

Gough's Cave 1 (Somerset, England): an assessment of body size and shape

TRENTON W. HOLLIDAY

Department of Anthropology, Tulane University, New Orleans LA 70118, USA

STEVEN E. CHURCHILL

Department of Biological Anthropology and Anatomy, Duke University, Durham NC 27710, USA

Synopsis. Stature, body mass, and body proportions are evaluated for the Cheddar Man (Gough's Cave 1) skeleton. Like many of his Mesolithic contemporaries, Gough's Cave 1 evinces relatively short estimated stature (ca. 166.2 cm [5' 5"]) and low body mass (ca. 66 kg [146 lbs]). In body shape, he is similar to recent Europeans for most proportional indices. He differs, however, from most recent Europeans in his high crural index and tibial length/trunk height indices. Thus, while Gough's Cave 1 is characterized by a total morphological pattern considered 'cold-adapted', these latter two traits may be interpreted as evidence of a large African role in the origins of anatomically modern Europeans.

INTRODUCTION

Reconstructed stature, body mass, and body shape are all variables of interest in any attempt to understand the paleobiology of prehistoric humans such as the 'Cheddar Man', or the Gough's Cave 1 specimen. The relative completeness of the Gough's Cave 1 postcranial skeleton allows each of these variables to be accurately reconstructed. Such variables are of interest both for evolutionary and non-evolutionary questions. For example, any body mass and/or stature differences between Mesolithic humans, such as Gough's Cave 1, and recent humans are unlikely to be evolutionary in nature. Nonetheless, they are of interest to paleobiologists since they may reflect the nutritional and overall health status of prehistoric populations. In contrast, body proportions vary among recent humans, presumably as the result of climatic selection. Yet body proportions appear to have a large genetic component, and, over evolutionarily short periods, since they are the result of apparently *long-term* climatic selection (based on migrant studies), they may provide evidence of population movements or migration from different climatic regimes (Holliday, 1997a).

Stature in Gough's Cave 1 is predicted from lower limb long bone lengths using Trotter and Gleser's (1958) standard formulae for Euroamericans (discussed in detail below). Body mass for the specimen is predicted using two methods outlined in Ruff *et al.* (1997). The first method involves computing the arithmetic average of predictions based on three separate body mass/femoral head diameter regressions derived from recent human skeletal material. In the second method, body mass is predicted from stature and bi-iliac breadth. In concert these two variables (stature and bi-iliac breadth) are known to provide an accurate estimate of body mass in living humans, and have an added advantage in that they are independent of the locomotor biomechanical stresses to which the femoral head is subject (Ruff *et al.*, 1997). Ruff's stature/bi-iliac breadth predictive formula is derived from data on living humans. Therefore, in order to use this method with fossils, stature was estimated using the Trotter and Gleser (1958) formulae, and a 5% correction factor was added to bi-iliac breadth to account for soft tissue. All formulae used to predict body mass were kindly provided by Prof. C.B. Ruff.

With regard to body shape or proportions, there are several means by which these features may be accurately reconstructed from skeletal remains; these means approximate some of the anthro-

pometric data taken on living human subjects. The measures that are used in this study reflect the following: 1) intralimb proportions (i.e., relative lengths of the proximal and distal limb segments), 2) limb/trunk proportions, 3) body linearity relative to overall body mass, and 4) body breadth relative to stature. For all analyses, Gough's Cave 1 is compared to other Late Pleistocene and Early Holocene associated skeletons as well as to a large sample of recent humans from across the western Old World (Africa and Europe). The fossils have been placed into Mesolithic (< 10,000 BP), Late Upper Paleolithic (LUP; 11,000–19,000 BP), Early Upper Paleolithic (EUP; 20,000–28,000 BP) and Neandertal (> 30,000 BP) samples, while the recent humans have been placed into three geographical subsamples: Europe, North Africa and Sub-Saharan Africa. Detailed discussion of these samples is found in Holliday (1995).

BODY SIZE

Stature

For all samples, stature was predicted using Trotter and Gleser's (1958) formulae for the tibia and femur; if both bones were present, the mean of the two resultant predictions was used. Formulae for Euroamerican males were used for Gough's Cave 1 and all comparative samples, with the exception of the recent Sub-Saharan Africans and the European EUP, for whom African-American formulae were used. These regression formulae are more appropriate because these two groups have a demonstrably more 'tropically-adapted' body shape which is more similar to that of African-Americans (Holliday, 1997a).

Table 1 presents summary statistics for predicted stature among Gough's Cave 1 and the comparative samples. The Gough's Cave specimen has a predicted stature of 166.2 cm, which falls just below the Mesolithic male mean of 167.5 cm. His predicted stature is much shorter relative to recent European males; he falls below their 25th percentile. Importantly, predicted stature values for the fossils are similar to those given in Frayer (1984), who used many of the same specimens, but temporally subdivided his samples differently than has been done here. As an example of the similarity of results, Frayer's (1984) Mesolithic sample had a predicted male stature of 167.8 cm, almost identical to our mean of 167.5 cm. Also, his Upper Paleolithic male mean of 174.3 cm is somewhat (although not

Table 1 Summary statistics (mean, standard deviation, number of specimens) for Gough's Cave 1, fossil and recent human male samples – predicted stature (in cm).

	Predicted stature
Gough's Cave 1	166.2
European Mesolithic	167.5, 4.8, 7
European Late Upper Palaeolithic	170.2, 6.6, 17
European Early Upper Palaeolithic	170.1, 7.9, 11
European Neandertals	166.7, 3.8, 4
Recent Europeans	171.6, 5.8, 311
Recent North Africans	167.4, 5.9, 75
Recent Sub-Saharan	164.7, 8.2, 62

statistically significantly) higher than our LUP and EUP means of 170.2 cm and 170.1 cm, respectively.

Not unexpectedly, our results suggest that stature in Europe is highest among Upper Paleolithic (both EUP and LUP) and recent Europeans. Neandertals and Mesolithic Europeans, on the other hand, are significantly shorter than recent Europeans (two-tailed *t* test, $p = 0.020$ and 0.048 , respectively). These results are similar to those reported by Frayer *et al.* (1993) and Formicola & Giannecchini (1999). With regard to the Mesolithic sample, this reduction in stature may be due to a drop in dietary protein. Such a drop could have followed decreased reliance on big game following the reforestation of Europe, a phenomenon documented by archaeologists for many early Holocene hunter-gatherers (Straus *et al.*, 1980; Geddes *et al.*, 1986).

Note that among the recent human groups, stature appears to decrease as one moves toward the equator. This is likely a secondary consequence of a decrease in body mass associated with increasingly hotter, more tropical temperatures, following Bergmann's rule (see below).

Body Mass

Table 2 gives predicted body mass summary statistics for Gough's Cave 1 and the comparative male sample. Among the recent human samples, there is a clear decrease in body mass (based on either predictive method) from higher to lower latitudes. This reflects adherence of humans to Bergmann's (1847) ecological rule (discussed below). The Gough's Cave 1 specimen has a predicted body mass of 64.8 kg based on femoral head size, and a mass of 67.3 kg based on stature and bi-iliac breadth. It is noteworthy that despite the fact that the two methods use very different anatomical features, the two predictions deviate from each other by less than 4%. Note, also that across all groups, the mean body mass estimates using the non-biomechanical (stature/bi-iliac breadth) method are close to those derived from the femoral head. The greatest difference between the two methods is found among the EUP sample, whose body mass

Table 2 Summary statistics for Gough's Cave 1, fossil and recent human males – predicted body mass (in kg).

	Femoral Head Method	Stature/BIB Method
Gough's Cave 1	64.8	67.3
European Mesolithic	66.9, 7.2, 7	66.0, 2.3, 6
European Late Upper Palaeolithic	67.7, 6.6, 14	67.4, 8.2, 6
European Early Upper Palaeolithic	65.8, 10.0, 10	69.6, 7.3, 6
European Neandertals	82.9, 4.3, 4	79.3, –, 1
Recent Europeans	69.3, 7.3, 134	71.0, 7.4, 126
Recent North Africans	59.0, 7.6, 73	61.3, 5.5, 60
Recent Sub-Saharan	54.7, 8.5, 53	53.6, 8.6, 49

prediction based on stature and bi-iliac breadth is 5.8% higher than the one based on femoral head diameter. Note, too, that while the Neandertal sample appears to be characterized by high body mass, there is relatively little evidence for a subsequent change in body mass in Europe from the EUP to the present (a result consistent with the findings of Ruff *et al.*, 1997). As for the specimen of interest, Gough's Cave 1 is not atypical among early Holocene Europeans in mass; he falls slightly below the Mesolithic male mean based on the femoral head prediction, and slightly above the mean for the stature/bi-iliac breadth prediction. He, like most of his Mesolithic cohorts, is light relative to recent Europeans; his femoral head-predicted and bi-iliac breadth/femoral length predicted weights fall on the 29th and 37th recent European male percentiles, respectively.

BODY SHAPE

Intralimb Proportions

Elongation of the distal limb segment relative to the proximal has been demonstrated to be associated with overall limb elongation in both the upper and lower limb (Meadows & Jantz, 1995), and is correlated with climatic variables (Roberts, 1978; Trinkaus, 1981). Distal limb segment elongation is typically quantified in the form of brachial (radius length/humeral length $\times 100$) and crural (tibial length/femoral length $\times 100$) indices. These skeletal measures are comparable to the anthropometric antebrachial index (forearm length/upper arm length $\times 100$) and calf/thigh index (calf length/thigh length $\times 100$), respectively, which are commonly taken on living people (Roberts, 1978).

Table 3 gives summary statistics for the brachial and crural indices of the Gough's Cave 1 specimen and fossil and recent human samples. Note that among the recent humans, the indices show a cline from lower to higher latitudes, with high indices in the former, and low indices in the latter. This is presumably the result of long-term climatic selection (discussed below). Within groups, male and female brachial and crural index values are similar (males do, however, tend to have higher brachial indices than females; Trinkaus, 1981; Holliday, 1995). Given the difficulty in assigning sex to some fossil specimens (as well as the already small size of the fossil sample), combined-sex means are given in Table 3. This does not affect the overall pattern, as will be evident below, when we discuss Gough Cave 1's relationship to other males from the comparative sample.

As is evident from Table 3, the Cheddar specimen, like other Late Pleistocene and early Holocene Europeans, has elongated distal limb segments in both the upper and lower limb. In fact, Gough's Cave 1 has indices not unlike the means of the recent African samples, and

Table 3 Summary statistics for Gough's Cave 1, fossil and recent human samples – brachial and crural indices.

	Brachial Index	Crural Index
Gough's Cave 1	77.1	88.9
European Mesolithic	77.5, 1.9, 10	85.5, 2.6, 10
European Late Upper Palaeolithic	78.6, 3.0, 17	85.1, 1.9, 22
European Early Upper Palaeolithic	77.9, 2.2, 17	85.4, 1.9, 13
European Neandertals	73.2, 2.5, 5	78.7, 1.6, 4
Recent Europeans	75.0, 2.5, 391	82.7, 2.4, 436
Recent North Africans	78.6, 2.4, 136	85.0, 2.3, 133
Recent Sub-Saharan	78.6, 2.8, 103	85.4, 2.4, 110

his crural index value actually falls above the Sub-Saharan African mean. It is not, however, too unusual to find a male European specimen today with a brachial index value equal to or higher than that of the Gough's Cave specimen; Gough's Cave 1 falls right on the 75th percentile for the recent European males ($n = 239$). However, his crural index would be extremely unusual in a sample of recent Europeans, since his value falls above the 99th percentile for recent European males ($n = 273$).

His values are not, however, unusual among European Mesolithic (nor Paleolithic) humans. His brachial index is virtually identical to the Mesolithic mean, and while his crural index is above the Mesolithic mean, one of the 10 Mesolithic specimens sampled (Téviec 11) has yet a higher crural index (89.1).

Limb/Trunk Proportions

The fact that limb/trunk proportions of modern humans covary with climate and geography has been documented for both skeletal (Holliday, 1995, 1997a) and anthropometric samples (via the relative sitting height index {sitting height/stature $\times 100$ }, Roberts, 1978). Given the largely complete (albeit poorly reconstructed) vertebral column of the Gough's Cave specimen, one can estimate skeletal trunk height (STH = summed dorsal vertebral elements T1-L5 + sacral ventral length; Franciscus & Holliday, 1992) as a body size or trunk length variable to which relative limb length may be assessed. As was done for the thoracic and lumbar vertebral column heights (Churchill & Holliday, 2002), STH is estimated from those vertebral elements preserved in Gough's Cave 1, using a least-squares regression for a complete recent human series ($n = 45$). The formula used is: $Y = 1.086x - 1.806$; $r^2 = 0.998$, where x (partial trunk height, or PTH) is the summed dorsal body heights for T4-L5, sacral ventral length, and the ventral body height of T1. The 'reconstruction' for display of the specimen necessitated further estimation. Thoracic vertebrae 6 and 7 were glued together with a mock intervertebral disk between them; thus their combined dorsal height was measured and the height of the intervening 'disk' (2.9 mm) was subtracted, yielding 39.8 as the estimate of combined T6-T7 dorsal height. The combined height of T8-T9 (42.5) and T11-T12 (48.1) were estimated in the same manner. The predictive equation based on the above measurements yields an STH of 483.9 mm, with a SE of the estimate of 1.6 mm. The 95% confidence limits for the prediction are 480.6–487.2 mm, a span which is only 1.4% of the prediction itself, indicating that STH can be accurately predicted in Gough's Cave 1.

As discussed in Churchill & Holliday (2002), the height of Cheddar Man's vertebral column (as reflected in thoracic and lumbar column heights) was short for a Mesolithic male. Thus, it is not surprising that the Gough's Cave specimen possesses a short STH, as well. The specimen's STH of 483.9 falls well below (although within one standard deviation of) the Mesolithic male mean of 511.6 ($n = 4$), and only one Mesolithic male, the diminutive Hoëdic 9, has a shorter trunk. However, the most important question that remains is how Gough's Cave 1 compares in terms of limb length relative to trunk height. In order to elucidate these patterns, limb segment length (maximum humeral, radius and tibial length and femoral bicondylar length) to trunk height ratios were computed for the comparative fossil and recent human sample, and are compared to Gough's Cave 1 in Tables 4 and 5. Sexual dimorphism in these traits exists, but is minimal (Holliday, 1995); thus, as was done with the brachial and crural indices, Gough's Cave 1 is compared to combined-sex samples. As was evident in intralimb proportions, among recent humans there is a clinal distribution of limb/trunk ratios, with Sub-Saharan Africans exhibiting the highest mean indices, the Europeans the lowest, and North Africans intermediate between the two groups.

Table 4 Summary statistics for Gough's Cave 1, fossil and recent human samples – upper limb segment/trunk height ratios.

	HL/STH	RL/STH
Gough's Cave 1	66.7	51.5
European Mesolithic	61.7, 3.7, 7	47.9, 2.7, 7
European Late Upper Palaeolithic	61.2, 2.8, 15	48.3, 2.4, 12
European Early Upper Palaeolithic	69.1, 4.0, 8	55.0, 2.7, 7
European Neandertals	64.0, 1.5, 3	47.0, 0.2, 3
Recent Europeans	63.6, 3.4, 124	47.9, 2.8, 123
Recent North Africans	66.0, 3.8, 62	51.9, 3.4, 62
Recent Sub-Saharans	69.6, 4.1, 51	55.0, 4.0, 51

Table 5 Summary statistics for Gough's Cave 1, fossil and recent human samples – lower limb segment/trunk height ratios.

	FL/STH	TL/STH
Gough's Cave 1	89.7	79.8
European Mesolithic	87.4, 3.9, 7	74.0, 4.0, 7
European Late Upper Palaeolithic	86.6, 3.4, 15	73.6, 3.5, 13
European Early Upper Palaeolithic	96.0, 5.1, 7	84.0, 4.6, 6
European Neandertals	89.1, 0.0, 2	71.2, 1.0, 2
Recent Europeans	88.6, 4.4, 123	73.6, 4.3, 124
Recent North Africans	94.2, 5.5, 63	79.8, 4.9, 60
Recent Sub-Saharans	97.7, 7.5, 51	84.1, 6.5, 51

For the upper limb/trunk height ratios (Table 4), Gough's Cave 1 differs not only from recent Europeans, but from Late Upper Paleolithic (LUP) Europeans, as well. In fact, relative to trunk height, the Cheddar specimen is somewhat long-armed, and is most similar to the recent North Africans in this regard. He is less long-armed, however, than the average recent Sub-Saharan African or European Early Upper Paleolithic (EUP) humans. While the distribution of sample means provides an overall pattern of differences, we may still ask how unusual would upper limb/trunk height ratios equal to or greater than that of Gough's Cave 1 be among recent Europeans? An examination of the male European distribution provides some insight. For the humeral length/trunk height ratio, he falls on the 75% percentile of recent European males, while for the radius length/trunk height ratio, he falls above the 85% percentile. Thus while he does exhibit a positive deviation from the mean, sampling a recent European male who shares his upper limb/trunk height (or greater) values could be as common as 1 in 4.

The lower limb/trunk height ratios reveal a slightly different pattern (Table 5). The Cheddar specimen's femoral length/trunk height ratio is very similar to the recent European mean, while his tibial length/trunk height ratio is 2.5 standard deviations above the recent European mean – indicating that he has an extremely long tibia relative to the height of his trunk. His percentile placement among the recent Europeans males reflects this dichotomy; he falls on their 60th percentile for the femoral length index, and above the 94th percentile for the tibial length index. With regard to the recent Africans, he falls below the Sub-Saharan African mean for both indices, and below the North African FL/STH mean. His TL/STH value, however, is identical to the North African average.

In comparison with other European fossils, Gough's Cave 1 possesses a relatively longer femur than the mean of all but one fossil sample (the long-limbed EUP), although he falls well within the range of all but the short-limbed Neandertal samples. His high relative tibial length index, however, is somewhat more unusual in the sense that he exceeds the range of the LUP sample, and, additionally, he evinces the highest TL/STH index of the Mesolithic sample. In fact, with regard to relative tibial length, among the fossil groups only the long-limbed EUP sample exceeds his value.

Body Linearity Relative to Mass

Another body shape feature known to covary with climate is relative body linearity. In living populations, the weight: height, or ponderal, index is used as a measure of this relationship (e.g., Newman, 1961; Schreider, 1964, 1975; Eveleth, 1966; Hiernaux *et al.*, 1975). This relationship is most easily quantified skeletally via relative femoral head size (i.e., antero-posterior femoral head diameter/femoral bicondylar length \times 100). This index should reflect relative linearity, since the femoral head is highly correlated with body mass, while femoral length is highly correlated with stature. This skeletal index was (not surprisingly) found to vary significantly between males and females, with males possessing relatively larger femoral heads than females (two-tailed *t* test, $p < 0.0001$), and thus Gough's Cave 1 is compared only to other males for this trait.

Table 6 reports the summary statistics for this trait among the comparative samples and the Cheddar specimen. Within the recent humans, there is a clear clinal pattern from Sub-Saharan Africa through North Africa and into Europe, such that the femoral head becomes relatively larger with increasing latitude (see also Ruff, 1994). With regard to fossil humans, note the extremely high indices exhibited by the male Neandertals. For this index, both Neandertal males (La Chapelle-aux-Saints 1 and La Ferrassie 1) fall beyond the 99th percentile of recent European males ($n = 134$). The other European fossils, including the Mesolithic males and the Gough's Cave 1 specimen himself are virtually identical to recent Europeans for this trait. Only the EUP sample slightly deviates from the European pattern of relatively large femoral heads; they are more similar to recent North Africans in that their femoral heads are somewhat smaller (although not as small as those of the Sub-Saharan Africans).

Body Breadth Relative to Stature

Bi-iliac breadth, or bi-cristal breadth, as it is sometimes called, is measured as the transverse diameter of the superior margin of the pelvic girdle. This raw measurement is correlated with climatic variables (Crogner, 1981; Ruff, 1994), but its fit with climate and/or geography significantly improves when it is scaled to a linear dimension of the body such as stature (Roberts, 1978; Ruff, 1991, 1993, 1994). For the samples presented here, stature is unknown, and therefore must be predicted from long bone length, e.g. femoral length. In such cases, then, predicted stature is each individual's femoral length subsequent to an arithmetic manipulation, (i.e., femoral length \times slope, + Y-intercept). Such prediction formulae inevitably introduce error into the analysis, however, since biologically speaking, many individuals are expected to fall well above or well below the predictive line. Thus, to avoid the introduction of further error, stature is not predicted for this analysis, but rather, femoral length (which is highly correlated with stature) is used in its stead.

The first means by which the body breadth to height relationship can be investigated is via the computation of ratios – in this case, bi-iliac breadth / femoral bicondylar length \times 100. Due to the fact that females have wider trunks relative to stature than do males, the values for this index are significantly different between the sexes (two-tailed *t* test, $p < 0.0001$), and therefore the Cheddar specimen is compared solely to males for this variable. Table 6 reports the summary statistics for the males in the comparative sample and the Cheddar specimen. Gough's Cave 1 lies well within 1 standard deviation of the Mesolithic, LUP and recent European male means. Likewise, his value is only 1.4 standard deviations above the North African mean. However, he falls over 3 standard deviations above the recent Sub-Saharan African mean; as discussed below, this group is characterized by some of the longest limbs and narrowest trunks of

Table 6 Summary statistics for Gough's Cave 1, fossil and recent human males – femoral head/femoral length ratios (FHAP/FL) and bi-iliac breadth/femoral length ratios (BIB/FL).

	FHAP/FL	BIB/FL
Gough's Cave 1	10.7	63.3
European Mesolithic	10.7, 0.5, 6	62.1, 3.2, 6
European Late Upper Palaeolithic	10.8, 0.7, 15	61.2, 5.1, 10
European Early Upper Palaeolithic	10.1, 0.4, 10	56.6, 3.2, 6
European Neandertals	12.3, 0.4, 4	69.8, –, 1
Recent Europeans	10.6, 0.5, 134	61.2, 3.4, 126
Recent North Africans	9.9, 0.6, 72	57.3, 4.4, 60
Recent Sub-Saharans	9.5, 0.6, 53	52.6, 3.0, 49

any humans. Interestingly, while based on extremely small samples, the earlier European fossil samples stand in marked contrast to each other and to recent Europeans. The Neandertals (albeit solely represented by the La Chapelle-aux-Saints 1 specimen) are characterized by an extremely high index, indicative of their broad body breadth relative to stature (Ruff, 1991, 1993, 1994; Trinkaus *et al.*, 1994). By way of contrast, the earliest modern European males (represented by 6 individuals) have low indices; in fact, their mean index falls between those of the North and Sub-Saharan Africans.

A second means of evaluating relative body breadth has been used extensively by Ruff (1991, 1993, 1994), and involves plotting relative bi-iliac breadth indices, like those calculated above, against stature in bivariate space. Using this method, one can evaluate the relationship between the 'size-corrected' index and a measure of overall size (in Ruff's case, stature; here again, femoral length is used in its stead). Ruff has shown that among recent humans, there is little overlap among broad geographically circumscribed samples for this bivariate relationship, and thus this method could provide some insight into the relative position of the Cheddar specimen. Figure 1 is a scatter plot of the bi-iliac breadth/femoral length ratios regressed on femoral length for the recent Sub-Saharan Africans (squares), the recent Europeans (crosses) and Gough's Cave 1 (star). The lines fitted to the recent samples are least-squares regression

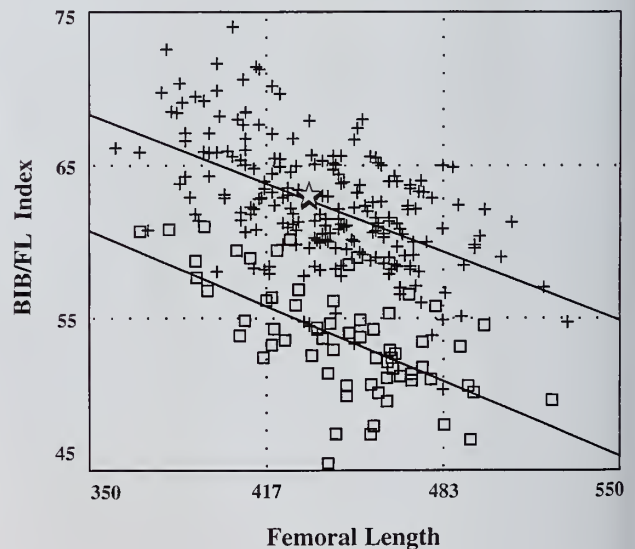


Fig. 1 Scatter plot of bi-iliac breadth/femoral length index on femoral length. Recent Europeans are indicated by crosses; recent Sub-Saharan Africans by squares. Gough's Cave 1 is indicated by a star. The lines for the two recent human samples are least-squares regression lines.

lines. As Ruff has found, there is good separation of the Europeans from the Sub-Saharan Africans throughout most of the size range. Informatively, Gough's Cave 1 falls squarely on the European regression line, far above the Sub-Saharan African line.

Multivariate Assessment of Body Shape

Any assessment of an individual's body size and proportions is at its base an assessment of that individual's total morphological pattern. While the individual analyses presented above when considered as a whole provide tantalizing clues as to the total morphological pattern of the Cheddar Man, these analyses are likely not as informative as would be a multivariate assessment based on the same morphological variables. In fact, a multivariate analysis may be expected to resolve some of the conflicting results obtained above. For example, in relative body linearity, relative body breadth and limb/trunk (excepting the tibia) proportions, the Gough's Cave specimen looks essentially like a recent European (albeit occasionally at the more linear end of the European range). In contrast, his tibia/trunk, brachial, and especially his crural index are more similar to those of more tropically-adapted groups (e.g., Africans).

What then, is the total morphological pattern of body size and shape exhibited by Gough's Cave 1? The way to discover this is to investigate overall body proportions in multivariate space, taking the variances and covariances of all the skeletal manifestations of body shape into account. Once this is done, Gough's Cave 1 will either continue to fall among recent Europeans, or he could possibly exhibit a somewhat different, more tropically-adapted pattern.

The variables to be used in the multivariate analysis and their abbreviations are found in Table 7. Note that these measurements are the same variables used to compute ratios and/or which were plotted in bivariate space. They should therefore provide an accurate reflection of total body shape. The method chosen for body shape extraction is that outlined by Mosimann and colleagues (Mosimann & James, 1979; Darroch & Mosimann, 1985; James & McCulloch, 1990). These morphometricians argue that an individual's overall size is best represented by the geometric mean of all the measurements taken on that individual. The geometric mean (or 'log size' as the authors denominate it) can then be used to create scale-free ratios, or 'shape' variables, between each of the individual's measurements and his geometric mean. The utility of the shape variables lies not in the 'removal' of size *per se*, but in the ability of the researcher to determine if there is a relationship between size and shape via correlation analyses. The application of this method to anthropological data sets is discussed in greater detail elsewhere (e.g., Falsetti *et al.*, 1993; Jungers *et al.*, 1995). In this study, since the primary interest is the body shape of Cheddar Man, discussion is limited to the analysis of shape variables. The variance-covariance matrix (VCM) of the shape variables for a combined sample of fossil and

Table 7 First two principal components of shape variables – fossil and recent humans.

	Eigenvector Coefficient	
	I	II
Femoral A-P head diameter (FHAP)	0.305	-0.860
Bi-iliac breadth (BIB)	0.591	0.451
Femoral bicondylar length (FL)	-0.246	0.070
Humeral maximum length (HL)	-0.178	0.037
Tibial maximum length (TL)	-0.404	0.124
Radius maximum length (RL)	-0.421	-0.009
Skeletal trunk height (STH)	0.591	0.187
Eigenvalue	0.0094	0.0032
% total variance	58.25	19.63

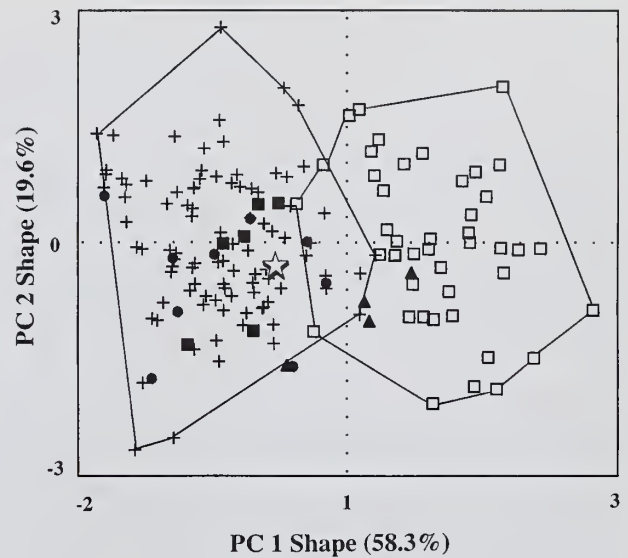


Fig. 2 Scatter plot of PC2 on PC1 (shape data). Crosses are recent Europeans, open squares are recent Sub-Saharan Africans, triangles are Early Upper Paleolithic, circles are Late Upper Paleolithic, closed squares are Mesolithic, star is Gough's Cave 1. Lines indicate range of the recent human samples.

recent humans ($n = 225$), all of whom preserve the measurements in question, was computed and then subjected to principal components analysis (PCA).

The eigenvector coefficients and eigenvalues for the first two principal components of the log shape data are found in Table 7. The first principal component (PC1) accounts for 58.3% of the total shape variance, and contrasts limb segment length (particularly the distal segments) with femoral head diameter, bi-iliac breadth and skeletal trunk height. The PC scores along this axis are not significantly correlated with overall size (i.e., the geometric mean; $r^2 = 0.008$, $p = 0.1758$). PC1 is readily interpreted as a climatic adaptation component, since it separates heavier, less linear individuals (more cold-adapted) from lighter, more linear individuals (more heat-adapted). The second principal component (PC2) accounts for 19.6% of the shape variance and contrasts bi-iliac breadth and trunk height with femoral head diameter. The scores along this axis are correlated with log size ($r^2 = 0.18$, $p < 0.0001$), and this component tends to segregate males (who on average have large femoral heads and relatively narrow pelvises) from the small femoral-head possessing and wider hip bearing females (albeit with considerable overlap).

Component scores for the European early modern fossils (including Gough's Cave 1), as well as the recent Sub-Saharan Africans and recent Europeans are plotted in Figure 2. Note that the separation of the groups is along the first principal axis. This axis contrasts individuals on the left, who possess short distal limbs, wide and relatively long trunks, and large femoral heads from those individuals on the right, who are characterized by relatively short and narrow trunks, long distal limb segments and smaller femoral heads. There is no separation of the groups (fossil or recent) along the second principal axis. Note that for the first principal component, there is relatively little overlap between the recent Sub-Saharan Africans (represented by open squares) and the recent Europeans (represented by crosses). Gough's Cave 1 (the star) and his contemporaries, the European Mesolithic specimens (indicated by dark squares) fall clearly among the recent Europeans, as do the LUP specimens

(indicated by circles). Only 2 of the 9 (22%) LUP specimens (Barma Grande 2 and Bichon 1) even fall in the region of overlap between the recent Sub-Saharan Africans and Europeans, and none of the Mesolithic sample does. In contrast, there is a tendency for the EUP specimens (indicated by triangles) to fall among the Sub-Saharan Africans and outside of the European sample range. This specific result is said to be indicative of a relatively recent African origin for the earliest modern Europeans, and is discussed in detail elsewhere (Holliday, 1995, 1997a). What is of most interest to this chapter is that the Gough's Cave specimen, despite possessing some 'non-typically' European traits, falls squarely among the Europeans in multivariate space, albeit toward the more linearly-built end of the distribution.

Discussion

Gough's Cave 1 is relatively unremarkable with regard to stature and body mass; he is small, yet similar to all European samples, save the heavier Neandertals. However, his body shape poses some interesting contrasts which need to be further explored. Among recent humans, clear differences in body shape manifest themselves among geographically-dispersed samples. In terms of relative sitting height, for example, some Australian Aboriginal and Sub-Saharan African groups evince mean relative sitting height indices as low as 47.0, while at the other extreme, many Inuit (Eskimo) samples evince mean indices of around 54.0 (Eveleth & Tanner, 1976). What this means is that among some of the more tropically-adapted groups worldwide, the head, neck and trunk comprise less than half (ca. 47% or less) of a person's stature. Yet another way of looking at this is that among these groups, the lower limb accounts for more than half (ca. 53+%) of a person's standing height. By way of contrast, among the Inuit and other cold-adapted groups, the head, neck and trunk make up well over half (ca. 54+%) of the average person's height, while the lower limbs make up considerably less than half (ca. 46% or less).

The explanation for empirical patterns such as the above is that they are due to climatic selection, and more specifically, reflect the adherence of recent humans to the ecological 'rules' of Bergmann (1847) and Allen (1877). These rules state that within a widespread species of warm-blooded animals, those in colder regions will tend to be heavier (Bergmann's rule) and evince shorter extremities (Allen's rule) than do their more tropical conspecifics. Theoretically, it is argued that we find this pattern because animals in cold regions minimize their surface area: volume ratio (SA:V) in order to better conserve body heat, since heat loss occurs through the skin (i.e., the animal's surface). On the other hand, heat loss in hot environments may be facilitated by increasing relative surface area. Changes in body size and shape can drastically affect the SA:V ratio, as discussed in Ruff (1994) and Holliday (1995).

But do these rules apply to fossil humans as well, or is this an over-extension of biological uniformitarianism? Limited fossil data suggest that prehistoric human populations were characterized by ecogeographical clines that were perhaps even steeper than those one finds today (Trinkaus, 1981, 1991; Stringer, 1989; Ruff, 1991, 1993, 1994). For example, the Kenyan Nariokotome *Homo erectus* skeleton (KNM-WT 15000) is said to be characterized by 'hyper-African' body proportions (Ruff and Walker, 1993), while European Neandertals are characterized by an extremely cold-adapted morphology (Trinkaus, 1981, 1986; Holliday, 1995, 1997b; Churchill, 1998).

How do the Gough's Cave 1 specimen and his contemporaries fit into this apparently climatically-driven geographical patterning? In order to address this question adequately, we must have at least some understanding of what the pattern in Europe was *before* the early

Holocene, i.e., what was the temporal pattern of body proportions in the European Pleistocene? In other words, were there temporal trends in body shape during this time period? The answer is an emphatic 'yes'. There is actually more *temporal* variability in body shape in Pleistocene Europe than there is *spatial* variability in the world today.

We begin with the European Neandertals. They exhibit a clearly cold-adapted physique, including low brachial and crural indices, low limb/trunk ratios, extremely large femoral heads and wide trunks. Those who succeed them in the region, however, hominins differentially referred to as the 'Cro-Magnons' or the Early Upper Paleolithic (EUP) humans, exhibit the opposite pattern – high brachial and crural indices, high limb/trunk proportions, *relatively* smaller femoral heads and narrower trunks. Succeeding the Cro-Magnons are the Late Upper Paleolithic (LUP), and subsequent Mesolithic populations. These later two samples have, in this analysis, been divided at the Pleistocene/Holocene boundary, with the Mesolithic sample (including Gough's Cave 1) being restricted to the latter epoch. This division may be biologically insignificant, however, since for virtually all analyses – univariate, bivariate or multivariate, the LUP and Mesolithic samples more closely resemble each other than they do any other group, fossil or recent (see also Holliday, 1995, 1997a).

Combined or separate, the real question of interest is what was the pattern of body shape in LUP and Mesolithic humans? Importantly, the 'shared' morphology of these two samples (including the specimen of interest) is in some regards paradoxical (Holliday, 1999). Late Upper Paleolithic and Mesolithic specimens retain the high brachial and crural indices of their presumed ancestors, the 'Cro-Magnons'. Yet unlike the Cro-Magnons, they tend not to possess relatively narrow trunks, relatively small femoral heads, or high limb/trunk ratios. Gough's Cave 1, as a general rule, follows this pattern. Like his contemporaries, his brachial and crural indices are near the upper extreme of the recent European sample. Likewise, as with others from his time period, his limb/trunk proportions are within the European range, although his values for HL/STH, RL/STH and particularly his TL/STH indices are somewhat more extreme than those of average Europeans today. Recall that he falls on the 75th, 85th and 94th percentiles, respectively, of the recent European male sample for these traits. For the other traits (relative femoral head size and relative body breadth), however, he falls very near the recent European mean, and is distinctly different from recent Africans. In multivariate space, however, he lies within the European scatter, and beyond the range of recent Sub-Saharan Africans, as do his Mesolithic contemporaries and the majority of the LUP sample. By way of contrast, the EUP sample tends to cluster more closely with the recent Africans.

Both in scientific articles (Framer, 1992; Framer *et al.*, 1993) and the popular press (Shreeve, 1995), it has been pointed out that the retention of high brachial and crural indices among Late Upper Paleolithic and Mesolithic humans is problematic for Trinkaus' (1981) argument that these indices reflect elevated gene flow (or population dispersal) from Africa associated with the origins of modern humans. After all, these workers argue, the glacial cold of Europe should have modified, at least by the end of the Pleistocene, any previously incoming population toward a more cold-adapted morphology. Yet with regard to brachial and crural indices, the LUP sample have an even more extreme (almost 'hyper-tropical') morphology than their EUP forebears.

As pointed out in Holliday (1999), this argument shows the problems that can arise when single traits are studied in isolation¹. In

¹We can, for the sake of argument, consider the brachial and crural indices a single trait, since they tend to covary, and are likely influenced by the same gene complexes. Likewise, they are almost certainly influenced by the same environmental factors.

the modern world, high brachial and crural indices tend to be associated with longer limbs. Not only have Trinkaus (1981) and Meadows & Jantz (1995) documented this, but Roberts' (1978) relative forearm index (the anthropometric equivalent of the brachial index) is also positively associated with temperature, and thus tends to be found in absolutely longer-limbed groups. However, while the association between these indices and limb length is a very real one, there remains much variability in these features (Holliday, 1999). For example, among the global sample of recent humans used for this analysis, correlations between the brachial index and total arm length (humeral length + radius length), and between the crural index and total lower limb length (femoral + tibial length) are significant, but are not particularly high (for the former relationship, $r = 0.12$, $p = 0.0036$, $n = 631$; for the latter, $r = 0.15$, $p = 0.0001$, $n = 680$). Thus, while there is a clear tendency among recent humans for brachial and crural indices to increase with overall limb length, there is also considerable variability in limb length, and how that length is distributed between the proximal and distal segments (and see Holliday & Ruff, 2001). As a result, there is much overlap in distal limb segment length proportions among individuals from broad geographic regions (Holliday, 1999).

Nevertheless, when the brachial indices of recent Europeans are compared to Mesolithic and Late Upper Paleolithic samples, two-tailed t tests detect significant differences between the recent and fossil Europeans (Mesolithic vs. Recent, $p = 0.004$; LUP vs. Recent, $p = 0.0002$). The crural index yields similarly significant differences (Mesolithic vs. Recent, $p = 0.01$; LUP vs. Recent, $p < 0.0001$). It is difficult to imagine that these differences are due to mere sampling error in the fossil record.

Thus, we are faced with a dichotomy. In multivariate analyses of shape, Mesolithic and LUP samples (unlike their EUP forebears) cluster among recent Europeans, yet their brachial and crural indices are significantly higher. Importantly, however, this does not mean that their limbs are long. In fact, while brachial and crural indices remained elevated from the EUP through the Mesolithic, total limb length *reduced* (Frayer, 1980, 1981, 1984, 1992; Jacobs, 1983, 1985; Holliday, 1995, 1999).

What, therefore, do the high brachial and crural indices of the Late Upper Paleolithic and Mesolithic humans, including Gough's Cave 1, mean? As argued in Holliday (1999), this is a clear example of mosaic evolution. It seems likely that climatic selection due to the glacial cold of Europe modified what had been a more tropically-adapted physique into a more cold-adapted one. Yet selection acted more or less equally on both the proximal and distal limb segments, leaving the later humans with shorter limbs (and thus better adapted to the cold), but permitting them to retain their relatively long distal limb segments².

Whether some other type of selection was maintaining these high ratios in spite of overall reduction in limb length, or whether they were selectively neutral is uncertain. The most likely conclusion is that the brachial and crural indices are genetic markers linking the Late Upper Paleolithic and Mesolithic populations to their 'Cro-Magnon' forebears. The logical extension of this argument is that contra Frayer (1992) and Frayer *et al.* (1993), these indices are, as Trinkaus (1981) first posited, indicative of African genes in the early modern Europeans.

In sum, while the total morphological pattern of the Cheddar Man's body proportions is European-like, it is those features for which he differs from the modern European condition that are of the

most interest. Specifically, it seems likely that his high brachial, crural indices, and TL/STH indices, reflective of relatively longer distal limb segments, are a retention from an earlier, largely African gene pool – a retention no longer seen in Europe today.

REFERENCES

- Allen, J.A. 1877. The influence of physical conditions in the genesis of species. *Radical Review*, 1: 108–140.
- Bergmann, C. 1847. Ueber die Verhältnisse der Warmeökonomie der thiere zu ihrer grosse. *Göttinger Studien*, 3: 595–708.
- Churchill, S.E. 1998. Cold adaptation, heterochrony, and Neandertals. *Evolutionary Anthropology*, 7: 46–61.
- & Holliday, T.W. 2002. Gough's Cave 1 (Somerset, England): A study of the axial skeleton. *Bulletin of the Natural History Museum London (Geology)*, 58: 1–11.
- Crognier, E. 1981. Climate and anthropometric variations in Europe and the Mediterranean area. *Annals of Human Biology*, 8: 99–107.
- Darroch, J.N. & Mosimann J.E. 1985. Canonical and principal components of shape. *Biometrika*, 72: 241–252.
- Eveleth, P.B. 1966. The effects of climate on growth. *Annals of the New York Academy of Science*, 134: 750–759.
- & Tanner, J.M. 1976. *Worldwide Variation in Human Growth*. International Biological Programme 8. Cambridge.
- Falsetti, A.B., Jungers, W.L. & Cole, T.M., III. 1993. Morphometrics of the callitrichid forelimb: A case study in size and shape. *International Journal of Primatology*, 14: 551–572.
- Formicola, V. & Giannecchini, M. 1999. Evolutionary trends of stature in Upper Paleolithic and Mesolithic Europe. *Journal of Human Evolution*, 36: 319–333.
- Franciscus, R.G. & Holliday, T.W. 1992. Hindlimb skeletal allometry in Plio-Pleistocene hominids with special reference to AL-288-1 ('Lucy'). *Bulletins et Mémoires de la Société d'Anthropologie de Paris*, n.s. 4, série 22: 1–16.
- Frayer, D.W. 1980. Sexual dimorphism and cultural evolution in the late Pleistocene and Holocene of Europe. *Journal of Human Evolution*, 9: 399–415.
- 1981. Body size, weapon use, and natural selection in the European Upper Paleolithic and Mesolithic. *American Anthropologist*, 83: 57–73.
- 1984. Biological and cultural changes in the European Late Pleistocene and Early Holocene. In: FH Smith & F Spencer (eds), *The Origins of Modern Humans: A World Survey of the Fossil Evidence*. New York, pp. 211–250.
- 1992. Evolution at the European edge: Neanderthal and Upper Paleolithic relationships. *Préhistoire Européenne*, 2: 9–69.
- , Wolpoff, M.H., Thorne, A.G., Smith, F.H. & Pope, G.G. 1993. Theories of modern human origins: The paleontological test. *American Anthropologist*, 95: 14–50.
- Geddes, D., Barbaza, M., Vaquer, J. & Guilaine, J. 1986. Tardiglacial and Postglacial in the eastern Pyrenees and western Languedoc (France). In: L.G. Straus (ed), *The End of the Paleolithic in the Old World*. BAR International Series 284. Oxford.
- Hiernaux, J., Rudan, P. & Brambati, A. 1975. Climate and the weight/height relationship in sub-Saharan Africa. *Annals of Human Biology*, 2: 3–12.
- Holliday, T.W. 1995. *Body Size and Proportions in the Late Pleistocene Western Old World and the Origins of Modern Humans*. Ph.D. thesis, University of New Mexico.
- 1997a. Body proportions in Late Pleistocene Europe and modern human origins. *Journal of Human Evolution*, 32: 423–448.
- 1997b. Postcranial evidence of cold adaptation in European Neandertals. *American Journal of Physical Anthropology*, 104: 245–258.
- 1999. Brachial and crural indices of European Late Upper Paleolithic and Mesolithic humans. *Journal of Human Evolution*, 36: 549–566.
- & Ruff, C.B. 2001. Relative variation in human proximal and distal limb segment lengths. *American Journal of Physical Anthropology*, 116: 26–33.
- Jacobs, K.H. 1983. *Hominid Body Size, Body Proportions, and Sexual Dimorphism in the European Upper Paleolithic and Mesolithic*. Ph.D. Dissertation, University of Massachusetts, Amherst.
- 1985. Evolution in the postcranial skeleton of late Glacial and early Postglacial European hominids. *Zeitschrift für Morphologie und Anthropologie*, 75: 307–326.
- James, F.C. & McCulloch, C.E. 1990. Multivariate statistical methods in ecology and systematics: Panacea or Pandora's box. *Annual Review of Ecology and Systematics*, 21: 129–166.
- Jungers W.L., Falsetti, A.B., & Wall, C.E. 1995. Shape, relative size and size-adjustments in morphometrics. *Yearbook of Physical Anthropology*, 38: 137–161.
- Meadows, L. & Jantz, R.L. 1995. Allometric secular change in the long bones from the 1800s to the present. *Journal of Forensic Sciences* 40: 762–767.
- Mosimann, J.E. & James, F.C. 1979. New statistical methods for allometry with application to Florida Red-winged Blackbirds. *Evolution*, 33: 444–459.
- Newman, M.T. 1961. Biological adaptation of man to his environment: heat, cold, altitude, and nutrition. *Annals of the New York Academy of Science*, 91: 617–633.
- Roberts, D.F. 1978. *Climate and Human Variability*. 2nd edition. Menlo Park.

²At least over the time period observed – at some point, apparently subsequent to the Mesolithic, European brachial and crural indices decreased to approximate the condition seen today.

- Ruff, C.B. 1991. Climate and body shape in hominid evolution. *Journal of Human Evolution*, **21**: 81–105.
- 1993. Climatic adaptation and hominid evolution: The thermoregulatory imperative. *Evolutionary Anthropology*, **2**: 53–60.
- 1994. Morphological adaptation to climate in modern and fossil hominids. *Yearbook of Physical Anthropology*, **37**: 65–107.
- , Trinkaus, E. & Holliday, T.W. 1997. Body mass and encephalization in Pleistocene *Homo*. *Nature*, **387**: 173–176.
- & Walker, A. 1993. Body size and body shape. In: A. Walker & R. Leakey (eds), *The Nariokotome Homo erectus Skeleton*. Cambridge, MA, pp. 234–265.
- Schreider, E. 1964. Ecological rules, body-heat regulation, and human evolution. *Evolution*, **18**: 1–9.
- 1975. Morphological variations and climatic differences. *Journal of Human Evolution*, **4**: 529–539.
- Shreeve, J. 1995. *The Neandertal Enigma: Solving the Mystery of Modern Human Origins*. New York.
- Straus, L.G., Clark, G.A., Altuna, J. & Ortea, J.A. 1980. Ice-Age subsistence in northern Spain. *Scientific American*, **242**: 142–152.
- Stringer, C.B. 1989. Documenting the origin of modern humans. In: E. Trinkaus (ed) *The Emergence of Modern Humans: Biocultural Adaptations in the Later Pleistocene*. Cambridge, pp. 67–96.
- Trinkaus, E. 1981. Neanderthal limb proportions and cold adaptation. In: C.B. Stringer (ed), *Aspects of Human Evolution*. London, pp. 187–224.
- 1986. The Neandertals and modern human origins. *Annual Review of Anthropology*, **15**: 193–218.
- 1991. Les hommes fossiles de la Grotte de Shanidar, Irak: Evolution et continuité parmi les hommes archaïques tardifs du Proche-Orient. *L'Anthropologie*, **95**: 535–572.
- , Churchill, S.E. & Ruff, C.B. 1994. Postcranial robusticity in *Homo*, II: Humeral bilateral asymmetry and bone plasticity. *American Journal of Physical Anthropology*, **93**: 1–34.
- Trotter, M. & Gleser, G.G. 1958. A re-evaluation of estimation of stature based on measurements of stature taken during life and of long bones after death. *American Journal of Physical Anthropology*, n.s. **16**: 79–123.