

Osbjorn M. Pearson  
*Doctoral Program in Anthropological  
Sciences, State University of New York  
at Stony Brook, Stony Brook, New York  
11794-4364, U.S.A.*

Frederick E. Grine  
*Departments of Anthropology and  
Anatomical Sciences, State University of  
New York at Stony Brook, Stony Brook,  
New York 11794-4364, U.S.A.*

Received 31 January 1995  
Revision received 30 September  
1996 and accepted 2 January  
1997

*Keywords:* Acheulean, Middle Stone  
Age, Cave of Hearths, Klasies  
River Mouth, radius, Neandertal,  
modern human.

## Re-analysis of the hominid radii from Cave of Hearths and Klasies River Mouth, South Africa

Two of the few postcranial fragments from the late Early Stone Age and/or the Middle Stone Age of southern Africa are the proximal radii from the Cave of Hearths and Klasies River Mouth. The Cave of Hearths fossil is metrically indistinguishable from both archaic (e.g., Neandertals) and recent humans, and presents a mosaic of primitive and modern features. The primitive include a relatively slender neck and thick cortical bone (the latter of which distinguishes recent humans from archaic, Early Modern, and Upper Paleolithic hominids); the modern includes an anteromedially (rather than medially) facing radial tuberosity. Its extreme collo-diaphyseal angle is unusual, although it can be matched by modern homologues. The neck-shaft angle of some Neandertal and Early Modern radii also appears to match that of the Cave of Hearths specimen. The Klasies River Mouth radius also has thick cortical bone of the neck. It is morphologically indistinguishable from Early Modern and Neandertal homologues. These, and other fossils, suggest a mosaic pattern of evolution in the postcranial skeleton of the late Early Stone Age and/or Middle Stone Age inhabitants of sub-Saharan Africa.

© 1997 Academic Press Limited

*Journal of Human Evolution* (1997) **32**, 577–592

---

### Introduction

It has been suggested that modern humans originated in sub-Saharan Africa during the terminal Acheulean (i.e., the late Early Stone Age, or ESA) or Middle Stone Age (MSA), and subsequently spread to other parts of the world (Bräuer, 1984; Rightmire, 1984; Stringer & Andrews, 1988; Stringer, 1992, 1994). Because only a handful of human postcranial fossils are known from the terminal ESA and the MSA of Africa, most research has focused upon the changes in cranial and mandibular morphology that accompanied the origin of modern humans. However, a number of morphological differences distinguish the postcrania of Neandertals from those of the Early Modern (or nearly modern) humans from the Levant (McCown & Keith, 1939; Vandermeersch, 1981; Trinkaus, 1981, 1983, 1984, 1992; Ruff *et al.*, 1993). Moreover, recent investigations of the proximal ulnae from the MSA of Klasies River Mouth (KRM) and Border Cave (BC), South Africa, have shown that they retain archaic proportions in the relative heights of their coronoid and olecranon processes (Churchill *et al.*, 1996; Pearson & Grine, 1996). The KRM ulna and a partial humerus from BC also possess thick cortical bone, a trait that is prevalent among archaic and Upper Paleolithic humans, but infrequent among recent people (Ruff *et al.*, 1993; Churchill *et al.*, 1996; Pearson & Grine, 1996; Pfeiffer & Zehr, 1996). Although comparative data have been made available for only the ulnae of the Early Modern samples from Skhul and Qafzeh, these elements have relatively-thick cortical bone (Churchill *et al.*, 1996). We suspect, however, that other elements in these Early Modern samples will also exhibit elevated levels of cortical thickness. Thus, there is some evidence for the retention of archaic postcranial traits among African hominids that have been argued to be among the earliest modern humans on the basis of skull morphology (Bräuer, 1984; Rightmire, 1984; Stringer & Andrews, 1988; but see Wolpoff, 1989; Frayer *et al.*, 1993). On the basis of these few fragments, there is evidence to suggest a mosaic appearance of the postcranial features that serve to distinguish recent humans from Neandertals and other archaic hominids.

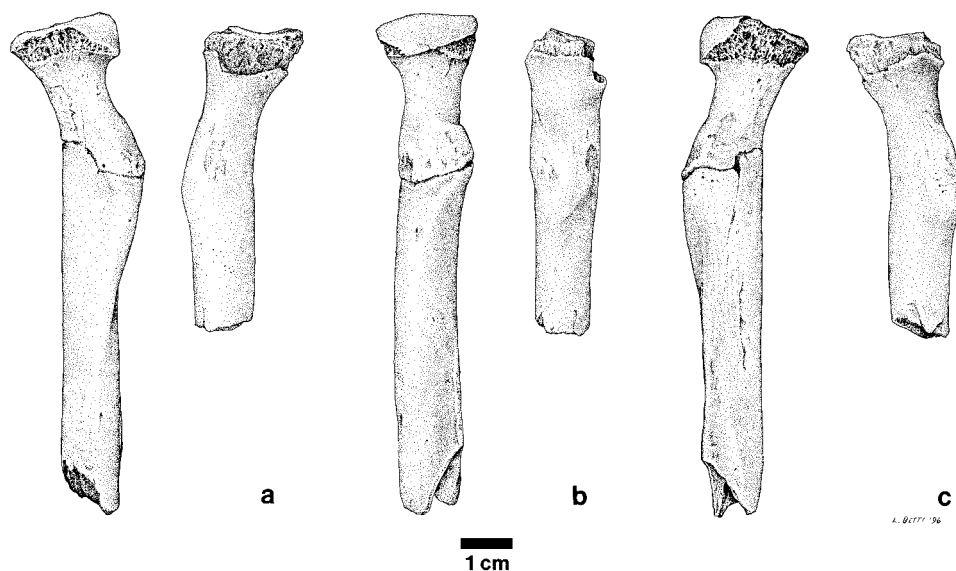


Figure 1. The Cave of Hearths (left) and Klasies River Mouth (right) radii in anterior (a), medial (b), and posterior (c) views.

Two other postcranial bones, the proximal half of a radius from the terminal ESA or MSA of the Cave of Hearths (CH), and a small proximal fragment of a radius from the MSA of KRM, deserve reconsideration in view of the evidence from the southern African MSA ulnae and humeral fragments.

The CH radius was originally described by Tobias (1971). A mandible is also known from the site. The mandible was excavated *in situ* from ESA levels with a late Acheulean industry. The radius, however, was recovered by J. W. Kitching from an assortment of bones that had fallen into a swallow hole in the cave. Its provenience is, therefore, not precisely known, although it most likely derives from either the late ESA or the MSA strata (Tobias, 1971).

The specimen comprises the proximal half or so of an adult right radius (Figure 1). Tobias (1971: p. 360) noted that it has “a relatively large head atop a disproportionately small neck; marked angulation of the neck on the shaft; a strongly-developed tubercle and a fairly robust shaft”. He concluded that the morphology of the radius coupled with the primitive features of the mandible suggested that the affinities of the CH hominids lay with “Neandertal and Neandertaloid” humans (Tobias, 1971: p. 363).

Another radius from southern Africa is of undoubted MSA context. It derives from the SAS Member of KRM (Deacon & Geleijnse, 1988; Rightmire & Deacon, 1991). It is from the left side and preserves the head, neck, and tuberosity (Figure 1). Singer & Wymer (1982: p. 146) provided only a cursory description of the specimen, stating that it had a weakly-developed tuberosity and was “suggestive of a small, lightly built individual”. They presented no comparative metric or morphological analysis.

### Materials and methods

Six linear measurements (Table 1) were recorded on the CH and KRM radii. These dimensions were recorded also for a large sample of recent humans, as well as for Upper

**Table 1 External measurements**

Group	Max n*	Maximum head diameter	Neck length†	Neck antero- posterior diameter‡	Neck medio- lateral diameter‡	Radial tuberosity	
						Length§	Width§
Recent humans¶	373	21.8 ± 2.3 (355)	32.7 ± 3.5 (351)	13.2 ± 1.8	12.5 ± 1.7	22.2 ± 2.7 (372)	13.6 ± 2.3
Early Moderns	6	23.3 ± 3.4 (5)	35.8 ± 1.8 (5)	12.1 ± 2.5 (5)	13.7 ± 2.8	24.1 ± 1.6	14.1 ± 2.5 (5)
Neandertals**	14	21.5 ± 2.4	35.3 ± 2.8	12.0 ± 1.6	11.0 ± 1.3	25.2 ± 5.1 (13)	13.7 ± 1.8
Cave of Hearths	1	22.9-25.0††	33.9	12.3	12.3	25.3	12.7
Klasies River Mouth	1	(20.0)-22.5‡‡	32.6	11.9	14.2	21.5	13.7

The numbers shown under each variable are the mean ± 1 S.D. Sample sizes less than the maximum n are shown in parentheses after the standard deviation.

\*This is the maximum sample size available. Fewer individuals were included for many measurements due to the fragmentary condition of many skeletons. The reduced sample sizes are indicated in parentheses.

†Measured from the centre of the proximal surface of the radial head to the proximodistal midpoint of the external surface of the radial tuberosity. This differs from Martin's neck length measurement M 1a (Bräuer, 1988) reported by Tobias (1971) for the Cave of Hearths fossil.

‡Measured at the midpoint between the distal edge of the rim of the radial head and the proximal edge of the radial tuberosity.

§Measured as the maximum proximodistal length and perpendicular mediolateral width of the radial tuberosity. The margins of the tuberosity were normally delineated by a sharp change in the angulation of the bone.

¶The sample of recent radii consists of 23 Australian Aborigines (ten males, four females, nine of indeterminate sex), 12 Neolithic Danes (all of unknown sex), 50 Alaskan Inuit (25 males, 25 females), 20 individuals (13 males, six females, one of unknown sex) from the North African Epipaleolithic site of Jebel Sahaba (Wendorf, 1968), 47 pre-European contact Khoisan from the Western Cape of South Africa (25 males, 21 females, one unknown sex), seven Sami from northern Norway (six males, one female), 72 African Americans (41 males, 31 females) from anatomy collections, 50 European Americans (25 males, 25 females) from anatomy collections, 61 Zulu (31 males, 30 females) from the Dart collection, five Aurignacian specimens (one male, one female, three of unknown sex), the radius of the Wadi Kubbania late Pleistocene Egyptian (Angel & Olsen Kelly, 1986), six Magdalenian individuals (four males, two females), 15 European Mesolithic individuals (eight male, five female, two of unknown sex), and the radius of the Neussing skeleton (of Solutrean age) (Gieseler, 1977).

||The Early Modern sample consists of skeletons described as possessing generally similar morphology to recent people and especially to Early Upper Paleolithic Europeans (McCown & Keith, 1939; Day et al., 1991; Vandermeersch, 1981; Trinkaus, 1983, 1984). These include Skhul II, Skhul IV (cast), Skhul V, Skhul VII, Qafzeh 9 (cast), and Omo 1 (cast).

\*\*The Neandertal sample consists of La Chapelle-aux-Saints, La Ferrassie 1 and 2, Le Régourdou 1 (cast), two Krapina radii (casts), Spy 1, Neandertal, Kebara 2 (cast), Tabun C1, Shanidar 3, and Shanidar 1, 4, and 6 (casts).

††The smaller value is our measurement of the maximum diameter of the preserved portion of the head; the larger is Tobias' (1971) estimate of the maximum pristine head diameter.

‡‡The lower value is our measurement of the damaged head; the larger number is our estimate of the maximum possible head diameter before the abrasion.

Paleolithic, Early (Mousterian or MSA) Modern human, and Neandertal homologues (Table 1). The collo–diaphyseal angle was measured in a sample of recent humans (African Americans, Zulu, and Khoisan).

The orientation of the CH radial tuberosity was noted and compared with data compiled by Trinkaus & Churchill (1988) for Neandertals and recent humans.

One feature that appears to differentiate the postcrania of archaic, Early Modern, and Upper Paleolithic hominids from recent humans is the relatively thicker cortical bone (and, by association, elevated resistance to bending, torsional, and other loading regimes) of the Pleistocene hominids (Endo & Kimura, 1970; Lovejoy & Trinkaus, 1980; Trinkaus, 1983, 1984; Trinkaus & Ruff, 1989; Ruff *et al.*, 1993; Grine *et al.*, 1995; Ruff, 1995). In order to assess the internal geometry of the CH and KRM radii, computed tomography (CT) scans were taken at the midpoint of the radial neck and at midshaft.<sup>1</sup> Seven measurements of cross-sectional geometry were recorded from the scans. These are cortical area (CA), total sub-periosteal area (TA), the ratio of cortical to total area (%CA), the maximum and minimum second moments of area ( $I_{\max}$  and  $I_{\min}$ ), and torsional strength (J). The “midshaft” CT scan of the CH radius was taken just proximal to its distal break. This level is likely a bit proximal, but almost certainly within 1 cm of its actual midshaft. It is, therefore, appropriate to compare this section with the midshaft sections from the comparative samples, in which the midshaft point was determined using articular length (Martin No. 2; Bräuer, 1988).

CT scans of the radial midshaft were recorded for three samples of recent humans: Khoisan individuals radiocarbon dated to the period before European contact (19 males, 19 females, and one of indeterminate sex), Zulu (25 males, 25 females), and African Americans (43 males, eight females). CT scans of the radial neck were recorded for the Khoisan and Zulu samples only.

All CT scans were taken in air using window and level settings of 4000 W and 1500 L. Daegling (1989) found these to be the optimum settings for a GE 9800 scanning defleshed bone immersed in water. Daegling & Grine (1991) used these settings on hominid mandibles, but found it necessary to increase the level setting to as much as 1750 L for some heavily mineralized specimens. Other investigators have recommended alternative settings (Ruff & Leo, 1986; Sumner *et al.*, 1989). Optimal CT settings vary by machine and whether the bones are scanned in water or air (Ruff & Leo, 1986; Sumner *et al.*, 1989). Researchers are advised to experiment to determine the best window and level settings for their machine and scanning protocol (Ruff & Leo, 1986).

The CH, Zulu, and African American radii were scanned with a GE 9800; the KRM and Khoisan radii were examined using a Siemens Somatom DRH. Cross-sections from hard copies were traced on to vellum and then digitized; the cross-sectional properties were computed using SLICE (Nagurka & Hayes, 1980).

## Results

### *Radial tuberosity orientation*

Trinkaus & Churchill (1988) presented a detailed study of the orientation of the radial tuberosity in modern and fossil humans. Elaborating upon the original observations by Fischer (1906), they noted that Neandertals tend to have a medially-directed tuberosity, while in modern humans it tends to face anteriorly or anteromedially. They observed only minimal

<sup>1</sup>Only the neck of the KRM specimen was scanned. Its midshaft section is not preserved.

overlap between the two groups. Furthermore, they found that the Neandertal morphology appears to be the primitive condition because it characterizes the proximal radii of AL 288-1, KNM-ER 1500 and OH 62, which have been attributed to *Australopithecus afarensis*, *Paranthropus boisei*, and *Homo habilis* (Johanson *et al.*, 1982, 1987; Grausz *et al.*, 1988; Wood, 1992).

The orientation of the CH radial tuberosity corresponds to position 2 of Trinkaus & Churchill (1988), in which the interosseous crest falls within the posterior third of the tuberosity. This is uncommon among Neandertals, with only two (11.8%) of 17 Neandertal radii exhibiting this pattern (Trinkaus & Churchill, 1988). On the other hand, this position is possessed by 59% of recent European Americans and 77.5% of Native Americans (Trinkaus & Churchill, 1988), with only 11.2 and 8% of these two samples showing a more medially-directed tuberosity.

Thus, the CH radius shares the derived pattern of an anteromedially facing tuberosity with anatomically modern humans, and departs from the archaic condition, in which the tuberosity is directed medially.

#### *Metrical features*

Measurements of the CH and KRM radii, as well as those of the modern and fossil samples are presented in Table 1. The relative size of the head is an important feature of the proximal radius. Unfortunately, the heads of the CH and KRM suffer from abrasion (Figure 1). We measured the maximum preserved head diameter of CH as 22.9 mm. Tobias (1971) estimated that the pristine maximum diameter would have been no more than 25 mm, and we accept his value as the greatest dimension possible for this measurement of CH. We measured the maximum diameter of the remaining portion of the head of KRM to be 20.0 mm, and estimate that the undamaged maximum would not have exceeded 22.5 mm.

The estimated maximum head diameters and the other values we recorded for the CH and KRM specimens fall within two standard deviations of the recent, Early Modern, and Neandertal sample means, with one exception (Table 1). The mediolateral (ML) neck diameter of the KRM radius is more than two standard deviations above the Neandertal mean; thus, it lacks the slender neck that characterizes Neandertals (Tobias, 1971; Trinkaus, 1983). While the CH radial neck is somewhat more slender than that of KRM, it is not unusual among recent humans. Tobias's (1971) estimates of the greatest diameter of the head (25 mm) and his measurement of the neck (11.9 mm compared with our measurement of 12.3 mm) provided the CH radius with the smallest neck:head ratio of any specimen in his comparative sample. The smaller neck diameter recorded by Tobias causes the CH radius to lie further from the recent human and closer to the Neandertal mean, but it is less than 2 S.D. away from either.

Although individual measurements of a fossil may not differ significantly from the means of a reference sample, it is possible that these measurements, when considered together, may describe a distinctive set of proportions. In order to assess whether the "overall" affinities of the CH and KRM radii lie with recent humans, Early Modern Humans (i.e., Skhul, Qafzeh, and Omo Kibish), or Neandertals, a canonical variates analysis was performed using all of the measurements recorded in Table 1. Both South African fossils were entered into the analysis as a separate "group" (Corruccini, 1978). The KRM and CH "groups" each consisted of two "individuals": one using the head diameter as measured, and the second employing the estimate of the pristine maximum dimension. In addition, Tobias's (1971) maximum neck diameter was used for the second CH "individual" in place of our larger anteroposterior (AP) and ML neck measurements.

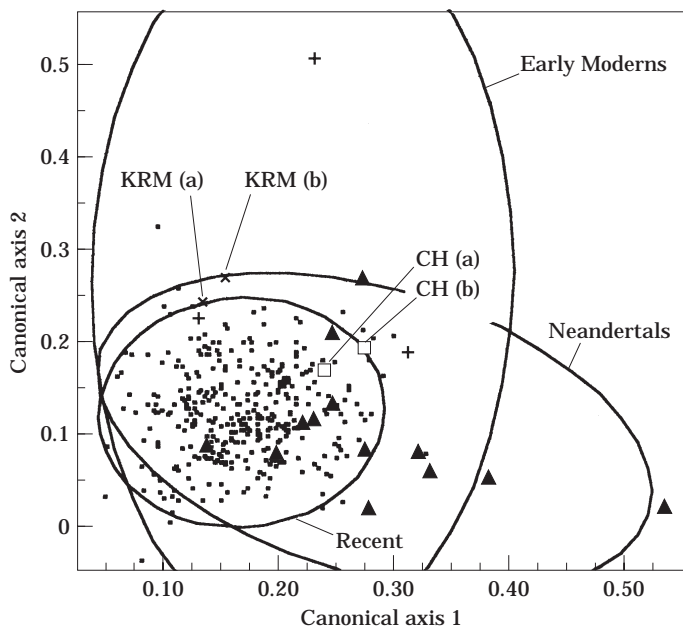


Figure 2. Canonical variates analysis of the Klasies River Mouth and Cave of Hearths radii compared with Early Modern, Neandertal, and recent homologues. Axis 1 accounts for 54.6% of the between-group variance; axis 2 accounts for 37.0%. Symbols are as follows: (●), recent humans; (+), Early Modern; (▲), Neandertal; KRM (a), specimen with the head diameter as measured; KRM (b), specimen with our estimated maximum head diameter; CH (a), specimen with our head and neck measurements; and CH (b), specimen with Tobias's neck diameter and estimated maximum head diameter.

**Table 2** Eigenvectors and between-group structure coefficients\* for the canonical variates analysis

Between-group variance:	Eigenvector 1 54.6%	Structure coefficients	Eigenvector 2 37.0%	Structure coefficients
Max. head diameter	0.007986	0.4293	0.010577	0.2754
Neck length	0.002645	0.7325	-0.002801	0.0641
Neck anteroposterior diameter	-0.021516	-0.3728	-0.046542	-0.4410
Neck mediolateral diameter	-0.024028	-0.7804	0.045691	0.8913
Tuberosity length	0.014665	0.9811	0.001562	-0.3019
Tuberosity breadth	0.012549	-0.3141	-0.000715	0.2975

\*Correlations between group means for each variable and average group positions on the canonical axis.

The results of the canonical variates analysis are shown in Figure 2 and Table 2. The comparative samples consisted of four Early Moderns, 13 Neandertals, and 341 recent humans. The first two canonical axes account for 54.6 and 37.0% of the between-group variance, respectively.

Both sets of measurements place the CH specimen within the 95% density ellipse of each of the comparative samples. The positions of CH (a) and (b) bracket a range of possible positions for the specimen. Our measurements [CH (a)] cause the CH radius to fall closer to the recent human centroid, while Tobias's [CH (b)] drive it toward the edge of the recent 95% density ellipse.



**Table 3** Radial neck–shaft angles recorded for recent human samples

		<i>n</i>	$\bar{X}$	S.D.	Observed range
Khoisan	Male	22	171.3	3.0	166–176
	Female	14	170.2	3.6	162–175
Zulu	Male	25	171.1	3.9	161–178
	Female	25	172.4	3.5	166–179
African American	Male	42	171.8	3.2	162–178
	Female	7	170.1	1.7	167–172

The unreconstructed and estimated dimensions of the KRM radius also delimit a range of positions the fossil could occupy in the canonical variates analysis. Using the smaller (damaged) head diameter, the KRM radius [KRM (a)] falls just outside the recent 95% density ellipse, near the periphery of the Neandertal ellipse, and well within the Early Moderns. The KRM specimen with the estimated maximum head diameter [KRM (b)] also falls within the Early Modern ellipse, but lies at the edge of the Neandertal ellipse and further from the recent humans.

In sum, the metrical features of the CH radius do not unequivocally establish a special affinity between it and any one of the comparative groups. It appears to possess a rather generalized morphometric condition that could be encountered in any of them. The KRM radius, likewise, does not appear to have a closer morphometric affinity to any one comparative group to the exclusion of the others. Its broad neck is more consistent with those of Early Modern humans than with the relatively-slender necks that are characteristic of Neandertals, but its position in discriminant space lies outside the 95% density ellipse of only the recent humans.

#### *Collo-diaphyseal angle*

[Tobias \(1971\)](#) considered one of the four main features of the CH radius to be the marked angulation of its neck and shaft. He recorded a neck–shaft angle of 162° for this specimen, and although he did not measure it for recent human radii, he noted that the published values of the Tabun I, Skhul IV and Skhul VII homologues closely approach this value. According to [Tobias \(1971\)](#), the angle of 162° that he obtained for the CH radius was measured as Martin No. 7. However, he recorded the maximum neck–shaft angle, which is apparent in anterolateral view [[Tobias, 1971: Figure 10\(c\)](#)], whereas the technique employed by Martin No. 7 uses an AP projection of the bone [[Figure 1](#); also [Tobias, 1971: Figure 10\(b\)](#)]. According to this technique, the CH radius has a collo–diaphyseal angle of 166°.

The collo–diaphyseal angle was recorded from AP radiographs for three samples of recent human radii ([Table 3](#)). The angle obtained by [Tobias \(1971\)](#) falls just within the lowest observed limits of all three samples (i.e., female Khoisan, and male Zulu and African Americans), but it falls below 2 S.D. of their means (although with reference to the Khoisan female and Zulu male samples, the difference is only 1 S.D.) ([Table 3](#)). The neck–shaft angle obtained by us falls just within 2 S.D. of the means for these recent human samples. The angles reported by [Tobias \(1971\)](#) for two of the three Neandertal specimens (Tabun, 166°; Neandertal, 167°; Spy, 172°), and for both specimens from Skhul that do not require an estimate (Skhul IV, 168°; Skhul VII, 166°) are identical to, or nearly the same as the values obtained by us for the CH radius ([Figure 3](#)).

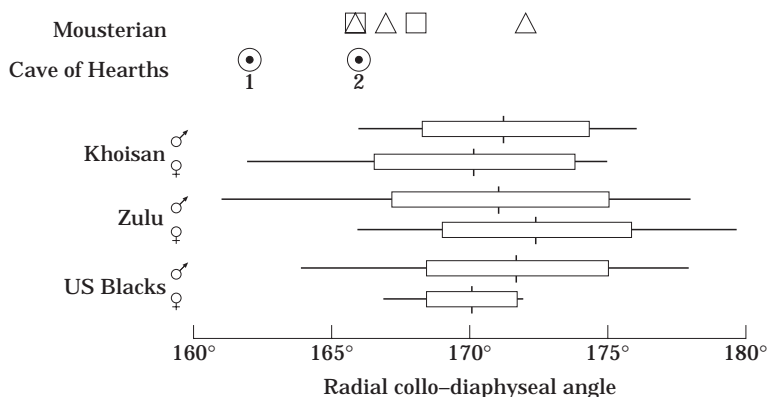


Figure 3. Collo-diaphyseal angles recorded for the Cave of Hearths radius compared with those for three recent human samples, Neandertals (triangles), and Early Modern specimens (squares) in Moustesian context. CH (1), angle of  $162^\circ$  obtained by Tobias (1971); CH (2), angle of  $166^\circ$  obtained by us.

Thus, the comparatively low collo-diaphyseal angle exhibited by the CH radius can be matched among recent human samples of African heritage, albeit with rather low frequency. It is, however, closely approached by possibly penecontemporaneous Neandertal and Early Modern human radii. The tendency for the radial neck and shaft to form a relatively straight axis may be a relatively recent human acquisition.

#### *Cross-sectional geometry*

The cross-sectional properties of the CH and KRM radial necks are compared with those recorded for recent African homologues in Table 4. The fossil values fall between the Zulu male and female means for TA, CA,  $I_{\max}$ ,  $I_{\min}$ , and J. The CH radius has a slightly larger circumference than the KRM radius; both are noticeably larger than many female Khoisan homologues, but considerably smaller than those of many Zulu males. The  $I_{\max/\min}$  index values of the CH and KRM radii are unremarkable compared with the recent samples, although the KRM neck appears to be somewhat rounder (i.e., it has an index value closer to 1.0) than many of the recent humans (Figure 4).

The most striking cross-sectional feature of the CH and KRM radial necks is their relatively-thick cortical bone (Table 3; Figure 4). Their %CA values fall at the high ends of the observed ranges for Khoisan and Zulu females, and Khoisan males, and while the KRM value falls in the upper part of the Zulu male range, the CH value exceeds it (Table 4; Figure 4). Of these recent human groups, Khoisan males have proportionately the thickest cortical bone of the radial neck, and three individuals in this sample (15.8%) equal or exceed both fossils in %CA. Figure 5 illustrates the relationship between size (represented by J) and relative cortical thickness (represented by %CA) in the CH and KRM radial necks, in comparison with recent human homologues. The cortical thickness in both fossils is evident in relation to their size, although this relationship is matched by some recent African homologues.

The cross-sectional properties recorded for the CH "mid-shaft" are compared with those for recent human radii in Table 5. Because the CH fragment was sectioned at a level somewhat proximal to the estimated actual midshaft, a degree of caution should be employed when comparing its cross-sectional properties with those of the comparative samples. This caveat notwithstanding, the CH "midshaft" section is of intermediate size with respect to TA,



**Table 4 Cross-sectional properties of the radial neck**

	n	TA	CA	%CA	I <sub>max</sub>	I <sub>min</sub>	J	I <sub>max</sub> /min
Cave of Hearths	1	132.86	106.35	80.05	1549.56	1194.93	2744.48	1.297
Klasies River Mouth	1	122.87	93.98	76.49	1201.56	1074.19	2275.75	1.119
Khoisan females	19	86.91 ± 21.84	51.29 ± 8.28	60.80 ± 10.89	614.82 ± 293.99	424.82 ± 179.10	1039.79 ± 461.36	1.444 ± 0.250
Khoisan males	19	93.92 ± 23.36	64.17 ± 16.52	68.97 ± 11.68	784.13 ± 361.88	582.21 ± 287.48	1330.34 ± 641.54	1.292 ± 0.199
Zulu females	25	117.85 ± 17.13	73.63 ± 12.96	63.27 ± 11.47	1034.60 ± 241.89	867.15 ± 241.57	1901.76 ± 477.07	1.209 ± 0.123
Zulu males	25	157.65 ± 23.41	99.53 ± 14.88	63.54 ± 7.32	1889.96 ± 496.53	1581.80 ± 482.45	3471.76 ± 970.24	1.213 ± 0.112

The numbers shown for each variable are the mean ± 1 S.D.

Symbols for the cross-sectional properties are as follows: TA = total subperiosteal area (mm<sup>2</sup>); CA = area occupied by cortical bone in the section (mm<sup>2</sup>); %CA = (TA/CA) × 100; I<sub>max</sub> = the maximum second moment of area in the section (mm<sup>4</sup>); I<sub>min</sub> = the minimum second moment of area of the section; J = the torsional strength of the section (mm<sup>4</sup>); I<sub>max</sub>/min = the maximum divided by the minimum second moments of area of the section.

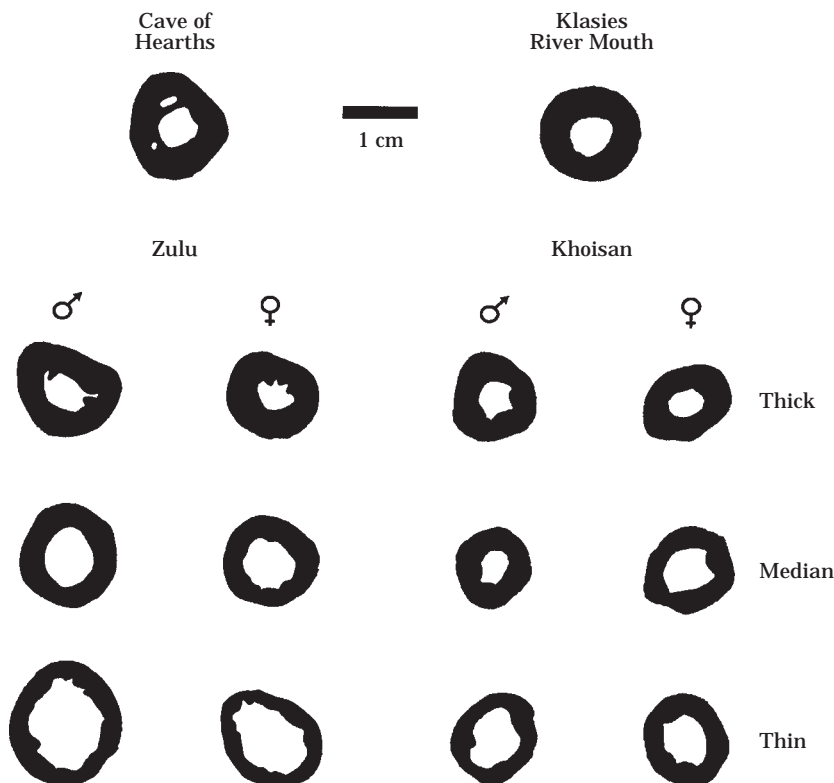


Figure 4. CT sections through the neck of the Cave of Hearths and Klasies River Mouth radii compared with those recorded for recent human samples. In each sample, the specimen with the highest %CA value is on top, that with the median value is in the middle, and that with the lowest value is on the bottom.

CA,  $I_{\max}$ ,  $I_{\min}$ , and J. These values for the CH radius tend to be larger than those of most Khoisan individuals (especially females), but they are smaller than those of many Zulu and African Americans. Although the cross-sectional values of the CH radius may have been slightly larger at its actual midshaft, any such increase would be unlikely to alter the present findings.

The  $I_{\max/\min}$  index value of 1.87 recorded for the CH "midshaft" section reveals it to have a relatively unequal distribution of bone around its bending axes. The Khoisan have the roundest midshaft sections of any of the three recent groups sampled, and the CH index value falls more than 2.0 S.D. above the Khoisan male mean and 1.5 S.D. above the Khoisan female mean. Endo & Kimura (1970) remarked that a round radial midshaft section tends to typify Neandertals, but Figure 6 reveals that there is a great deal of variability in radial cross-sectional shape. Some recent humans have a more flaring interosseous crest than Neandertals, but others do not. The CH radius has a distinct and moderately-flaring interosseous crest. In this feature, it differs from many Neandertals and more closely resembles the condition of many recent radii. However, given the degree of variability in this trait, the importance of this feature should not be overemphasized.

As might be expected, the "midshaft" of the CH radius also possesses thick cortical bone (Table 5). Its %CA value of 89.4 exceeds the mean of any of the recent human samples

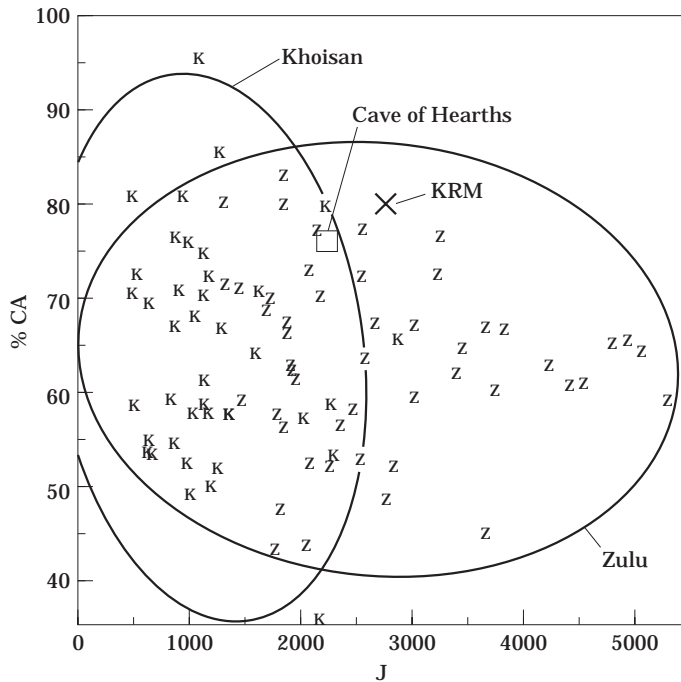


Figure 5. Plot of %CA versus J for cross-sections of the Cave of Hearths and Klasies River Mouth radial necks. 95% density ellipses surround the Khoisan and Zulu pooled-sex samples.

examined here, but falls within 2 S.D. of all of them. Thus, it is possible to encounter individuals with similarly thick, or even thicker cortical bone in all three modern human populations.

Archaic, Early Modern, and Upper Paleolithic humans have relatively thicker cortical bone, on average, than do recent humans (Lovejoy & Trinkaus, 1980; Ben-Itzhak *et al.*, 1988; Ruff *et al.*, 1993; Grine *et al.*, 1995; Ruff, 1995). The comparatively-thick cortical bone of the CH and KRM radii, therefore, tends to resemble more closely that displayed by Pleistocene hominids than that of recent humans.

## Discussion

There is some evidence that the postcranial skeletons of the MSA inhabitants of southern Africa possessed a mosaic of primitive and derived features (Churchill *et al.*, 1996; Pearson & Grine, 1996). The most ubiquitous of the primitive features appears to be relatively-thick cortical bone. However, the possession of thick cortical bone does not differentiate archaic hominids from Upper Paleolithic or Early Modern humans (Ruff *et al.*, 1993; Churchill *et al.*, 1996). The relatively thinner cortical bone of recent populations may have developed as a result of decreased activity levels (Ruff *et al.*, 1993; Trinkaus *et al.*, 1994; Lieberman, 1996). The CH and KRM radii fragments conform to this pattern, with comparable levels of cortical thickness being encountered at low frequencies in several recent populations of African heritage. Interestingly, among the recent human samples included in this study, the pre-contact, foraging Khoisan (especially males) tend to have the thickest cortical bone of the

**Table 5 Cross-sectional properties of the radial midshaft**

	n	TA	CA	%CA	I <sub>max</sub>	I <sub>min</sub>	J	I <sub>max/min</sub>
Cave of Hearths	1	120.29	107.57	89.43	1588.84	850.15	2438.99	1.869
Khoisan females	18	80.96 ± 12.48	60.25 ± 12.73	74.38 ± 10.70	634.24 ± 195.18	409.29 ± 143.90	1043.53 ± 332.71	1.573 ± 0.193
Khoisan males	19	92.87 ± 24.01	77.17 ± 19.71	83.47 ± 7.40	845.13 ± 417.43	590.06 ± 265.60	1435.19 ± 674.06	1.416 ± 0.191
Zulu females	25	104.04 ± 14.97	81.38 ± 11.49	78.54 ± 6.71	1061.02 ± 336.27	694.17 ± 198.71	1755.19 ± 516.70	1.530 ± 0.246
Zulu males	25	143.47 ± 22.14	113.57 ± 13.40	79.83 ± 6.77	2054.94 ± 663.55	1348.98 ± 427.68	3403.93 ± 1012.68	1.556 ± 0.350
African American females	8	119.27 ± 15.36	84.23 ± 18.50	70.47 ± 13.00	1402.06 ± 376.52	838.65 ± 279.97	2240.71 ± 627.80	1.710 ± 0.254
African American males	43	144.11 ± 19.84	109.73 ± 15.19	76.55 ± 7.96	2098.67 ± 585.92	1315.98 ± 339.06	3414.65 ± 889.38	1.606 ± 0.264

The numbers shown for each variable are the mean ± 1 S.D. The abbreviations for the properties are the same as in Table 4.

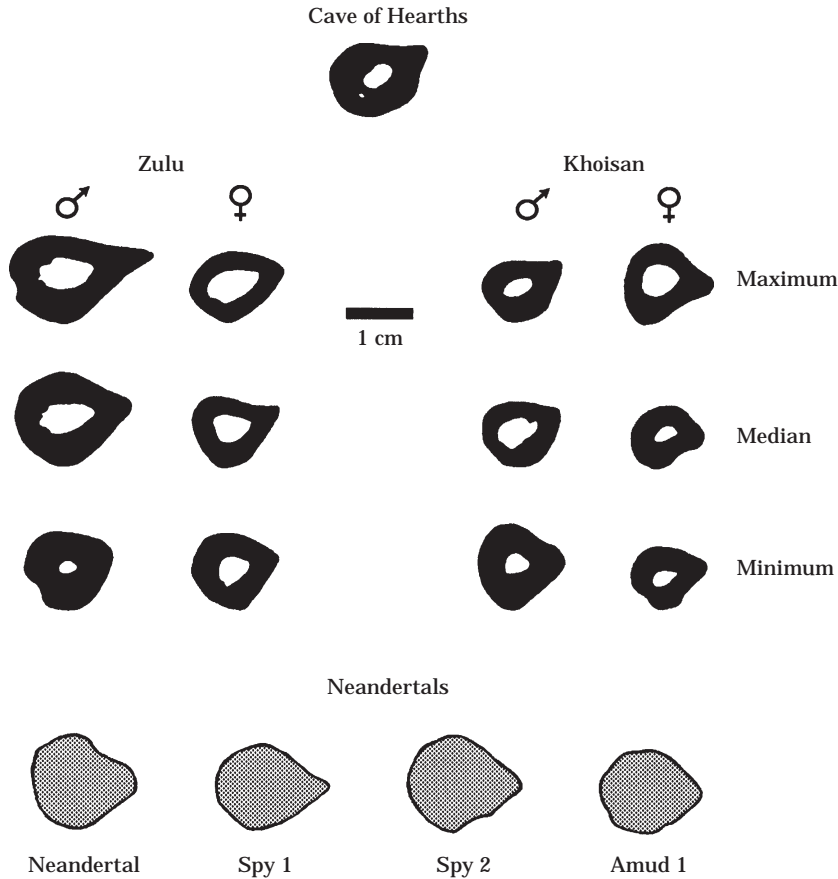


Figure 6. Cross-section of the "midshaft" of the Cave of Hearths radius compared with those recorded for recent human samples, and with outlines of midshaft sections of Neandertal radii. Individuals in each sample are ordered; that with the highest  $I_{\max/\min}$  index value is on top, that with the median value is in the middle, and that with the lowest value is on the bottom. Neandertal sections are taken from Endo & Kimura (1970).

radial neck and midshaft. Ruff *et al.* (1993) also found pre- and proto-historic Amerindians to have relatively more robust femora than a sample of industrialized whites.

Other archaic morphology is also apparent in the CH radius. Tobias (1971) had earlier suggested that its relatively slender neck and large head caused it to resemble Neandertal homologues. The present analysis, however, shows that it does not unequivocally group with Neandertals, even when Tobias's (rather than our) measurements are used. Nevertheless, it is noteworthy that the CH radius falls closer to the Neandertal centroid than does the KRM fragment. Tobias's (1971) measurements of the CH neck and estimate of maximum head diameter increase this tendency.

The notable collo-diaphyseal angulation of the CH radius is encountered at low frequencies in two recent African populations, but is matched by some Neandertal and Early Modern homologues. It is possible that a low neck-shaft angle is an archaic feature, retained by the Early Modern individuals from the Levant.

On the other hand, the CH radius shares a derived feature with recent humans: an anteromedially oriented radial tuberosity. In this respect, it differs from Neandertals and earlier hominids [e.g., *Australopithecus anamensis*, *Paranthropus robustus*, and *Homo erectus* (Robinson, 1953; Grine & Susman, 1991; Heinrich *et al.*, 1993; Leakey *et al.*, 1995)] While the CH radial tuberosity is fairly large, its orientation resembles that of recent humans.

The KRM radius has a stout neck, in which it differs from the Neandertal condition and resembles modern humans.

Thus, the CH and KRM radii display what appears to be a combination of primitive and derived traits. Among the former, the CH fossil displays relatively thick cortical bone, a rather slender neck, and a low collo-diaphyseal angle, and the KRM fragment exhibits comparatively-thick cortical bone. Among the apparently derived features, the CH radius possesses an anteromedially-orientated tuberosity and a flaring interosseous crest. In addition, the KRM neck is comparatively stout, which is partly (if not largely) responsible for providing it with an overall morphometric profile that falls within the Early Modern envelope, and within the observed ranges of recent African radii.

### Summary and conclusions

Re-analysis of the CH radius reveals that it exhibits a generalized set of metrical proportions that can be matched within recent human, Early Modern (i.e., Skhul, Qafzeh, and Omo Kibish), and Neandertal samples. The CH radius exhibits thick cortical bone in its neck and shaft, and it has a rather slender neck. Its slender neck resembles archaic rather than modern homologues, and the thick cortical bone aligns it with either archaic, Early Modern, or Upper Paleolithic hominids. On the other hand, it exhibits an anteromedially-orientated tuberosity, a feature it shares with Early Modern and recent humans in contrast to the majority of Neandertals and other archaic hominids.

The KRM radial fragment presents an overall morphometric profile that falls within the Early Modern and just within the Neandertal, and outside the recent human 95% density ellipse in discriminant space. Like the CH specimen, its neck also has a comparatively thick cortical bone. Externally, the KRM radial neck is rather stout. This condition differs from Neandertals and resembles Early Modern and recent humans.

The relatively thick cortical bone possessed by the CH and KRM radii is exhibited by other human postcrania from the MSA of southern Africa. Like these other specimens (e.g., the KRM ulna), the CH and KRM radii also exhibit derived features in common with modern humans. Thus, both fossils conform to the mosaic pattern of primitive and derived features that appears to have characterized other parts of the postcranial skeleton of the inhabitants of southern Africa in the late ESA and/or MSA.

### Acknowledgements

We are grateful to G. Avery, P. V. Tobias, and R. J. Clarke, who permitted us to measure and CT scan the Klasies River Mouth and Cave of Hearths radii. We also thank F. Thackeray, J. McKee, A. G. Morris, M. L. Wilson, I. Tattersall, F. Wendorf, D. Hunt, E. Trinkaus, D. Pilbeam, C. Stringer, R. Kruszynski, R. Orban, H. de Lumley, D. Grimaud-Herve, S. Simone, J. F. Bussière, J.-J. Hublin, M. Chech, H.-E. Joachim, G. Grupe, P. Schröter, M. Berner, N. Lynnerup, and P. Holck for permission to examine the fossil and recent human skeletons in their care. The donation of the Spy remains by the heirs of Professor Max Lohest



(1857–1923) to the Institut Royal des Sciences Naturelles de Belgique is acknowledged. We are grateful also to those who helped us obtain the CT scans: B. Day of Stony Brook Hospital; S. Beningfield, J. Michie, M. Sadler and L. Munro of Groote Schuur Hospital, Cape Town; N. Inglestone, E. Kruger, A. Fennell, and C. Goldsmith of Johannesburg General Hospital. We thank R. Rayner for his generous hospitality, and Y. Lam, D. Strait, and three anonymous reviewers for insightful comments on the manuscript. L. Betti-Nash skillfully prepared the illustrations. This work was supported by an NSF predoctoral fellowship to O.M.P. and NSF DBS-9120117 to F.E.G.

## References

- Angel, J. L. & Olsen Kelly, J. (1986). Description and comparison of the skeleton. In (F. Wendorf & R. Schild, Eds) *The Wadi Kubbaniya Skeleton: A Late Paleolithic Burial from Southern Egypt*, pp. 53–70. Dallas: Southern Methodist University Press.
- Ben-Itzhak, S., Smith, P. & Bloom, R. A. (1988). Radiographic study of the humerus in Neandertals and *Homo sapiens sapiens*. *Am. J. phys. Anthropol.* **77**, 231–242.
- Bräuer, G. (1984). A craniological approach to the origin of anatomically modern *Homo sapiens* in Africa and implications for the appearance of modern Europeans. In (F. H. Smith & F. Spencer, Eds) *The Origins of Modern Humans: A World Survey of the Fossil Evidence*, pp. 327–410. New York: Alan R. Liss.
- Bräuer, G. (1988). Osteometrie. In (R. Knussman, Ed.) *Anthropologie*, pp. 160–231. Stuttgart: Gustav Fischer Verlag.
- Churchill, S. E., Pearson, O. M., Grine, F. E., Trinkaus, E. & Holliday, T. W. (1996). Morphological affinities of the proximal ulna from Klasies River Mouth Main Site: archaic or modern? *J. hum. Evol.* **31**, 213–237.
- Corruccini, R. S. (1978). Morphometric analysis: uses and abuses. *Yearb. phys. Anthropol.* **18**, 134–150.
- Daegling, D. J. (1989). Biomechanics of cross-sectional size in the hominoid mandibular corpus. *Am. J. phys. Anthropol.* **80**, 91–106.
- Daegling, D. J. & Grine, F. E. (1991). Compact bone distribution and biomechanics of early hominid mandibles. *Am. J. phys. Anthropol.* **86**, 321–339.
- Day, M. H. (1969). Omo human skeletal remains. *Nature* **222**, 1135–1138.
- Day, M. H., Twist, M. H. C. & Ward, S. (1991). Les vestiges post-crâniens d'Omo I (Kibish). *L'Anthropol.* **95**, 595–610.
- Deacon, H. J. & Geleijense, V. B. (1988). The stratigraphy and sedimentology of the main site sequence, Klasies River Mouth, South Africa. *S. Afr. Archaeol. Bull.* **43**, 5–14.
- Endo, B. & Kimura, T. (1970). Postcranial skeleton of Amud Man. In (H. Suzuki & F. Takai, Eds) *The Amud Man and His Cave Site*, pp. 231–406. Tokyo: Academic Press of Japan.
- Fischer, E. (1906). Die Variationen am Radius und Ulna des Menschen. *Z. Morph. Anthropol.* **9**, 147–247.
- Frayser, D. W., Wolpoff, M. H., Thorne, A. G., Smith, F. H. & Pope, G. G. (1993). Theories of modern human origins: the paleontological test. *Am. Anthropol.* **95**, 14–50.
- Geiseler, W. (1977). Das jungpaläolithische Skelett von Neuessing. In (P. Schröter, Ed.) *75 Jahre Anthropologische Staatssammlung München*, pp. 39–51. Munich: Anthropologischen Staatssammlung München.
- Grausz, H. M., Leakey, R. E., Walker, A. C. & Ward, C. V. (1988). Associated cranial and postcranial bones of *Australopithecus boisei*. In (F. E. Grine, Ed.) *Evolutionary History of the "Robust" Australopithecines*, pp. 127–132. New York: Aldine de Gruyter.
- Grine, F. E., Jungers, W. L., Tobias, P. V. & Pearson, O. M. (1995). Fossil *Homo* femur from Berg Aukas, northern Namibia. *Am. J. phys. Anthropol.* **97**, 151–185.
- Grine, F. E. & Susman, R. L. (1991). Radius of *Paranthropus robustus* from Member 1, Swartkrans Formation, South Africa. *Am. J. phys. Anthropol.* **84**, 229–248.
- Heinrich, R. E., Rose, M. D., Leakey, R. E. & Walker, A. C. (1993). Hominid radius from the Middle Pliocene of Lake Turkana, Kenya. *Am. J. phys. Anthropol.* **92**, 139–148.
- Johanson, D. C., Lovejoy, C. O., Kimbel, W. H., White, T. D., Ward, S. C., Bush, M. E., Latimer, B. M. & Coppens, Y. (1982). Morphology of the Pliocene partial hominid skeleton (A.L. 288-1) from the Hadar Formation, Ethiopia. *Am. J. phys. Anthropol.* **57**, 403–452.
- Johanson, D. C., Masao, F. T., Eck, G., White, T. D., Walter, R. C., Kimbel, W. H., Asfaw, B., Manega, P., Ndessokia, P. & Suwa, G. (1987). New partial skeleton of *Homo habilis* from Olduvai Gorge, Tanzania. *Nature* **327**, 205–209.
- Leakey, M. G., Feibel, C. S., McDougall, I. & Walker, A. C. (1995). New four-million-year-old hominid species from Kanapoi and Allia Bay, Kenya. *Nature* **376**, 565–571.
- Lieberman, D. E. (1996). How and why humans grow thin skulls: experimental evidence for systemic cortical robusticity. *Am. J. phys. Anthropol.* **101**, 217–236.

- Lovejoy, C. O. & Trinkaus, E. (1980). Strength and robusticity of the Neandertal tibia. *Am. J. phys. Anthropol.* **44**, 489–506.
- McCown, T. D. & Keith, A. (1939). *The Stone Age of Mount Carmel, II: The Fossil Human Remains from the Lavallois-Mousterian*. Oxford: Clarendon Press.
- Nagurka, M. L. & Hayes, W. C. (1980). An interactive graphics package for calculating cross-sectional properties of complex shape. *J. Biomechanics* **13**, 59–64.
- Pearson, O. M. & Grine, F. E. (1996). Morphology of the Border Cave hominid ulna and humerus. *S. Afr. J. Sci.* **92**, 231–236.
- Pfeiffer, S. & Zehr, M. K. (1996). A morphological and histological study of the human humerus from Border Cave. *J. hum. Evol.* **31**, 49–59.
- Rightmire, G. P. (1984). *Homo sapiens* in sub-Saharan Africa. In (F. H. Smith & F. Spencer, Eds) *The Origins of Modern Humans: A World Survey of the Fossil Evidence*, pp. 295–235. New York: Alan R. Liss.
- Rightmire, G. P. & Deacon, H. J. (1991). Comparative studies of the late Pleistocene human remains from Klasies River Mouth, South Africa. *J. hum. Evol.* **20**, 131–156.
- Robinson, J. T. (1953). *Telanthropus* and its phylogenetic significance. *Am. J. phys. Anthropol.* **11**, 445–502.
- Ruff, C. B. (1995). Biomechanics of the hip and birth in early *Homo*. *Am. J. phys. Anthropol.* **98**, 527–574.
- Ruff, C. B. & Leo, F. P. (1986). Use of computed tomography in skeletal structure research. *Yearb. phys. Anthropol.* **29**, 181–196.
- Ruff, C. B., Trinkaus, E., Walker, A. & Larsen, C. S. (1993). Postcranial robusticity in *Homo*. I. Temporal trends and mechanical interpretation. *Am. J. phys. Anthropol.* **91**, 21–53.
- Singer, R. & Wymer, J. (1982). *The Middle Stone Age at Klasies River Mouth*. Chicago: University of Chicago Press.
- Stringer, C. B. (1992). Reconstructing human evolution. In (M. J. Aitken, C. B. Stringer & P. A. Mellars, Eds) *The Origin of Modern Humans and the Impact of Chronometric Dating*, pp. 179–195. Princeton, NJ: Princeton University Press.
- Stringer, C. B. (1994). Out of Africa—a personal history. In (M. H. Nitecki & D. V. Nitecki, Eds) *The Origins of Anatomically Modern Humans*, pp. 149–172. New York: Plenum.
- Stringer, C. B. & Andrews, P. (1988). Genetic and fossil evidence for the origin of modern humans. *Science* **239**, 1263–1268.
- Sumner, D. R., Olson, C. L., Freeman, P. M., Lobick, J. J. & Andriacci, T. P. (1989). Computed tomographic measurement of cortical bone geometry. *J. Biomechanics* **22**, 649–653.
- Tobias, P. V. (1971). Human skeletal remains from the Cave of Hearths, Makapansgat, Northern Transvaal. *Am. J. phys. Anthropol.* **34**, 335–368.
- Trinkaus, E. (1981). Neandertal limb proportions and cold adaptation. In (C. B. Stringer, Ed.) *Aspects of Human Evolution*, pp. 187–224. London: Taylor and Francis.
- Trinkaus, E. (1983). *The Shanidar Neandertals*. New York: Academic Press.
- Trinkaus, E. (1984). Western Asia. In (F. H. Smith & F. Spencer, Eds) *The Origins of Modern Humans: A World Survey of the Fossil Evidence*, pp. 251–293. New York: Alan R. Liss.
- Trinkaus, E. (1992). Morphological contrasts between the Near Eastern Qafzeh-Skhul and late archaic human samples: grounds for a behavioral difference? In (T. Akazawa, K. Aoki & T. Kimura, Eds) *The Evolution and Dispersal of Modern Humans in Asia*, pp. 277–294. Tokyo: Hokusen-sha Publishing Co.
- Trinkaus, E. & Churchill, S. E. (1988). Neandertal radial tuberosity orientation. *Am. J. phys. Anthropol.* **75**, 15–21.
- Trinkaus, E. & Ruff, C. (1989). Diaphyseal cross-sectional morphology and biomechanics of the Fond-de-Forêt 1 femur and the Spy 2 femur and tibia. *Anthropol. Préhistoire* **100**, 33–42.
- Trinkaus, E., Churchill, S. E. & Ruff, C. B. (1994). Postcranial robusticity in *Homo*. II: Humeral bilateral asymmetry and bone plasticity. *Am. J. phys. Anthropol.* **93**, 1–34.
- Vandermeersch, B. (1981). *Les Hommes Fossiles de Qafzeh (Israël)*. Paris: CNRS.
- Wendorf, F. (1968). Site 117: a Nubian Final Paleolithic graveyard near Jebel Sahaba, Sudan. In (F. Wendorf, Ed.) *The Prehistory of Nubia*, pp. 954–995. Dallas: Fort Burgwin Research Center and Southern Methodist University Press.
- Wolpoff, M. H. (1989). Multiregional evolution: the fossil alternative to Eden. In (P. Mellars & C. B. Stringer, Eds) *The Human Revolution*, pp. 97–141. Princeton: Princeton University Press.
- Wood, B. (1992). Origin and evolution of the genus *Homo*. *Nature* **355**, 783–790.