferrassie 1	1.09	2.34	2.79	−0.07
La Ferrassie 2	0.40	1.70	4.92	2.86
Krapina 213	—	—	—	0.30
Krapina 214	—	—	—	4.01
Neandertal 1	0.95	2.65	2.90	−0.60
St.-Césaire 1	—	—	3.02	—
Shanidar 1	—	—	1.62	—
Shanidar 4	—	2.11	4.09	1.46
Shanidar 5	—	0.52	—	—
Shanidar 6	—	—	5.48	—
Spy 2	2.58	3.59	3.09	−1.68
Tabun 1	0.40	0.92	3.91	2.67

femora. As with the comparison of anatomical neck length to its vertical diameter (Grine et al., 1995), the Berg Aukas femoral neck length is unexceptional from a modern human perspective, although relatively short for an archaic *Homo*.

This moderate neck length (for an archaic *Homo*) is associated with the lowest known (presumably) nonpathological human femoral neck shaft angle. Its value of 106° (Grine et al., 1995, p.163) is below all other known values for archaic *Homo* (being approached by KNM-WT 15000 at 110° and Amud 1 at 113°) (Walker and Leakey, 1993; Trinkaus, 1993) and 3.4 and 4.1 standard deviations below the means of two Holocene human groups with the lowest mean neck shaft angles [Khoisan males (Grine et al., 1995) and Japanese Jomon foragers (Ishisawa, 1931), respectively] and below a minimum value of 110° for a sample of 1376 recent humans from 15 populations (Anderson and Trinkaus, 1998).

Femoral diaphyseal shape

The distribution of 80% I_{man} versus I_{min} (Fig. 3) reflects the pattern previously noted (Ruff, 1995; Trinkaus et al., 1998; Trinkaus and Ruff, 1999). In this, Early Archaic *Homo*

have platymeric proximal femoral diaphyses, reflecting the biomechanical loads imposed on their femora from long femoral necks and platypelloid pelves. The Eurasian Late Archaic *Homo* sample has relatively round proximal femoral diaphyses, with the two exceptions being the early (terminal Middle Pleistocene) Krapina specimens. Most of the early modern humans exhibit platymeric femora, with the exception of the very linear Qafzeh-Skhul sample. This is reflected in their *z*-scores, which are positive to minimally negative for the early sample and negative (except for the Krapina femora) for the late archaic sample (Table 3).

The Middle Pleistocene remains exhibit considerable variability. Two Broken Hill femora are quite round, one is relatively platymeric, and the Tabun E1 femur is close to the early modern human line. The Berg Aukas femur is in the middle of the early modern human and overall distributions (Table 3). It is therefore relatively platymeric, more similar to the Early Archaic *Homo* sample than it is to the Late Archaic *Homo* group, falling very close to specimens such as KNM-ER 736 and 803a and Gesher Benot Ya'aqov 1. However, it fits well within
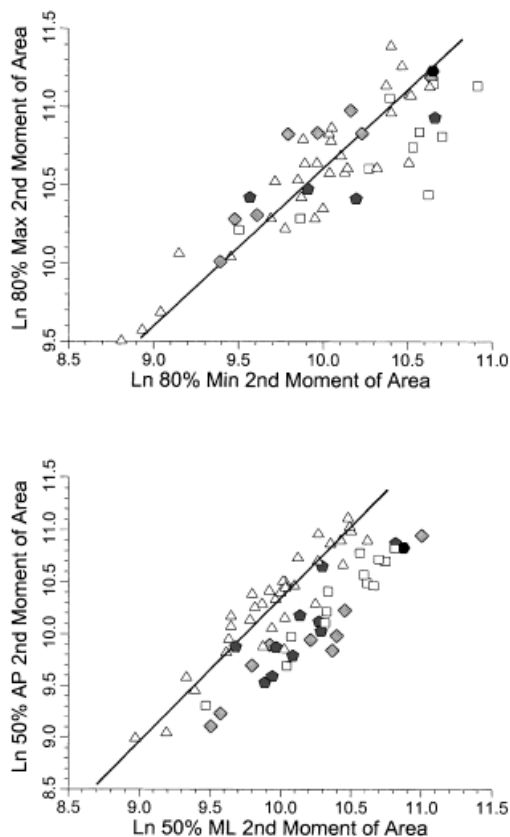
Fig. 3. Bivariate distributions of perpendicular second moments of area for the subtrochanteric (80%) level (above) and the midshaft (50%) level (below). The subtrochanteric distribution employs maximum and perpendicular to maximum second moments of area (I_{max} versus I_{min}), whereas the midshaft one plots anteroposterior versus mediolateral ones (I_x versus I_y). Symbols: solid hexagon, Berg Aukas femur; gray diamonds, early archaic *Homo*; dark gray pentagons, middle archaic *Homo*; open squares, late archaic *Homo*; open triangles, early modern humans. The reduced major axis line for the early modern human sample is provided.

the variable distribution of the Middle Pleistocene femora.

In the midshaft, Berg Aukas falls with the majority of the archaic *Homo* specimens. It lacks any evidence of a pilaster, since it only has a slight projection of the linea aspera dorsally (Fig. 2). There is a marked medial buttress, one of the largest known for an archaic *Homo* femur, being approached by those of Amud 1, La Ferrassie 1 and Saint-Césaire 1 (Trinkaus et al., 1991, 1998; Trinkaus and Ruff, 1999). Therefore, even though the major axis is oriented anterolat-

eral to posteromedial, as is reflected in its theta value of 139°, the anteroposterior and mediolateral second moments of area (I_x versus I_y) are very similar (Table 1).

With the exceptions of the Broken Hill E690 and Castel di Guido 1 femora, all of the archaic *Homo* femora fall on the rounded side of the early modern human distribution (Fig. 3). The mean *z*-scores for the Early, Middle and Late Archaic *Homo* samples are −3.31, −2.44 (−2.96 without Broken Hill E690 and Castel di Guido 1), and −2.85, respectively. The Berg Aukas femur with a *z*-score of −3.51 falls well within the ranges of archaic *Homo* femora and outside of the range of the largely pilastric early modern human femora.

Femoral diaphyseal robusticity

Even though the Berg Aukas femur is large, its level of robusticity (strength scaled to appropriate measures of body size and limb length) is less apparent relative to other Pleistocene *Homo* femora. This ambiguity derives from the combined contributions of body proportions, body mass and activity level to the hypertrophy of the weight-bearing locomotor skeleton (Ruff et al., 1993).

In comparisons of both midshaft cortical areas and polar moments of area to femoral lengths, there is a consistent pattern. Late Archaic *Homo* specimens are generally on the high side of the early modern human distribution, with mean *z*-scores of 1.49 and 1.53 (Fig. 4 and Table 3). The Early Archaic *Homo* femora plus the Middle Pleistocene Broken Hill E690 femur, all of which derive from Africa or the neighboring Near East, have more modest levels of relative cortical area and polar moments of area, being slightly higher on average than the early modern human sample (mean *z*-scores of 0.52 and 0.36, respectively).

Berg Aukas has a *z*-score of 1.39 for relative cortical area, well within the Late Archaic *Homo* plus Zhoukoudian range (mean: 1.57) but overlapping those of Aïn Maarouf 1 and KNM-ER 803a. It has a *z*-score of 1.00 for the relative polar moment of area, between the mean values for the Early (plus Broken Hill; 0.36) and Late (plus Zhoukoudian; 1.59) Archaic *Homo* samples. Is Berg

TABLE 3. *z-Scores for comparisons of femoral cross-sectional properties*

	80% I_{max}/I_{min}	50% I_x/I_y	50% CA/Len	50% J/Len
Berg Aukas	**−0.10**	**−3.51**	**1.39**	**1.00**
Early Archaic *Homo*				
Aïn Maarouf 1	—	−1.75	1.73	1.42
KNM-ER 736	−0.26	−3.81	(−0.78)	(−1.11)
KNM-ER 737	1.06	−4.54	0.34	0.57
KNM-ER 803a	−0.02	−3.71	1.60	1.72
KNM-ER 1472	0.96	−1.91	1.06	0.51
KNM-ER 1481a	0.42	−2.74	0.19	−0.44
KNM-ER 1808mn	2.17	−3.46	(0.53)	(1.44)
Gesher Benot Ya'aqov 1	−0.03	−2.87	0.14	−0.47
OH 28	1.30	−5.02	−0.39	−0.01
Middle Archaic *Homo*				
Broken Hill E689	−2.04	—	—	—
Broken Hill E690	1.23	−0.23	(0.76)	(−0.08)
Broken Hill E793	—	−1.81	—	—
Broken Hill E907	−1.73	—	—	—
Castel di Guido 1	—	−0.53	—	—
Ehringsdorf 5	—	−2.91	—	—
Tabun E1	−0.26	−3.02	—	—
Zhoukoudian F1	—	−3.57	(2.50)	(2.25)
Zhoukoudian F2	—	−3.35	—	—
Zhoukoudian F4	—	−3.39	—	—
Zhoukoudian F5	—	−3.41	—	—
Zhoukoudian F6	—	−2.20	—	—
Late Archaic *Homo*				
Amud 1	−0.55	−3.29	1.40	0.93
La Chapelle 1	−2.57	−3.45	2.20	2.08
La Ferrassie 1	−4.11	−3.89	0.60	0.56
La Ferrassie 2	−1.41	−3.35	1.35	1.80
Fond-de-Forêt 1	—	−2.91	1.01	1.13
Krapina 213	0.31	—	—	—
Krapina 214	0.48	—	—	—
Neandertal 1	−2.04	−1.99	0.95	1.08
St.-Césaire 1	−1.74	−1.67	2.33	2.29
Shanidar 4	—	−2.87	2.51	2.87
Shanidar 5	—	−3.10	1.89	2.32
Shanidar 6	—	−2.39	1.61	1.95
Spy 2	−1.95	−2.89	1.09	1.01
Tabun 1	−1.00	−3.58	0.93	0.39
Tabun 3	—	−1.62	—	—

Aukas one of the more robust earlier Pleistocene archaic *Homo* femora, similar to a modestly built Late Pleistocene archaic *Homo*, or can its relative diaphyseal hypertrophy be otherwise explained?

Relative femoral head size

To assess the relative size of the Berg Aukas femoral head, it needs to be scaled to a measure of body mass. However, the only possible indications of body mass are either the femoral head itself or calculations based on estimated stature (from its reconstructed length) and body breadth (from ecogeographical patterning given its inferred paleoclimatological context) (Ruff et al., 1997). Alternatively, it can be compared to femoral length, bearing in mind that such a comparison assumes similar body proportions across

the comparative samples, an assumption known to be false.

Such a comparison for Pleistocene *Homo* places Berg Aukas at the top of the distribution, exceeded in relative femoral head size only by three European Neandertals (Fig. 5 and Table 2). Its *z*-score of 2.48 is close to the mean (2.67) of the European Late Archaic *Homo* sample and well above the more modest values for most of the late Near Eastern specimens and the three Early Archaic *Homo* specimens. The Berg Aukas femur has a large femoral head, but not one which is exceptional relative to at least one Pleistocene hominid sample.

Relative gluteal tuberosity size

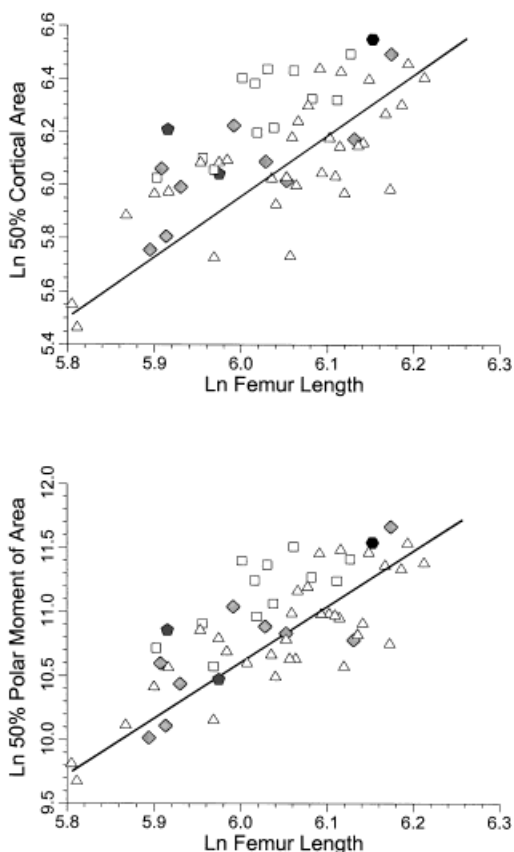The gluteal tuberosities of many Pleistocene archaic and early modern humans

Fig. 4. Bivariate distributions of midshaft (50%) cortical area (above) and polar moment of area (below) versus femoral biomechanical length. Symbols as in Fig. 3. The reduced major axis line for the early modern human sample is provided.
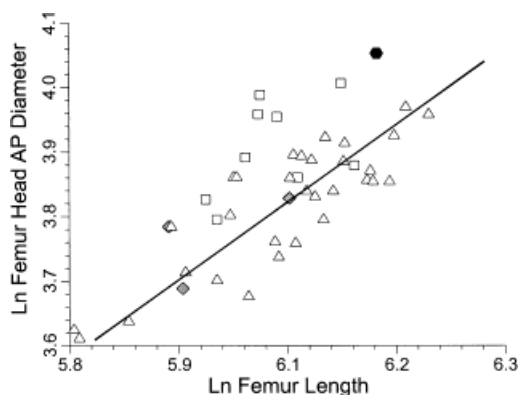

Fig. 5. Bivariate distribution of femoral head antero-posterior diameter versus femoral length. Symbols as in Fig. 3. The reduced major axis line for the early modern human sample is provided.

are large and rugose (Trinkaus, 1976). The Berg Aukas tuberosity is similarly marked, descending from a third trochanter just below the level of the lesser trochanter and becoming increasingly rugose and concave as it descends distally onto the dorsal proximal diaphysis. Its maximum breadth of 9.0 mm is located proximally, at the distal end of the third trochanter, and the tuberosity narrows to ca. 7.5 mm distally.

Even though it is difficult to assess actual muscle size from osteological attachment dimensions and only a portion of M. gluteus maximus inserts into the gluteal tuberosity (the remainder blending into the iliotibial tract), the size of the gluteal tuberosity appears to provide a reasonable indication of M. gluteus maximus hypertrophy (and by extension that of the hip musculature generally, given the need for balance between synergists and antagonists).

Gluteal tuberosity breadth relative to femoral length largely separates archaic *Homo* and early modern human femora; the only overlap involves the modest tuberosity dimensions for Broken Hill E690 (possibly underestimated given surface abrasion to the specimen) and La Chapelle-aux-Saints 1 and the pronounced one for DolníVĕstonice 13 (Fig. 6). It places Berg Aukas among the more gracile of the specimens, with a *z*-score of −0.02. An alternative approach is to compare gluteal tuberosity breadth to femoral head diameter, assuming that the latter is better reflecting body mass than is femoral length across these ecogeographically variable samples (Fig. 6). The result is a general uniformity of early modern human and archaic *Homo* femora, with only three small Late Archaic females (La Ferrassie 2, Krapina 214 and Tabun 1) plus the early KNM-ER 1481a being robust outliers (Fig. 6 and Table 2). Berg Aukas, with its modest gluteal tuberosity breadth and large femoral head, is an unusually low outlier.

DISCUSSION
Paleoenvironmental context

The Pleistocene paleoenvironments of southwestern Africa are poorly known, but it appears from geological evidence (Ward et
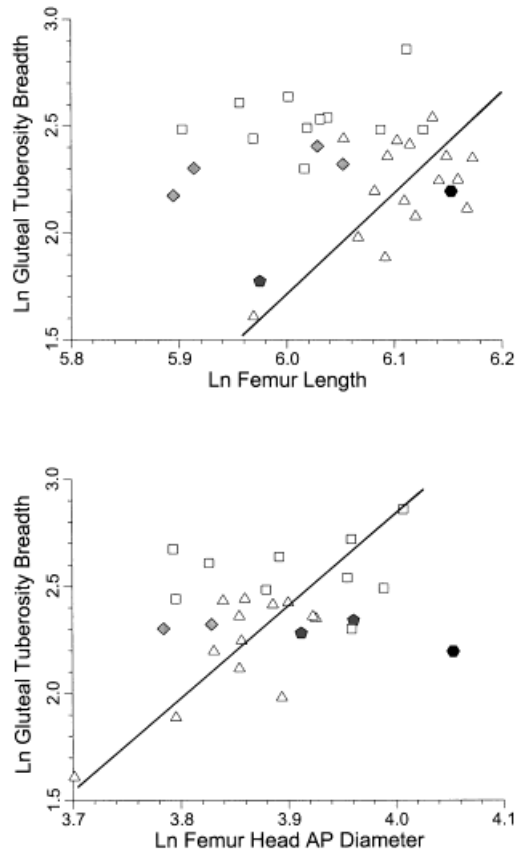
Fig. 6. Bivariate distributions of gluteal tuberosity breadth versus femoral biomechanical length (above) and femoral head diameter (below). Symbols as in Fig. 3. The reduced major axis line for the early modern human sample is provided.

current arid to extreme-arid environment progressively developed in conjunction with the late Miocene origin of the Benguela current.

The scattered Middle Pleistocene archeological evidence and geological evidence for at least ephemeral lakes (e.g., Shackley, 1980; Sandelowsky, 1983), as well as the presence of the Berg Aukas hominid femur, indicate that there were periods during which rainfall was sufficient to support a savanna grassland and associated fauna.

We can only assume that the Berg Aukas hominid was associated with the post-Miocene (probably Pleistocene) micro-mammalian fauna represented in one of the clusters of breccia blocks from the Berg Aukas mine dump (Conroy, 1996). Ten extant mammalian genera are exclusive to this cluster, the majority of which are associated with semi-arid to desert conditions (Skinner and Smithers, 1990).

It is therefore likely that the paleoenvironmental context of the Berg Aukas hominid was similar to that of modern Namibia, warm and semi-arid to arid. A linear human body form, such as is associated with such environments (Ruff, 1994), appears most likely for this individual based on its paleoenvironmental context.

Diaphyseal shape

The subtrochanteric and midshaft diaphyseal cross sections of the Berg Aukas femur fit best within the variable Middle Archaic *Homo* sample. The specimen is fully nonpilastric, and its midshaft structural distribution of bone places it close to most of the other archaic *Homo* femora (all except two unusual Middle Pleistocene specimens). Proximally it is less rounded than the Neandertals and closer to the earlier (and lower latitude) specimens. However, it is unclear whether the trend toward rounder proximal femoral diaphyses through later archaic *Homo* was the result of changing load patterns in this region from trends in pelvic aperture shape (Ruff, 1995) or was a combination of such aperture changes combined with ecogeographically influenced patterning in pelvic breadth (Ruff, 1991).

al., 1983) that it remained relatively warm in the Pleistocene and that Namibia was semi-arid to arid throughout this period. A serious limitation to Pleistocene paleoclimatic reconstructions of Namibia is the paucity of time successive mid-to-late tertiary vertebrate fossil localities (Shackley, 1980; Senut et al., 1992; Pickford et al., 1994). This problem has been alleviated partially by the discovery of a dozen fossiliferous localities in northern Namibia, of which the richest, both in terms of taxonomic diversity and specimen abundance, is the Berg Aukas mine (Senut et al., 1992; Conroy, 1996). In general, the biostratigraphic evidence at Berg Aukas largely supports other evidence (Siesser, 1980) suggesting that Namibia's

Femoral robusticity and body proportions

Analyses of Pleistocene *Homo* femoral and tibial diaphyseal robusticity, which take into account body proportions, estimated body mass, and inferred activity levels (e.g., Ruff et al., 1993; Trinkaus, 1997; Trinkaus et al., 1998, 1999, Trinkaus and Ruff, 1999), have shown that there is a trend (with individual variation) through Pleistocene *Homo* in which average femoral and tibial robusticity declines very slowly through time across these groups. The apparent gracility of many of the Early Archaic *Homo* and warm climate Middle Archaic *Homo* femora and tibiae is the product of their ecogeographically influenced linear body proportions. The apparent hyper-robusticity of the Late Pleistocene Neandertals disappears once their hyperarctic body proportions are taken into account, and the moderately to strongly linear body proportions of northwestern Old World early modern humans (Holliday, 1997a) account for most of their apparent gracility relative to at least that of the Neandertals.

Assessment of the robusticity of the Berg Aukas femur relative to these archaic *Homo* femora must therefore take into account inferred ecogeographically determined body proportions. Given a warm paleoclimate for Pleistocene Namibia, the Berg Aukas individual would be expected to have had linear body proportions, although not necessarily as linear as those seen among Pleistocene and recent equatorial Africans (Ruff, 1994). Assuming this, its level of femoral cortical bone hypertrophy would indicate a level of robusticity similar to those of African and Near Eastern Early/Middle Archaic *Homo*. However, if one infers less linear body proportions for this individual, the indicated level of robusticity would decrease accordingly. The modest size of the Berg Aukas gluteal tuberosity relative to femoral length (and more so relative to femoral head size) either indicates little development of its hip musculature or, more likely, a linear body shape.

However, since femoral head size is proportional to body mass (Jungers, 1988; McHenry, 1988; Ruff et al., 1991), scales relatively similarly across the genus *Homo* once variation in body proportions are taken into ac-

count (Ruff et al., 1993), and remains stable once growth is completed (Ruff et al., 1991), the relatively large size of the Berg Aukas femoral head indicates cold adapted body proportions, somewhere between the average for the hyperarctic European Neandertals and temperate populations.

An inference of a hyperarctic body form does not fit appropriately with the known nature of Pleistocene Namibian environments. It would also imply that the Berg Aukas femur had one of the more gracile of the known Pleistocene human femoral diaphyses. In addition, its relatively platymeric proximal femur contrasts with those of the cold-adapted Neandertals with their broad pelves, suggesting that it did not possess the very broad bi-iliac breadth of those late archaic humans.

It remains possible that the femoral length estimate employed here is in error. A shorter one would increase the degree of capitular hypertrophy (similar to the more extreme European Neandertals), and the resultant diaphyseal robusticity would fall among the more robust of Early and Middle Archaic *Homo* (if given warm climate proportions) or in the middle of the Neandertals (if given cold adapted body proportions). A longer femoral length would make the relative head size less pronounced and indicate less of a cold-adapted body mass to stature proportion, but it would make it gracile for an archaic *Homo* femur in terms of diaphyseal hypertrophy and especially hip musculature development.

Given both the anatomical basis for the length estimate employed here and the reasonable level of diaphyseal and gluteal hypertrophy for the individual if provided with relatively warm climate (but not equatorial) body proportions, it is the exceptionally large size of the femoral head that is anomalous. Femoral head dimensions respond primarily to levels of hip joint reaction force during development, which implies an elevated level of biomechanical loading during development if a more moderate level (for a Pleistocene hominid) during mature life.

This correlates with its exceptionally low neck shaft angle. Neck shaft angles are high in infancy and then decrease steadily during the first decade and a half of life (Humphry,

1889; Billing, 1954; Houston and Zaleski, 1967; Yamaguchi, 1993) [a pattern also evident in juvenile Late Pleistocene *Homo* femora (Trinkaus and Ruff, 1996)]. The degree of decrease in the angle, and its eventual level in adulthood, is largely determined by the level of loading of the lower limb from locomotor activity during development. This is evident from both clinical studies (e.g., Houston and Zaleski, 1976; Laplaza et al., 1993; Yamaguchi, 1993; Saji et al., 1995) and patterns across recent humans in which the mean neck shaft angle is positively correlated with the level of sedentism and mechanization of the society (Anderson and Trinkaus, 1998).

The implication of the anomalously large femoral head, low neck shaft angle, and moderate diaphyseal robusticity (for a warm climate archaic *Homo* specimen) is that this individual experienced unusually high levels of lower limb loading during development, combined with average locomotor loading levels for a Pleistocene foraging population during mature life. What is unknown, given the absence of any other bones of this individual, is whether this unusual combination was associated with any localized or systemic pathological condition, or merely represents an extreme of individual variation with respect to lower limb loading during development.

ACKNOWLEDGMENTS

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