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Body mass and encephalization in Pleistocene *Homo*

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Many dramatic changes in morphology within the genus *Homo* have occurred over the past 2 million years or more, including large increases in absolute brain size and decreases in postcanine dental size and skeletal robusticity. Body mass, as the 'size' variable against which other morphological features are usually judged, has been important for assessing these changes[1–5]. Yet past body mass estimates for Pleistocene *Homo* have varied greatly, sometimes by as much as 50% for the same individuals[2,3,6–12]. Here we show that two independent methods of body-mass estimation yield concordant results when applied to Pleistocene *Homo* specimens. On the basis of an analysis of 163 individuals, body mass in Pleistocene *Homo* averaged significantly (about 10%) larger than a representative sample of living humans. Relative to body mass, brain mass in late archaic *H. sapiens* (Neanderthals) was slightly smaller than in early 'anatomically modern' humans, but the major increase in encephalization within *Homo* occurred earlier during the Middle Pleistocene (600–150 thousand years before present (kyr BP)), preceded by a long period of stasis extending through the Early Pleistocene (1,800 kyr BP).

It is generally acknowledged, even by those who have used other methods, that the best means of estimating body mass from skeletal or fossil remains, when feasible, is to use features that have some direct functional relationship to body mass[9,11,12]. For hominids, the skeletal dimensions used most often have been lower limb long bone diaphyseal and articular breadths[2,3,6,7,9]. Diaphyseal breadths of fossil hominids are problematic as body mass estimators because relative to body size they are systematically larger than modern humans, probably as a response to increased mechanical loading[5]. In contrast, articulations are much less environmentally sensitive[13,14], and thus are potentially better body-size indicators. The articular dimension used here as a body-mass estimator is femoral head breadth because it is available for many fossil *Homo* specimens, is easily measured and highly reproducible, and because several investigators have provided information on the relationship between femoral head breadth and body mass in modern humans[6,13,15] (see Methods).

The second method used here to estimate body mass does not rely on any assumptions about the mechanical relationship between a particular skeletal feature and body size (support of body weight). Rather, in this approach body mass is estimated directly from reconstructed stature and body breadth. A modern worldwide anthropometric sampling of 56 population/sex-specific means[16] was used to derive multiple regressions of body mass on stature and bi-iliac (maximum pelvic) breadth (Methods).

Figure 1 compares femoral head and stature/bi-iliac estimates of body mass for 75 Pleistocene *Homo* specimens. The mean absolute difference between estimates is about 5 kg (7.6%), and the mean directional difference is less than 1 kg (1.1%). Paired t-tests between results are not significant ($P \geq 0.30$). Thus, equations based on femoral head size and stature/bi-iliac breadth yield similar body mass estimates when applied to Pleistocene *Homo*, with very little systematic bias. Because the two techniques are based on different rationales and skeletal dimensions, yet nevertheless converge on the same result, this increases confidence in both.

Skeletal dimensions for 163 Pleistocene *Homo* specimens, dated 10–1,950 kyr BP, were derived from previously published sources and personal measurements[5,10,17]. Most regions of the Old World (except Australia) are represented, although the majority of the sample is from Europe (55%), with the remainder from Africa (27%), western Asia (15%) and eastern Asia (3%). (Data for individual specimens are given in Supplementary Information.) The resulting body mass estimates are shown in Fig. 2a, together with 51 sex/population-specific means for a worldwide sampling of living humans (ref. 16, excluding five Pygmy data points). More than three-quarters (125/163) of the Pleistocene specimens fall above the living human mean. On average, Pleistocene specimens are 7.4 kg larger (mean ± s.e., 65.6 ± 0.7 kg) than living humans (58.2 ± 1.0 kg), a highly significant 12.7% difference in body mass ($P < 0.0001$, t-test).

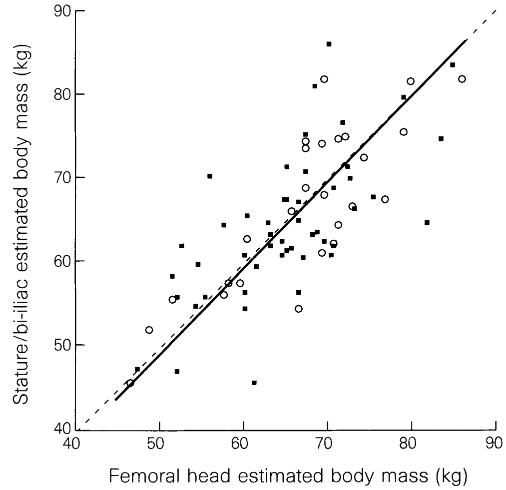

Figure 1 Comparison between body mass estimated from stature and bi-iliac breadth, and body mass estimated from femoral head breadth in 75 Pleistocene *Homo* specimens. Empty symbols, measured bi-iliac breadth; filled symbols, estimated bi-iliac breadth. Solid line, reduced major axis regression ($y = 1.04 \times x - 3.4$; $r = 0.738$). Dotted line indicates equivalence of y and x.

There is some indication in Fig. 2a that body mass is lower in the Early Pleistocene and rises to peak values in the Late Pleistocene. However, this is largely an artefact of two confounding variables: sex

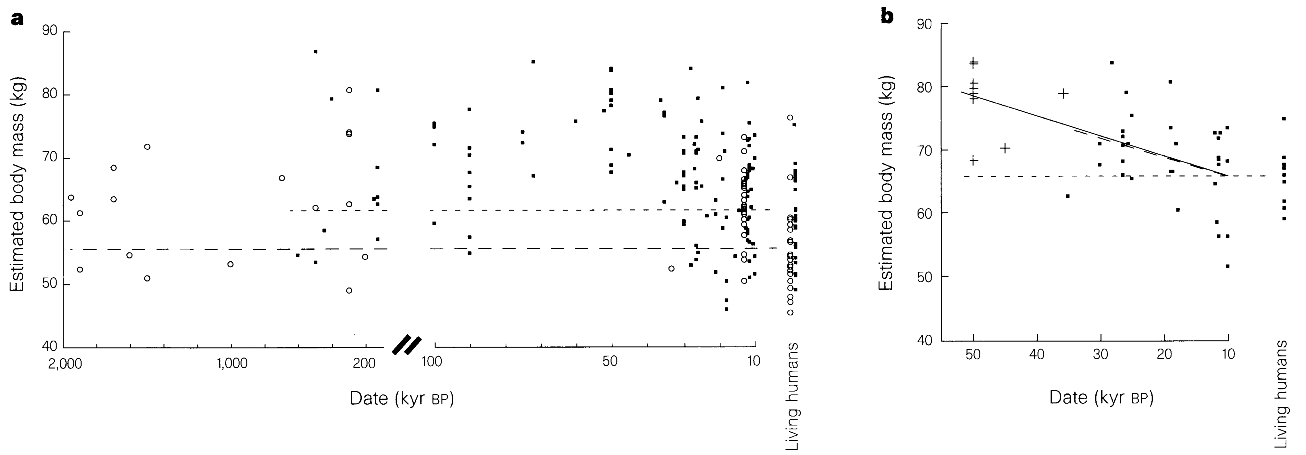

Figure 2 Changes through time in body mass of *Homo*. **a**, Total sample. Empty symbols, lower latitude (<30° N) (dashed line through living mean); closed symbols, higher latitude (dotted line through living mean). Note change in temporal (x) axis scale at 100 kyr BP. **b**, Higher-latitude males. Crosses, archaic *H. sapiens*; squares, early anatomically modern (EAM) and living *H. sapiens* (dotted line through living mean). Solid line, least-squares regression through total Pleistocene sample ($y = 0.318 \times x + 62.6$; $r = 0.582$); dashed line, least-squares regression through EAM sample ($y = 0.299 \times x + 62.9$; $r = 0.334$).

Table 1 Body-mass and brain-mass data

Sample	Temporal range (kyr BP)	Body mass (kg)* (mean ± s.e. (n))	Cranial capacity (cc)† (mean ± s.e. (n))	Brain mass (g)‡ (mean ± s.e. (n))	Encephalization quotient‡ Associated specimens (mean ± s.e. (n))	Encephalization quotient‡ Sample means (mean)
Living worldwide	–	58.2 ± 1.0 (51)	1,349	1,302	–	5.288
Pecos Pueblo	–	55.5 ± 1.2 (29)	1,308 ± 23 (29)	1,263 ± 22 (29)	5.349 ± .103 (29)	–
Late Upper Paleolithic	10–21	62.9 ± .9 (71)	1,466 ± 35 (23)	1,412 ± 33 (23)	5.479 ± .083 (18)	5.406
Early Upper Paleolithic	21–35	66.6 ± 1.3 (33)	1,517 ± 30 (15)	1,460 ± 28 (15)	5.467 ± .142 (10)	5.352
Late archaic *H. sapiens*	36–75	76.0 ± 1.4 (17)	1,498 ± 45 (14)	1,442 ± 42 (14)	4.984 ± .165 (8)	4.781
Skhul-Qafzeh	90	66.6 ± 2.2 (10)	1,501 ± 45 (6)	1,444 ± 42 (6)	5.369 ± .083 (4)	5.293
early Late Pleistocene	100–150	67.7 ± 2.4 (10)	1,354 ± 41 (8)	1,307 ± 39 (8)	4.682 (1)	4.732
late Middle Pleistocene	200–300	65.6 ± 5.1 (6)	1,186 ± 32 (17)	1,148 ± 30 (17)	–	4.257
middle Middle Pleistocene	400–550	67.9 ± 6.4 (5)	1,090 ± 38 (12)	1,057 ± 36 (12)	–	3.818
late Early to early Middle Pleistocene	600–1,150	58.0 ± 4.3 (3)	856 ± 52 (7)	835 ± 50 (7)	–	3.400
Early Pleistocene	1,200–1,800	61.8 ± 4.0 (5)	914 ± 45 (5)	890 ± 43 (5)	3.064 (1)	3.458

* Data from Fig. 2, except that Early Pleistocene sample does not include earliest (pre-1,800 kyr BP) specimens (see text). Pecos Pueblo body weights from femoral head and bi-iliac/stature formulae.

† Average cranial capacity for living worldwide sample from Beals *et al.*[29]; Pecos Pueblo cranial capacities from Hooton's original grave cards[30]; Pleistocene *Homo* cranial capacities from the literature and personal measurement.

‡ See Methods for derivation of brain mass from cranial capacity, and encephalization quotient.

and geography. Modern and fossil *Homo* males are larger than females, and there is a bias towards males in our Late Pleistocene sample (72 of 114 sexable specimens). Ecogeographic patterning in body mass has been demonstrated in modern humans, with populations from higher latitudes being larger on average than those from lower latitudes[16]. The same is true for Pleistocene *Homo*: in our sample specimens from over 30° N latitude are significantly larger than those from under 30° N latitude (ANCOVA, controlling for sex and date, $P < 0.005$). All of the Pleistocene *Homo* specimens included here and dated before 600 kyr BP are from tropical regions (Fig. 2a). The apparent sudden increase in average body mass during the later Middle Pleistocene is largely a result of the inclusion of higher-latitude specimens beginning during this time period. If the effects of latitude and sex are controlled through ANCOVA, the pooled Pleistocene *Homo* sample is still 9.2% larger on average than living humans ($P < 0.0001$).

Body mass appears to decline after about 50 kyr BP. Figure 2b shows that within higher-latitude (>30° N) males there is a significant decrease (16%, $P < 0.0001$) in average body mass between 50 and 10 kyr BP. The trend is very similar whether or not archaic *Homo sapiens* (Neanderthals) are included. By the Terminal Pleistocene (10–15 kyr BP) body mass is not significantly different from that of living higher-latitude males (0.3% difference). The same is also true of higher-latitude females (3.7% difference). However, lower-latitude Terminal Pleistocene males and females are still significantly larger (11–12%, $P < 0.01$) than lower-latitude living samples.

The body-mass data are paired with cranial capacity and brain-mass data in Table 1, temporally subdivided within the Pleistocene. Because of uncertainty regarding the cranial–postcranial affinities of very early *Homo*[18], only specimens dated to 1,800 kyr BP or later are included in this analysis. (All individual cranial data are listed in Supplementary Information.)

Early to early Middle Pleistocene (1,800–600 kyr BP) *Homo* was about one-third less encephalized than Recent humans, and there was no increase in encephalization quotient (EQ) throughout this time period (Table 1). By the early Late Pleistocene (150–100 kyr BP), EQ had increased to values within about 10% of those of Recent humans. However, early Late Pleistocene and late archaic *H. sapiens* are significantly lower in EQ than pooled 'early anatomically modern' (EAM) *H. sapiens* (Skhul-Qafzeh and Upper Palaeolithic samples) ($P < 0.01$, t-test of individually associated specimens). The same results holds true whether or not Recent humans are pooled with EAM *H. sapiens*, or the early Late Pleistocene individual with associated data (Tabun C1) is pooled with late archaic *H. sapiens*.

Because EQs in general, and any EQ in particular, are subject to a number of limitations, encephalization within *Homo* was also evaluated by plotting log(cranial capacity) against log(body mass)

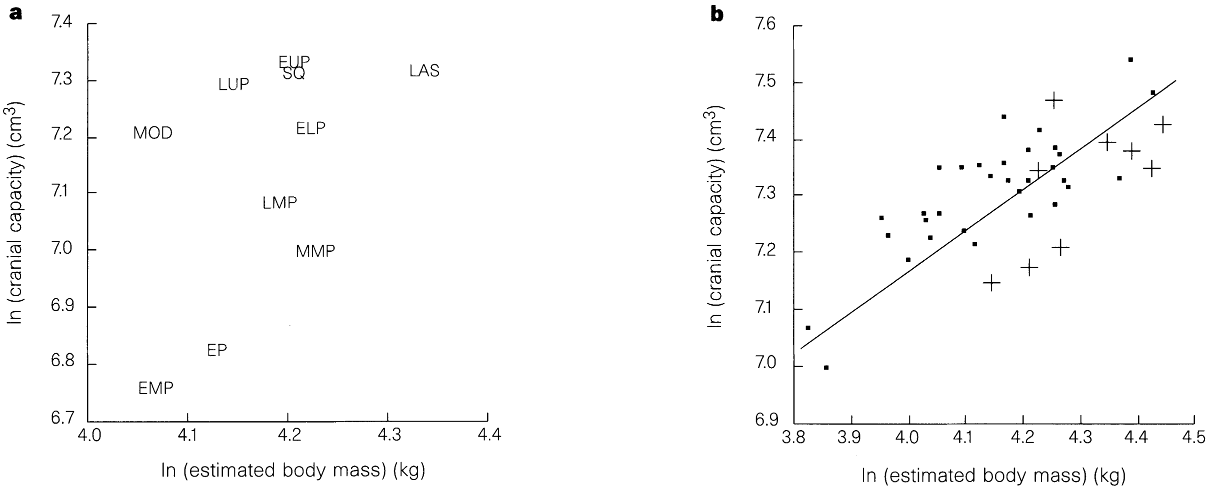

Figure 3 Log-transformed brain mass versus body mass in Pleistocene *Homo*. **a**, Temporal group means. MOD, living humans; LUP, Late Upper Palaeolithic; EUP, Early Upper Palaeolithic; SQ, Skhul-Qafzeh; LAS, late archaic *H. sapiens*; ELP, early Late Pleistocene; LMP, late Middle Pleistocene; MMP, middle Middle Pleistocene; EMP, early Middle Pleistocene; EP, early Pleistocene (see Table 1). **b**, Late Pleistocene individuals. Squares, pooled EUP, LUP and SQ individuals; crosses, pooled LAS and ELP individuals; solid line, reduced major axis regression through total pooled sample.

(Fig. 3). Figure 3a is a plot of the sample mean data from Table 1. The data appear to be best characterized by three major 'trajectories': an Early to middle Middle Pleistocene trajectory, a late Middle to early Late Pleistocene to late archaic *H. sapiens* trajectory, and a trajectory that includes Recent and EAM *H. sapiens*. Variation in cranial capacity between these three groups with body mass as a covariate is highly significant ($P < 0.0001$, ANCOVA; Tukey tests, $P < 0.01$, all pairwise comparisons). Alternatively, the middle and late Middle Pleistocene groups could be viewed as transitional between an earlier (EP–EMP) and later (ELP–LAS) trajectory, with Recent and EAM *H. sapiens* again forming a third trajectory; this interpretation would be more consistent with the EQ data in Table 1. Figure 3b is a plot of all of the individually associated brain and body masses for the Late Pleistocene samples. Although there is substantial overlap between archaic and EAM *H. sapiens*, they are significantly different ($P < 0.01$); this result holds true whether or not the one early Late Pleistocene specimen is included.

Pilbeam and Gould[1] suggested that the scaling of brain size to body size in *Homo* followed a single log-linear trajectory that eventually separated humans from australopithecines as well as other primates. Walker[19], in part on the basis of the discovery of the early *Homo* KNM-WT 15000, proposed that *Homo* was characterized by two brain-size/body-size scaling trajectories or 'grades': one for *H. habilis/H. erectus* and one for modern *H. sapiens*. With more specimens and more accurate means of estimating body mass, it now appears that there were at least three trajectories, or grades of brain size relative to body size within *Homo*, even excluding very early *H. habilis* or *H. rudolfensis* specimens, which may represent another grade[4]. Other previously proposed temporal trends may also now be evaluated with more confidence. For example, the presence of a directional trend in absolute brain size in Early to Middle Pleistocene *Homo* has been debated, with interpretations hampered by the lack of body-mass data for the same time period[20,21]. Our results support a stasis in relative brain size within *Homo* between 1,800 and at least 600 kyr BP. Opinions regarding the relative encephalization of Late Pleistocene archaic *H. sapiens* (Neanderthals) have varied widely[9,12]. Our findings indicate that Neanderthals were slightly less encephalized than Recent and EAM *H. sapiens*, but closer in this respect to modern humans than to middle Middle Pleistocene and earlier *Homo*.

Our results also indicate that a decrease in average absolute brain size over the past 35,000 years within *H. sapiens* was paralleled by a corresponding decrease in average body size, supporting earlier suggestions of a general correlated size reduction in the human skeleton since the early Upper Palaeolithic[22]. This decrease continued through the Neolithic, at least in Europe[23]. Recent secular increases in body size have characterized European and many other higher-latitude populations, whereas many tropical populations have experienced flat or even negative secular trends in size over the same time period[24]. Our body mass results for tropical and higher latitude samples are consistent with these recent trends. Viewed in this light, although some living humans may be expressing a genetic potential for greater body size retained from earlier hunter-gatherer (Upper Palaeolithic) ancestors[25], this phenomenon has been largely limited to higher-latitude populations. ☐

Methods

Femoral head estimation of body mass. Equations from three studies of a diverse sampling of modern humans were used[6,13,15]. In one study, estimates had been derived for males and females separately[13]; in the other two only a combined sex sample had been analysed[6,15]. For the Pleistocene sample, the two combined sex equations were always used and the male or female equation used when sex could be determined (otherwise, a mean of the male and female equation results was used). All equations are for raw (non-logged) data (BM, body mass; FH, femoral head breadth (mm)):

$$\mathrm{BM} = 2.239 \times \mathrm{FH} - 39.9;\ r = 0.98\ \text{(derived by us from raw published data) (ref. 6)} \qquad (1)$$

$$\mathrm{BM} = 2.268 \times \mathrm{FH} - 36.5;\ r = 0.92\ \text{(ref. 15)} \qquad (2)$$

$$\begin{aligned} \mathrm{BM} &= 2.741 \times \mathrm{FH} - 54.9;\ r = 0.50\ \text{(males)}; \\ \mathrm{BM} &= 2.426 \times \mathrm{FH} - 35.1;\ r = 0.411\ \text{(females) (ref. 13)} \end{aligned} \qquad (3)$$

Estimates from equation (3) were adjusted downwards by 10% as recommended by the authors. When applied to 94 Pleistocene *Homo* specimens with intact femoral heads, correlations between pairs of body mass estimates using the above equations were all 0.97 or better, with a mean difference between results of 4%. The mean of the three estimates was used in the study.

Stature/bi-iliac estimation of body mass. The stature/bi-iliac equations were derived from modern anthropometric data given in ref. 16 (BM, body mass (kg); ST, stature (cm); BI, bi-iliac breadth (cm)):

$$\begin{aligned} \mathrm{BM} &= 0.373 \times \mathrm{ST} + 3.033 \times \mathrm{BI} - 82.5;\ r = 0.90\ \text{(males)}; \\ \mathrm{BM} &= 0.522 \times \mathrm{ST} + 1.809 \times \mathrm{BI} - 75.5;\ r = 0.82\ \text{(females)} \end{aligned} \qquad (4)$$

(Note that the equation for females is different from that published in ref. 16 because of correction of an error in one of the original data points (Aleut females: correct body mass = 53.4 kg)). The sex-specific formula was used when possible; otherwise the mean of the male and female formulae was used. Before applying these formulae, skeletal bi-iliac breadth was converted to living bi-iliac breadth using the equation (both dimensions in cm):

$$\text{living BI} = 1.17 \times \text{skeletal BI} - 3 \qquad (5)$$

derived from comparisons within modern humans[16]. Bi-iliac breadth of the Pleistocene specimens was either measured directly or estimated from closely related fossils and/or from known clinal variation in bi-liiac breadth[16,17]. Stature was estimated from preserved long bone lengths using equations derived from appropriately proportioned modern reference samples. Details are given in Supplementary Information.

Combined body mass estimates. When both an intact femoral head and bi-iliac breadth were available, the mean of the femoral head and stature/bi-iliac estimates was used ($n = 26$). Otherwise, either the femoral head, when available ($n = 67$) or the estimated stature/bi-iliac ($n = 70$) estimate was used.

Brain mass and EQ. Brain mass was derived from cranial capacity using a least-squares regression of 27 primate species that had data available for both parameters[26,27], corrected for logarithmic transformation bias:

$$\text{brain mass} = 1.147 \times \text{cranial capacity}^{0.976}\ (r^2 = 0.995) \qquad (6)$$

Encephalization quotient was derived from Martin's[28] relationship between brain mass (g) and body mass (kg) in mammals:

$$\text{EQ} = \text{brain mass}/(11.22 \times \text{body mass}^{0.76}) \qquad (7)$$

Encephalization quotients (EQ) relating brain mass to body mass were derived in two ways, using individually associated crania and postcrania, and using mean brain mass and body mass within temporally defined groups. The EQs derived using the group means are based on many more specimens, but because they do not use individually matched data they could potentially be biased in several ways. However, other methods of limiting these samples, for example by using only individuals from the same sites and/or sex, produce similar results. Also, where they can be compared, the individually associated and mean data values for the same temporal periods are similar (Table 1). For associated specimens, sex and latitudinal biases in EQ should be minimal: within the Pecos and Pleistocene EAM samples sex differences in EQ average less than 2%, and among modern humans higher- and lower-latitude populations appear to average less than a 4% difference in EQ (mean data from Beals *et al.*[29] and our worldwide sample[16]).

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Deficits in auditory temporal and spectral resolution in language-impaired children

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Between 3 and 6 per cent of children who are otherwise unimpaired have extreme difficulties producing and understanding spoken language[1]. This disorder is typically labelled specific language impairment. Children diagnosed with specific language impairment often have accompanying reading difficulties (dyslexia)[2], but not all children with reading difficulties have specific language impairment[3]. Some researchers claim that language impairment arises from failures specific to language or cognitive processing[4–6]. Others hold that language impairment results from a more elemental problem that makes affected children unable to hear the acoustic distinctions among successive brief sounds in speech[7–11]. Here we report the results of psychophysical tests employing simple tones and noises showing that children with specific language impairment have severe auditory perceptual deficits for brief but not long tones in particular sound contexts. Our data support the view that language difficulties result from problems in auditory perception, and provide further information about the nature of these perceptual problems that should contribute to improving the diagnosis and treatment of language impairment and related disorders.

We measured the detection threshold for a brief tone presented before, during or after two different masking noises in eight children diagnosed with specific language impairment, and in eight control children with normal language skills who matched the others in age and non-verbal intelligence (Table 1). Before beginning the tests with the brief tones, we introduced the children to the listening task by measuring their detection thresholds for a long tone presented in the temporal centre of a 'bandpass' noise that included frequencies at and near the tone frequency. The points above the schematic

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