

VARIATION IN HUMAN BODY SIZE AND SHAPE

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■ **Abstract** Evolutionary trends in human body form provide important context for interpreting variation among modern populations. Average body mass in living humans is smaller than it was during most of the Pleistocene, possibly owing to technological improvements during the past 50,000 years that no longer favored large body size. Sexual dimorphism in body size reached modern levels at least 150,000 years ago and probably earlier. Geographic variation in both body size and shape in earlier humans paralleled latitudinal clines observed today. Climatic adaptation is the most likely primary cause for these gradients, overlain in more recent populations by nutritional effects on growth. Thus, to distinguish growth disturbances, it is necessary to partition out the (presumably genetic) long-term differences in body form between populations that have resulted from climatic selection. An example is given from a study of Inupiat children, using a new index of body shape to assess relative body mass.

INTRODUCTION

Body size and shape vary considerably among living human populations. Mean body mass (weight) varies by 50% or more, within sex, in a worldwide sampling of populations (Ruff 1994), even if Pygmies are not considered. Mean body height (stature) and breadth (bi-iliac or maximum pelvic breadth) also vary between the same samples, although in different ways. Variation in height is smaller (about 10%) and does not follow any particular geographic trend. Variation in breadth is larger (about 25%) and shows a clear latitudinal gradient. The explanation for this difference, and some other systematic human body shape differences, may lie in basic physiological adaptive mechanisms, as discussed below.

There is abundant evidence that both body size and shape were even more variable among Plio-Pleistocene hominins (e.g., Jungers 1988, Ruff 1991, Aiello 1992, McHenry 1992) and, within geographically dispersed taxa, followed clines that were similar to those found among modern humans (Trinkaus 1981; Ruff & Walker 1993; Ruff 1994; Holliday 1997a,b). General temporal trends in body size are also apparent in the fossil record (e.g., Ruff et al. 1997). An appreciation of such variation among human ancestors is important for several reasons: (a) Body size (and within-taxon variation in body size) is related to many other characteristics

of a species, including life history parameters, ecology, and social organization (Calder 1984, Schmidt-Nielson 1984); thus, it is often used to predict these traits in fossil taxa [notwithstanding some significant problems in doing so (see Smith 1996)]. (b) Body size is the usual “denominator” for assessing key evolutionary trends in the hominin lineage, including changes in relative brain size (encephalization), tooth size (megadontia), bone strength (robusticity), and gut size (Pilbeam & Gould 1974; McHenry 1976, 1984, 1988; Ruff et al. 1993, 1997; Aiello & Wheeler 1995; McHenry & Coffing 2000). (c) Differences in body shape have been used as population or taxonomic markers among past hominins and to identify migrational and possible interbreeding events (Trinkaus 1981; Holliday 1997a,b; Duarte et al. 1999; Ruff et al. 2002). (d) The body size and shape of earlier humans can serve as effective baselines for assessing more recent temporal or geographic variation, for example, the effects of changes in subsistence strategy and the significance of recent secular trends (Fruyer 1984, Tobias 1985, Ruff et al. 1997) (see below). Appreciation of long-standing differences in body form between human populations can help inform decisions regarding the most appropriate methods for assessing the health and nutrition of living individuals. Both absolute measures of body size (height, weight) and relative indices reflecting body shape [body mass index (wt/ht^2)] are often used as standards for evaluating growth and under- and over-nutrition (WHO 1995). To the extent that these characteristics vary systematically in response to factors other than health and nutrition, such standards may not be universally applicable across populations.

EVOLUTIONARY TRENDS IN BODY SIZE

Methodological Considerations

Because body size reconstruction in the fossil record almost always depends on extrapolation from fragmentary remains, it is important to clearly understand the rationale behind different reconstruction methods. A purely statistical approach considers the relationship between body mass (or stature) and skeletal/dental features in a modern reference sample and applies resulting prediction equations to the fossil fragments, perhaps preferring those equations with the smallest estimation errors in the modern sample. The problem with such an approach is that it implicitly assumes equality—proportional and/or functional—between the reference sample and the individual to which it is applied, which may or may not be true. For example, equations for predicting stature from long bone lengths developed in European samples severely overestimate stature in East Africans because of their relatively longer limb-to-trunk lengths (Allbrook 1961). This result is predictable given known systematic differences in limb proportions among modern human populations (Roberts 1978). The same rationale applies to reconstruction of stature in the *Homo erectus* KNM-WT 15000, who also had apparently very long limbs (Ruff & Walker 1993). Another example would be the use of tooth

size to predict body mass in the hominin lineage, a common practice in primate paleontology (e.g., Gingerich et al. 1982, Conroy 1987) but one that is obviously biased in this case because of temporal (and probably taxonomic) differences in relative tooth size among hominins (Pilbeam & Gould 1974, McHenry 1984, McHenry & Coffing 2000, Teaford et al. 2002). Another not-so-obvious example is the use of long-bone diaphyseal breadth to predict body mass in hominins, a commonly employed procedure in the past (McHenry 1976, Oleksiak 1986, Rightmire 1986, Hartwig-Scherer 1994). It is evident that long-bone diaphyses change their diameters in response to mechanical loading (Trinkaus et al. 1994) and that Plio-Pleistocene hominins had relatively thicker diaphyses than modern humans (Ruff et al. 1993, 1994; Ruff 1998). Thus, use of diaphyseal cross-sectional dimensions and a modern reference sample will lead to systematic overestimates of body mass in fossil hominins.

These examples illustrate the importance of considering the functional significance of skeletal/dental traits when using them for body size reconstruction. In many cases this will involve their mechanical significance because mechanical factors have such a pervasive influence on skeletal form (see references above). The mechanics of weight-bearing in bipeds, in fact, argues for the use of lower limb-bone dimensions for body mass reconstruction in hominins. Articular dimensions have been shown to be less sensitive to differences in activity level than are diaphyseal breadth dimensions (Ruff et al. 1994, Trinkaus et al. 1994, Lieberman et al. 2001); thus, they should more accurately reflect variations in body mass without the potentially confounding effects of individual behavioral differences. For these reasons, lower limb articular size, and particularly femoral head size (because the femoral head is often preserved and is easily measurable), is an effective predictor of body mass in hominins (Ruff et al. 1991, 1997; McHenry 1992; Grine et al. 1995).

Mechanically based methods for estimating body mass can be distinguished from morphometric methods (Ruff 1994, 2000b) that rely on direct reconstruction of body dimensions from preserved bone dimensions. The latter usually involve estimation of stature or body length, followed by estimation of body mass from stature, assuming some specified relationship between the two (Mathers & Henneberg 1995, Porter 1995). Using a cylindrical model of the human body (Ruff 1991), body mass should be predictable from stature and body (cylinder) breadth. In fact, body mass estimates from stature and bi-iliac breadth in living humans are remarkably good (Ruff 1994, 2000b). It is critical when estimating stature, or bi-iliac breadth (if necessary), to use appropriate modern reference samples, i.e., modern populations with body proportions similar to the specimens being estimated (Holliday & Ruff 1997). Fortunately, strong geographical trends in body shape, as well as information gleaned from more complete specimens, can provide guidance with the more usual fragmentary specimens (Ruff et al. 1993; Ruff & Walker 1993; Trinkaus & Ruff 1999a,b). Body mass estimates from femoral head size and a multiple regression using stature and bi-iliac breadth give similar results, on average, when applied to Pleistocene hominin specimens (Ruff et al. 1997).

General Temporal Trends

Figure 1 shows body mass estimates for individual specimens of Pleistocene *Homo* species derived from regressions on femoral head size and/or bi-iliac breadth and stature (Ruff et al. 1997), mean estimates for other Plio-Pleistocene hominin taxa taken from the literature, mainly McHenry (1992), and modern human sex-specific population means from a worldwide sampling, not including Pygmies (Ruff 1994). All estimates for skeletal/fossil specimens were derived from postcranial elements. The Pleistocene *Homo* specimens include 163 individuals used in a previous analysis (Ruff et al. 1997) plus two recently described Middle Pleistocene specimens from Yinnuishan, China (Rosenberg et al. 1999) and Atapuerca, Spain (Arsuaga et al. 1999). Three other specimens attributed to *Homo habilis sensu stricto* (Olduvai 8 and 36 and KNM-ER 3735), whose body masses were estimated by McHenry (1992), are shown enclosed in parentheses because their attribution to the genus *Homo* has been questioned (Wood & Collard 1999). [Other early *Homo* specimens plotted here, including KNM-ER 3228, 1481, and 1472, are not definitely attributable to any particular species but appear to be most similar in morphology to later *H. ergaster/erectus* rather than *H. habilis sensu stricto* (McHenry 1994b, McHenry & Coffing 2000).] Among the *Homo* specimens, those from higher (above 30°) and lower latitudes are distinguished by different symbols. (All *Australopithecus* specimens are from lower latitudes.) Two dotted lines representing the mean body masses of the modern higher- and lower-latitude samples are plotted for reference. Because of differences in data sampling density, the temporal axis is given in three different scales with break points at 2 million and 100,000 years ago.

Several temporal trends in hominin body mass are apparent from Figure 1. First, there is a marked increase in body size with the appearance of early *Homo* (except *H. habilis sensu stricto*) about 2 million years ago. This contrast between *Homo* and earlier and contemporaneous australopithecines has been previously noted (e.g., McHenry 1994a, Wood & Collard 1999, McHenry & Coffing 2000). The explanation for the increase in body size in *Homo* is not clear but may be related to a commitment to a fully terrestrial lifestyle, inhabitation of more open environments, increased foraging distances, and/or dietary shifts (Foley 1987, Wheeler 1992, McHenry 1994a, Leonard & Robertson 1997, Klein 1999). The lack of such an increase in *H. habilis sensu stricto*, with its attendant behavioral implications, is one argument against the inclusion of this taxon within the genus *Homo* (Wood & Collard 1999).

Second, there is an increase in average body size at about 500,000 years ago, corresponding to the first hominin postcranial remains recovered from higher latitudes. It is well documented that among modern humans body mass is distributed clinally, increasing in higher latitudes (Roberts 1978, Ruff 1994, Katzmarzyk & Leonard 1998), as reflected in the living-human data points in Figure 1. This has been interpreted as an example of Bergmann's Rule (Mayr 1956), which is generally explained as an adaptation to decreased heat loss in colder environments.

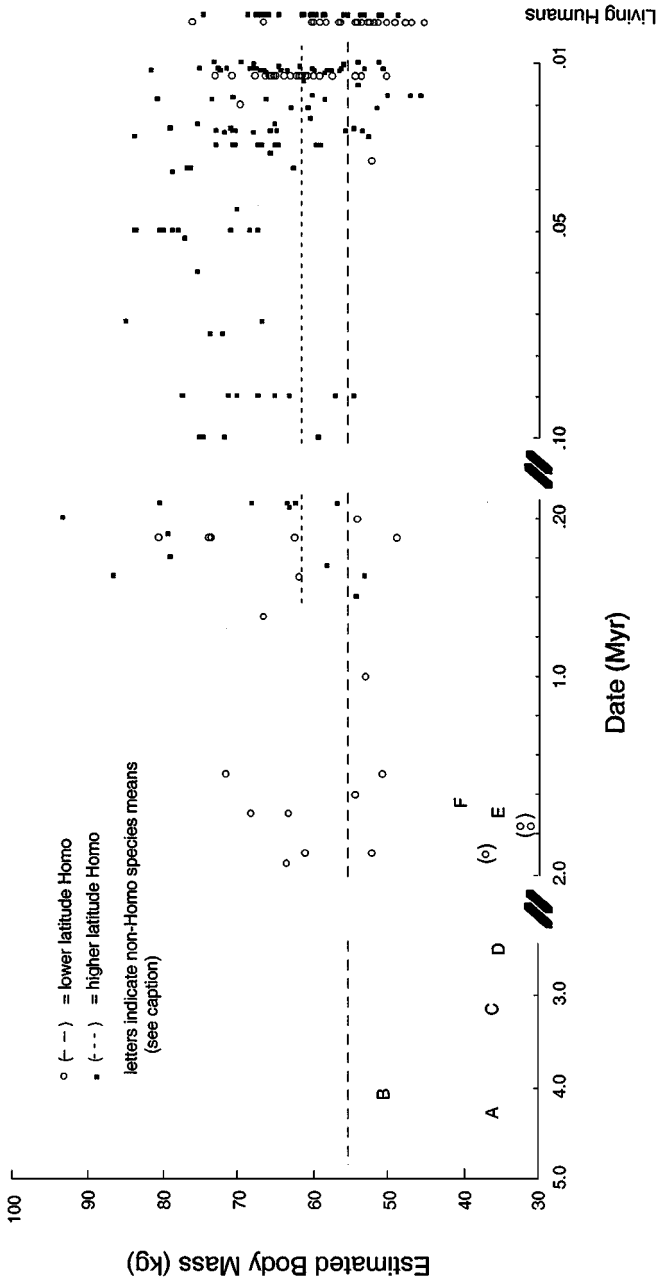


Figure 1 Estimated body mass of Plio-Pleistocene hominins. Letters represent species means of early taxa: A, *Ardipithecus ramidus*; B, *Australopithecus anamensis*; C, *Australopithecus afarensis*; D, *Australopithecus africanus*; E, *Paranthropus robustus*; F, *Paranthropus boisei*. (A) Based on similarity in size of humerus to middle of range for *A. afarensis* (White et al. 1994); (B) Leakey et al. 1995; (C-F): McHenry 1992. Symbols represent individual *Homo* specimens (Ruff et al. 1997, Arsuaga et al. 1999, Rosenberg et al. 1999). Symbols in parentheses are individual *H. habilis sensu stricto* (McHenry 1992). Living humans are sex/population-specific means (Ruff 1994). Open symbols, lower latitude; solid symbols, higher latitude; dotted and dashed lines through living human means for higher and lower latitudes, respectively. Myr, millions of years before present. (Adapted from Ruff 2001, with permission from Elsevier Science.)

Thus, it would be expected that a range expansion into colder climates would increase the average body mass (and total range in body mass) of the genus *Homo*. Body masses for individual Pleistocene *Homo* specimens are generally above the means for living humans from the same latitudinal zones, on the order of 10% higher on average (Ruff et al. 1997). The difference is even greater if only archaic *Homo* specimens (Neandertals and other specimens dated to before 100,000 years ago) are considered: Higher-latitude archaic *Homo* specimens average almost 20% greater in body mass than the means for living higher-latitude populations. This figure may be somewhat inflated by a male preservational bias in the fossil record (Ruff et al. 1997), but even so, it is evident that Middle Pleistocene and early Late Pleistocene humans were significantly larger on average than living humans. A large body size is also consistent with evidence from material culture from this time period, such as very large Middle Pleistocene throwing spears (Thieme 1997).

Third, there is a decline in average body mass beginning about 50,000 years ago. The decline is best demonstrated among higher-latitude samples and is equivalent whether or not archaic humans (Neandertals) are included (Ruff et al. 1997). Lower-latitude samples with body mass estimates are unfortunately rare in the Late Pleistocene. However, similar declines in the Late Pleistocene and early Holocene in other body dimensions, including estimated stature and cranial size, have been demonstrated in many areas of the world, including Europe, the Mediterranean region, sub-Saharan Africa, South Asia, and Australia (Frayer 1980, 1984; Kennedy 1984b; Meiklejohn et al. 1984; Jacobs 1985; Henneberg 1988; Brown 1992; Henneberg & Steyn 1993; Formicola & Giannecchini 1998). The decline continues through the Neolithic, after which it is reversed in European samples. No reversal in this negative trend in size has been reported for lower-latitude samples, except possibly for some very recent increases in some areas over the past few decades (Katzarzyk & Leonard 1998). As a result, living higher-latitude populations are about as large as terminal Pleistocene samples, whereas living lower-latitude populations are smaller on average than they were 10,000 years ago (Figure 1) (see Ruff et al. 1997).

Several reasons, not mutually exclusive, have been proposed for the Late Pleistocene–Early Holocene decline in human body size (see references above). These include technological improvements that decreased the selective advantage of a larger body (which is also metabolically expensive to maintain), a decline in nutritional quality, climatic factors (adaptation to a warming environment), and reduced gene flow (inbreeding). A reduction in body size has been observed in many, although not all, populations undergoing a transition from a foraging to a food producing economy, especially an intensive agricultural economy (Cohen & Armelagos 1984a). Explanations for this trend usually focus on increases in malnutrition, overcrowding, and spread of infectious diseases. Institution of a class system with resulting social inequities in resource allocation may also be a factor in some populations (Bogin & Keep 1999). However, because body size reduction occurred in many areas of the world prior to the adoption of food production (or where food production was never adopted, i.e., Australia), this factor may be

contributory but does not fully explain the trend. Given the timescales involved and the known effects of malnutrition on growth, it seems likely that changes associated with food production were developmental rather than genetic in nature. Recent positive secular trends over the past few hundred years are also most likely to be developmental and related to increased nutritional and overall health levels (Van Wieringen 1986, Eveleth 1994, Stinson 2000). Such positive trends have not been observed in many areas of the world, primarily in lower latitudes that have not enjoyed the same improvements in environment (Malina et al. 1983, Tobias 1985, Pretty et al. 1998). At the same time, the positive secular trend in body size in (mainly) higher-latitude populations may have leveled off over the past few decades (Kimura 1984, Stinson 2000).

One possible explanation for these observations is that the Late Pleistocene reduction in body size was due primarily to genetic factors, possibly reduced selection for large body size in association with technological improvements (Frayer 1984), whereas the succeeding fluctuations (decrease, then, in higher latitudes, increase) in body size in the Holocene were due to environmental effects on growth, e.g., nutrition. Thus, many higher-latitude populations may have recently achieved their maximum “genetic potential” in body size (stature), originally established in the terminal Pleistocene, whereas many lower-latitude populations have not. Additional Late Pleistocene body-mass data from lower-latitude samples would be useful in further testing this hypothesis.

Sexual Dimorphism

Figure 2 shows sexual dimorphism in estimated body mass for early hominin taxa and regional/temporal groupings of *H. sapiens*. Mean male and female body masses for *Australopithecus*, *Paranthropus*, and early *Homo* are from McHenry & Coffing (2000), mean sex-specific body masses for Pleistocene *H. sapiens* are from the data set used in Ruff et al. (1997), and values for individual living human populations ($n = 19$) are from Ruff (1994). The mean sexual dimorphism (male/female) in body mass in the living human populations is about 15%, similar to average figures derived from other living population samples (Stini 1974, McHenry & Coffing 2000). Sexual dimorphism is similar in higher-latitude (mean 15.5%) and lower-latitude (mean 14.7%) living samples ($p > 0.75$, t test). The same is true for the Late Upper Paleolithic sample—the only Pleistocene sample with a sufficient number of individuals from higher and lower latitudes to subdivide in this way—with 16.1% and 15.1% sexual dimorphism for higher and lower latitudes, respectively. Thus, whereas latitude affects average body mass, it appears not to affect sexual dimorphism in body mass in any systematic way. This is the pattern that would be expected if sexual dimorphism in body mass in humans were more influenced by environmental/behavioral factors other than climate per se.

All taxonomic or regional/temporal groupings of *Homo* specimens have levels of body-mass sexual dimorphism comparable to those of modern humans (7%–18%) (Figure 2). In contrast, most earlier and contemporary australopithecines,

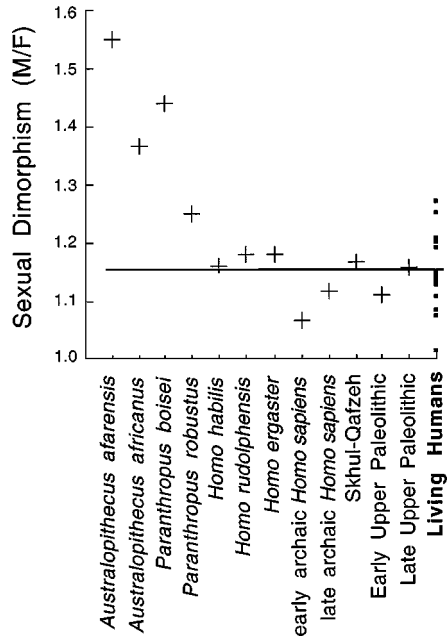


Figure 2 Sexual dimorphism in body mass in hominin taxa or regional/temporal groupings. See text for origin of data. “Early archaic *Homo sapiens*” corresponds to “early Late Pleistocene” in Ruff et al. 1997. Line indicates living human mean.

including *A. afarensis* and *A. africanus*, and *Paranthropus boisei*, show clearly elevated levels of sexual dimorphism (37%–55%). *Paranthropus robustus* is slightly elevated (25%) although just within the range of modern human populations. Some of the estimates for the earlier species are heavily dependent on taxonomic attributions, which can be problematic for isolated postcranial elements; thus, such estimates can change substantially if groups are redefined or additional specimens are added to particular taxa (McHenry 1992, 1994a; McHenry & Coffing 2000). For example, based on newly identified and some reclassified specimens from Swartkrans, South Africa, Susman et al. (2001) estimated body-mass sexual dimorphism to be about 40% in *P. robustus*, equivalent to that in *P. boisei* and *A. africanus* (Figure 2), and even larger in *Homo sp.* from the site, about 80%. This latter figure is similar to earlier estimates of sexual dimorphism in *H. habilis* more broadly defined (*sensu lato*) (McHenry 1992). Another problem in such comparisons is that almost none of the earlier specimens have any associated indicators of sex; thus, sex assignment is made on the basis of size alone (larger = male, smaller = female), often across different sites and temporal ranges, which may exaggerate the degree of estimated dimorphism. In contrast, all of the Late Pleistocene sex assignments shown in Figure 2 for *H. sapiens* are based either on associated pelvic or cranial material or on comparisons within site-specific samples.

Perhaps the most conservative assessment of the data shown in Figure 2 is that sexual dimorphism in body mass definitely reaches modern levels with archaic *Homo sapiens*¹, and very possibly earlier with *H. ergaster/erectus*, but was likely larger in australopithecines and possibly some early species of *Homo*. The behavioral and ecological significance of increased sexual dimorphism in body size in at least some early hominin taxa has been debated (see McHenry 1991, 1992, 1994a; Plavcan & Van Schaik 1997; Plavcan 2001 and references therein). The lack of concurrent marked sexual dimorphism in canine tooth size may imply a social/behavioral system unique among primates (Plavcan & Van Schaik 1997, Plavcan 2001). To the extent that sexual dimorphism in body size reflects social organization, the data for archaic *H. sapiens* indicate that by the Late Pleistocene, at least, patterns of social organization may have been similar to those of modern human foragers. This is concordant with evidence from lower limb bone structure, which indicates a sexual division of labor in archaic *H. sapiens* similar to that of modern hunter-gatherers (Ruff 1987, 2000a).

More recent variations in body-mass sexual dimorphism, not shown in Figure 2, likely reflect more subtle differences in subsistence strategy, diet, and possibly sex-related buffering against the environment (Stini 1974; Frayer 1980, 1984; Meiklejohn et al. 1984; Jacobs 1985; Stinson 1985; Jantz & Jantz 1999). Secular trends in stature over the past few hundred years have been in similar directions for males and females of the same populations (e.g., Meredith 1976, Bogin & Keep 1999), although again with possible subtle differences in magnitude (Jantz & Jantz 1999).

EVOLUTIONARY TRENDS IN BODY SHAPE

There is abundant evidence that many early hominin taxa (australopithecines and *H. habilis sensu stricto*) had basic body proportions that were significantly different from those of modern humans. Upper limbs were large relative to lower limbs, and body breadth (and mass) was large relative to stature (McHenry 1978, Johanson et al. 1987, Leakey et al. 1989, Hartwig-Scherer & Martin 1991, Ruff 1991, Aiello 1992, McHenry & Berger 1998, Asfaw et al. 1999). These differences are probably best accounted for by retained arboreal capabilities combined with the allometric effects of small body size, which itself may be related to locomotor patterns (see above). By 1.5 million years ago body proportions, together with body size, in *H. ergaster/erectus* were well within the range of modern human variation (Ruff & Walker 1993). From this point on, within the *Homo* lineage, a fully terrestrial

¹The Sima de los Huesos skeletal sample from Atapuerca, Spain, dated to about 200,000 years ago, preserves the remains of many individuals (Arsuaga et al. 1999). Most lower limb remains from the site have not yet been formally described, but a number of acetabular breadths are given in the above reference, some of which have sexually diagnostic regions of the pelvis preserved. The males average 60 mm and the females 52 mm, a 15% difference.

lifestyle can be inferred, with variations in body shape viewed as adaptations to environmental variables other than basic locomotor behavior.

One environmental variable that has long been postulated to influence modern human body shape is climate (see references in Ruff 1994). Relative limb length (Allen's Rule) and body breadth vary systematically with temperature in modern human populations, with those from colder environments having relatively shorter limbs (and shorter distal segments within limbs) and wider bodies than those from warmer environments (Roberts 1978, Trinkaus 1981, Ruff 1994). These clinal variations, and the observed cline in body mass discussed earlier, can all be viewed as part of the same adaptive strategy to reduce body surface area/body mass in colder climates and increase it in warmer climates (Schreider 1964; Ruff 1991, 1994). Of course, body proportions can be affected by other environmental variables as well. For example, relative limb length may increase with improved nutrition and health status (Tanner et al. 1982). However, this factor cannot explain the relatively longer limbs observed in modern tropical populations, most of whom are more nutritionally deprived than higher-latitude populations. Thus, genetic factors (climatic selection) are likely involved (Stinson 2000). Interestingly, there is evidence that body (bi-iliac) breadth is not as affected by nutritional or other developmental influences as limb length proportions, perhaps in part because of stabilizing selection owing to obstetric requirements (Ruff 1994). In terms of climatic adaptation, changes in absolute body breadth will always affect surface area-to-body mass ratios, whereas changes in stature will not (Ruff 1991). Thus, (skeletal) body breadth shows very strong latitudinal trends, whereas stature does not (Ruff 1994).

Where possible to evaluate, body proportions in earlier hominins have been found to follow the same geographic clines as modern humans. Thus, for example, Neandertals have relatively short distal limb segments (Trinkaus 1981) and broad bodies (Ruff 1994), whereas the opposite is true for KNM-WT 15000, a juvenile *H. ergaster/erectus* from East Africa (Ruff & Walker 1993). Furthermore, with the discovery of new fossil specimens over the past several years, it is now apparent that the Neandertal body type is actually part of a broader pattern shared with other higher-latitude archaic *Homo* specimens. These new specimens include the Yinnuishan female, dated to about 280,000 years ago (Rosenberg et al. 1999), and the Atapuerca "Pelvis 1" male, dated to at least 200,000 years ago (Arsuaga et al. 1999). Both specimens preserve enough of the pelvis to allow measurement or accurate estimation of bi-iliac breadth. Yinnuishan also preserves an ulna from which forearm length can be assessed. The Atapuerca Sima de los Huesos remains are all unassociated, but an approximate ulnar length can be calculated from a complete humerus recovered at the same site ("Humerus II") (Carretero et al. 1997). The pairing of the pelvis and humerus is reasonable, because both were at the upper end of the size range represented at the site and so very likely represented large males. Ulna length was calculated from humeral length using a regression formula based on a combined sample of modern East Africans and Pecos Pueblo

Amerindians (Ruff 1995): $ulna = 0.873 \cdot humerus - 12.4$ ($r = 0.910$, standard error of estimate = 8.4 mm). This is a conservative estimate in terms of testing whether the Atapuerca specimen had relatively short limbs because East Africans have typically tropical proportions (long forearms); using only the Amerindians as a reference sample would produce an ulna length estimate several millimeters shorter.

Figure 3 plots ulna length against bi-iliac breadth for the Yinnuishan and Atapuerca specimens, together with similar data for several other Pleistocene specimens and some modern comparative samples. The modern samples include East African (Ruff 1995) and combined Alaskan Inupiat (Eskimo) and Aleut skeletal samples. Because modern males have relatively longer forearms than females (Trinkaus 1981), sexes are distinguished in the plot.

As expected, the modern tropical sample has much longer forearms relative to body breadth than the high-latitude sample: There is no overlap between same-sex individuals from the two groups. Interestingly, a line indicating equivalent

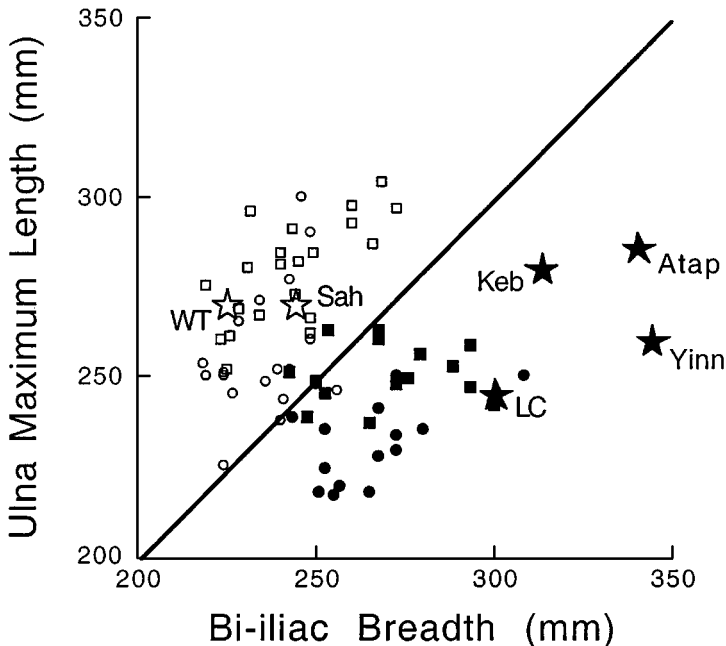


Figure 3 Ulna maximum length against bi-iliac (maximum pelvic) breadth in Pleistocene and modern *Homo*. Open symbols, modern East Africans; filled symbols, modern Eskimos/Aleuts; squares, males; circles, females. Open stars, KNM-WT 15000 and Sahaba 16; filled stars, La Chapelle 1, Kebara 2, Atapuerca “Pelvis 1”, Yinnuishan (see text); diagonal line, equivalent ulnar and bi-iliac measures.

ulnar length and bi-iliac breadth, included in the plot, almost perfectly divides the two groups. Multiple analyses of variance (ANOVA) indicate that both sex and latitude have highly significant effects on proportions in the modern samples ($p < 0.0001$). The Yinnuishan and Atapuerca specimens are “hyper-arctic,” with very wide bodies and short forearms. Two Neandertals with pelvises sufficiently preserved to measure or estimate bi-iliac breadth [Kebara 2 (Rak & Arensburg 1987) and La Chapelle 1 (Boule 1911, Ruff et al. 1993)] also fall in the high latitude range. (Ulna length for La Chapelle was estimated from its radius length using a formula derived from modern East Africans and Pecos Amerindians: $ulna = 1.008 \cdot radius + 16.2$, $r = 0.988$, standard error of estimate = 3.2 mm.) The Atapuerca and La Chapelle specimens are quite similar in proportions, with Yinnuishan falling below these two. The extreme proportions of Yinnuishan may be attributable in part to sexual dimorphism: The difference between this female specimen and the Atapuerca and La Chapelle 1 males is about equal to the average difference between modern females and males from the same latitudinal zone (Figure 3). Kebara 2 (also a male) is somewhat less hyper-arctic, reflecting the longer forearms (and possibly somewhat more linear body form) characteristic of Near Eastern as opposed to European Neandertals (Trinkaus 1981, Ruff 1994, Ruff et al. 2002).

Two Pleistocene specimens from tropical regions are also included in Figure 3: KNM-WT 15000, a juvenile male *H. ergaster/erectus* (Walker & Leakey 1993), and Jebel Sahaba 26, a female from a terminal Pleistocene site in Nubia (Wendorf 1968). The juvenile status of KNM-WT 15000 should have relatively little effect on comparisons (Ruff & Walker 1993). Both specimens fall close to the average proportions for sex-matched modern individuals from East Africa.

Thus, the available evidence supports latitudinal clines in body shape in earlier *Homo* similar to those found in modern humans. This in turn suggests a similar physiological mechanism as an explanation, i.e., climatic adaptation. As noted earlier, there are very few available Middle and Early Late Pleistocene specimens from lower latitudes, and none with enough postcranial elements to directly assess body proportions. These would provide very useful comparisons with archaic *Homo* specimens from higher latitudes because the latter show the most extreme examples of apparent adaptation to colder climates. Without this direct contrast it can be argued, for example, that the broad pelvises of higher-latitude archaic *Homo* have more phylogenetic rather than physiological implications (Arsuaga et al. 1999). However, other less direct evidence also supports a latitudinal cline in body shape within the Middle Pleistocene. The complete tibia from Broken Hill, Zambia (E691), is very long, in the Pleistocene equaled in length only by specimens with high crural indices (long tibias relative to femora) (Kennedy 1984a). On the basis of shaft external breadth or cross-sectional properties to length proportions, the Broken Hill tibia and other lower-latitude tibias from the Middle Pleistocene are clearly distinct from the broadly contemporaneous higher-latitude Boxgrove 1 tibia (Stringer et al. 1998, Trinkaus et al. 1999). The most parsimonious explanation is that the Boxgrove specimen had a relatively wide body and short limbs (like

Neandertals, Atapuerca, and Yinnuishan), whereas the lower latitude specimens had relatively narrow bodies and longer limbs (like KNM-WT 15000).

The transition in Europe from Neandertals to “early anatomically modern” (Late Paleolithic) humans 40,000 to 25,000 years ago and subsequent changes in morphology within the latter group, are especially interesting in that they may provide evidence of adaptation following migration to a new climatic zone if these populations were derived from farther south, as suggested by the preponderance of current evidence (Klein 1999). The lack of change between European Early and Late Paleolithic samples in distal-to-proximal limb length proportions (crural and brachial indices) was initially puzzling in this regard because a reduction would have been predicted if climatic adaptation were taking place (Trinkaus 1981). However, more recent work has shown that relative to measures of trunk (vertebral column) height, limb length did decrease significantly within the Upper Paleolithic in Europe, beginning at proportions similar to those of sub-Saharan Africans and ending at proportions similar to those of modern Europeans (Holliday 1997a). Comparisons of long bone lengths to bi-iliac breadths in available European Upper Paleolithic specimens ($n = 15-19$, about a third from the Early Upper Paleolithic) also indicate significant reductions in limb length to body breadth between the Early and Late Upper Paleolithic (unpublished results based on data given in Ruff et al. 1997, supplementary information). Thus, body shape did change significantly in Upper Paleolithic Europeans after exposure to colder climatic conditions, although the change was mosaic in nature, beginning with a general reduction in limb lengths followed by a reduction in distal-to-proximal limb element proportions. The possible significance of this difference in timing has been further explored elsewhere (Ruff et al. 2002).

RELATIVE BODY MASS IN LIVING POPULATIONS

What can the patterns of variation in body size and shape observed in pre-Holocene humans tell us about more recent human variation? If the body size of terminal Late Pleistocene humans does indeed represent a genetic target (or limit) for body size in living humans, then data on such populations, prior to the major changes in diet, social organization, etc., characteristic of the Holocene, could serve as effective baselines for evaluating current body size. As noted earlier, there is evidence that many living populations from developing countries may not be as large as their Pleistocene ancestors. Of course, this does not address the issue of whether maximum potential body size is desirable or not (for a review see Stinson 1992).

Here I concentrate on another issue: how differences in relative body mass, i.e., body shape, between modern populations should be used in health assessment. The above review indicates that body shape varies systematically along latitudinal clines in both modern humans and Pleistocene *Homo*. Nutrition and health status do not seem to explain these trends, which are, however, consistent with

climatic adaptation. The temporal depth of such clines and their persistence despite other confounding factors argues that they represent long-standing mechanisms of adaptation within our lineage and are probably at least in part genetically based.²

The body mass index (BMI), weight/height² (also known as Quetelet's Index), is widely employed in assessing relative under- or over weight status of living individuals and populations (WHO 1995). Standard percentiles for BMI at various ages during childhood and in adults have been developed from U.S. population surveys (WHO 1995). However, questions have been raised concerning the applicability of such standards to other populations, owing to the effects of varying body proportions and lean body mass fraction on the index (Garn et al. 1986) (some of these limitations were also noted in the WHO recommended guidelines cited above). The effects of differences in relative lower limb length (or relative sitting height) on body mass indices have been known for many years (Bardeen 1923).

Arctic populations represent an extreme in modern human body shape variation, with relatively short limbs and wide bodies (see Figure 3). This contributes to their high weight-for-height indices, despite the fact that they do not have increased skinfold thicknesses compared with U.S. standards (Schaefer 1977, Johnston et al. 1982, Jamison 1986). This pattern is apparent among Eskimo (Inupiat and Inuit) children and adults and has led to recommendations that different standards be developed for identifying obesity in these populations (Schaefer 1977, Jamison 1986). One approach would be to develop population-specific weight-for-height standards for such groups. The problems with this approach are that (a) it would necessarily rely on a relatively small data set and would not take advantage of the very extensive samples available in large population surveys that allow more secure statistical inferences (e.g., Hamill et al. 1979), and (b) results could be confounded by very recent and marked secular changes occurring in some of these groups in diet, lifestyle, and anthropometrics (Schaefer 1970, Jamison et al. 1978).

An alternate approach would be to use a different index of relative weight that is less affected by, or incorporates, variations in body build including relative limb length and relative (skeletal) body breadth. Sitting height is a commonly taken anthropometric measurement that reflects trunk height, i.e., a body length measure that does not include the limbs. Sitting heights of Eskimo children were found to be similar to those of age-matched U.S. whites and blacks, despite large differences in stature (Johnston et al. 1982). Bi-iliac breadth is the best available trunk breadth measurement (see Ruff 1991). As noted above, it also shows strong systematic differences between human populations. The product of trunk height and bi-iliac breadth provides an index of "trunk frame size" (Ruff & Jamison 2002). The ratio of body mass to trunk frame size can then be considered a "trunk frame index" (TFI). Both sitting height and bi-iliac breadth are expressed in cm and body mass in kg; the resulting ratio is multiplied by 1000.

²Note that this does not imply any close genetic ties between earlier *Homo* species and modern humans from the same geographic regions, but rather the operation of the same adaptational principles to both earlier and more recent populations.

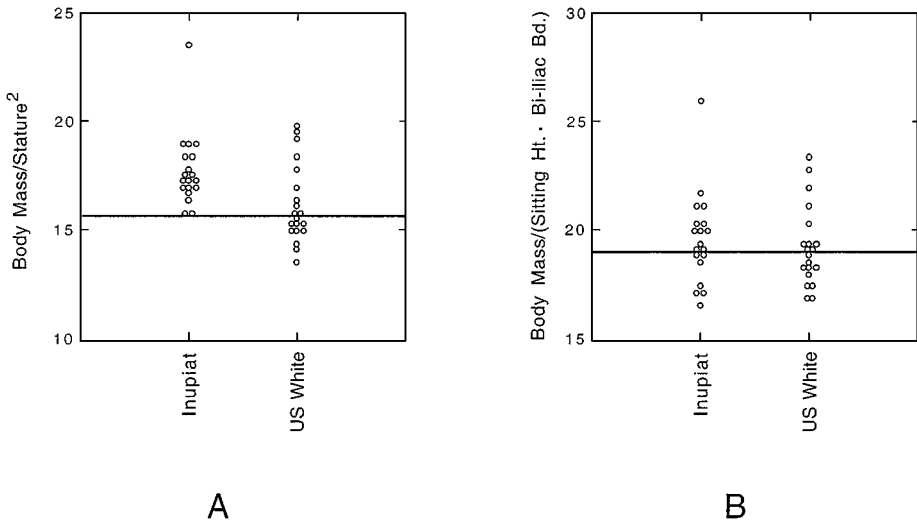


Figure 4 Two body mass indices applied to 9-year-old Inupiat and U.S. white children (see text for derivation of samples). Horizontal lines indicate U.S. white medians. (A) Traditional body mass index (BMI); (B) trunk frame index (TFI).

Figure 4 compares use of the TFI and BMI indices as applied to Inupiat and U.S. white children. The Inupiat data are from northern Alaska and were collected around 1970 by Jamison and colleagues (Jamison 1978, 1986, 1990). Individual raw anthropometric data were obtained courtesy of P.L. Jamison (personal communication). The U.S. white data are from the Denver Growth Study, collected over several decades (McCammon 1970), although all of the measurements included here were taken in the 1950s. Individual data for 20 subjects (10 males and 10 females), followed longitudinally from near birth to late adolescence, were obtained from the study database (R.M. Siervogel, personal communication). An age of 9 years was chosen for comparisons, because it avoids complications owing to differences in timing of the adolescent growth spurt and is an age with little sexual dimorphism in the BMI, allowing pooling of males and females (WHO 1995). (The same similarity between the sexes at this age, within group, was confirmed here for both BMI and TFI.) Anthropometric data were available at this age for 19 Inupiat children (13 females and 6 males, “nonhybrids” only).

BMI is significantly higher in Inupiat than in U.S. whites ($p < 0.01$, t test). In fact, all of the Inupiat children fall above the median BMI for the Denver sample (Figure 4A). In contrast, there is no significant difference between Inupiat and U.S. white children for TFI ($p > 0.50$), and the distribution of individual data points, with the exception of one high Inupiat outlier, is very similar in the two groups (Figure 4B).

These Inupiat children, like other Eskimo children, do not have large skinfolds. Mean skinfold breadths for 9-year-old boys and girls, respectively, are 8.1 mm and 10.0 mm for triceps and 5.5 mm and 7.1 mm for subscapular [unlike BMI, there is sexual dimorphism for skinfolds at this age (WHO 1995)]. The triceps skinfolds are slightly below, and the subscapular skinfolds slightly above the 50th percentiles for 9-year-olds based on U.S. standards (WHO 1995) or the Denver Growth Study sample (Hansman 1970).

Thus, for the Inupiat sample as a whole, the TFI appears to more faithfully represent relative fatness than does the BMI. The same may be true on an individual basis. The one high outlier for both BMI and TFI is also a high outlier for skinfold values (above the 90th percentile for her age according to the same reference samples), i.e., both indices successfully identified her as overweight relative to direct subcutaneous fat measurements. The next highest BMIs among the Inupiat were from two boys, both above the 85th percentile for their age, the recommended cutoff for "at risk for overweight" (WHO 1995). Interestingly, despite identical BMIs in these boys (18.9), skinfold breadths were high in one (13.0 mm and 9.0 mm for triceps and subscapular, respectively) but not in the other (6.0 mm and 5.0 mm). The individual with the large skinfolds had a relatively high TFI of 21.7—the second highest index in the group—whereas the individual with the moderate skinfolds had a TFI of 20.1, closer to the median of the group (see Figure 4). The identical BMIs but differing TFIs can be attributed to body build differences: The individual with the smaller skinfolds was relatively larger in both bi-iliac breadth and sitting height (> 1 sample standard deviation above the other boy for bi-iliac breadth/stature and sitting height/stature). Thus, the BMI tended to overestimate his fatness level, whereas the TFI, which incorporates trunk shape, did not. A noncorrespondence between secular changes in skinfold measurements and BMI has also been noted for Eskimo (Inuit) adults (Leonard 2000), which could be due to similar body shape differences (see Schaefer 1970).

Although this discussion has focused on identification of overweight status in Inupiat, an equally valid question could be posed regarding underweight. As Jamison (1990) has noted, we cannot tell from current weight-for-height data based on U.S. standards where a borderline malnourished Inupiat child would fall. The same reasoning applies, of course, to populations in other areas of the world where malnutrition is severe and that also exhibit apparently intrinsic (genetic) differences in body proportions from U.S. standards, e.g., relatively longer limbs and narrower bodies in lower-latitude populations. Incorporation of such proportional differences into body mass indices should provide more sensitive and less population-biased measures of under- and overweight. The apparent developmental lability of some body proportions, e.g., lower limb length relative to stature (Tanner et al. 1982), does not negate this argument. It is important to recognize such secular trends in skeletal proportions if soft tissue differences are to be distinguished from general body shape changes. For example, Takahashi (1986) found that among Japanese older adolescent and younger adult women, stature had increased more than body mass in the 1970s and early 1980s, which the author attributed primarily to dietary

and lifestyle changes resulting from a desire “to be slimmer” and “to keep from getting fat.” However, no clear secular trend in skinfold thicknesses could be discerned. The implication is that (skeletal) body breadth did not increase as fast as stature during this time period. In fact, just such a secular trend was found among Japanese-Americans living in Hawaii (Froehlich 1970) as well as in other populations with secular increases in stature (see Ruff 1994 for a discussion). Thus, the inclusion of a body breadth measurement in the Japanese analysis could have provided better discrimination of actual soft tissue changes.

CONCLUSIONS

Both body size and body shape vary systematically in modern humans, and did so in earlier humans as well. Subsequent to the development of full bipedality and prior to the adoption of food production, the most important environmental influences on size and shape were likely climate and technological sophistication. Nutritional and overall health levels may account for an increasing proportion of variation during the Holocene, including very recent secular trends. Differences in body form among modern humans are thus likely to result from an interaction between long-term genetic factors, including climatic adaptation, as well as developmental environment, including diet and disease. In assessing anthropometric variation in living populations, it is important to consider the influence of both kinds of factors in order to distinguish one from the other. Methodologies that incorporate critical dimensions of body form can shed new light on human adaptation in both paleontological and neontological contexts.

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