

Mechanical determinants of bone form: Insights from skeletal remains

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Abstract

Analysis of skeletal remains from humans living in the past forms an important complement to observational and experimental studies of living humans and animal models. Including earlier humans in such analyses increases the range of variation in both behavior and body size and shape that are represented, and can provide insights into the adaptive potential of the modern human skeleton. I review here a variety of studies of archaeological and paleontological remains that have investigated differences in skeletal structure from a mechanical perspective, focusing in particular on diaphyseal strength of the limb bones. Several conclusions can be drawn from these studies: 1) there has been a decline in overall skeletal strength relative to body size over the course of human evolution that has become progressively steeper in recent millennia, probably due to increased sedentism and technological advancement; 2) differences in pelvic structure and hip mechanical loadings affect femoral shape; 3) activity patterns affect overall strength and shape of both the lower and upper limb bones; and 4) responsiveness to changes in mechanical loading varies between skeletal features (e.g., articulations versus diaphyses) and by age.

Keywords: Mechanics, Skeleton, Archaeology, Paleontology

Introduction

The modern human skeleton represents an end point of several million years of ongoing adaptation since our separation into an independent evolutionary lineage. This long archaeological and paleontological record should be of interest to human biologists for several reasons. First, it provides a temporal context for interpreting living human variation. For example, geographic clines in body shape observable today can be shown to be an ancient characteristic of humans (probably climatically determined) and are thus likely to be primarily genetically rather than environmentally based, with implications for assessing modern nutritional status from body form¹. As another example, it is evident

that bone strength relative to body size has declined in recent humans compared to our earlier ancestors², likely due to increased sedentism and technology that has reduced mechanical demands on the body. Bone fragility with aging in modern industrialized countries can be seen as, in part, a consequence of this temporal trend towards reduced bone strength, coupled with reduced activity levels^{3,4}.

The second reason for considering ancient human skeletal remains is that ancient humans encompass a wider range of morphological and behavioral variation than living humans¹. This is certainly true in comparisons with very early human ancestors, who were in some ways more ape-like in morphology and behavior than modern humans⁵. Even later human ancestors of our own genus (*Homo*) show some significant morphological differences from modern humans⁶, and given the huge range of technological sophistication and subsistence strategies represented in the archaeological and fossil record⁷, were probably subjected to a correspondingly large range of mechanical environments. Thus, in a way human ancestors represent a series of "natural experiments" that may shed light on the general process of bone adaptation to various mechanical stimuli, for example, to variation in hip morphology or activity level^{6,8}. Finally, *intra*-popula-

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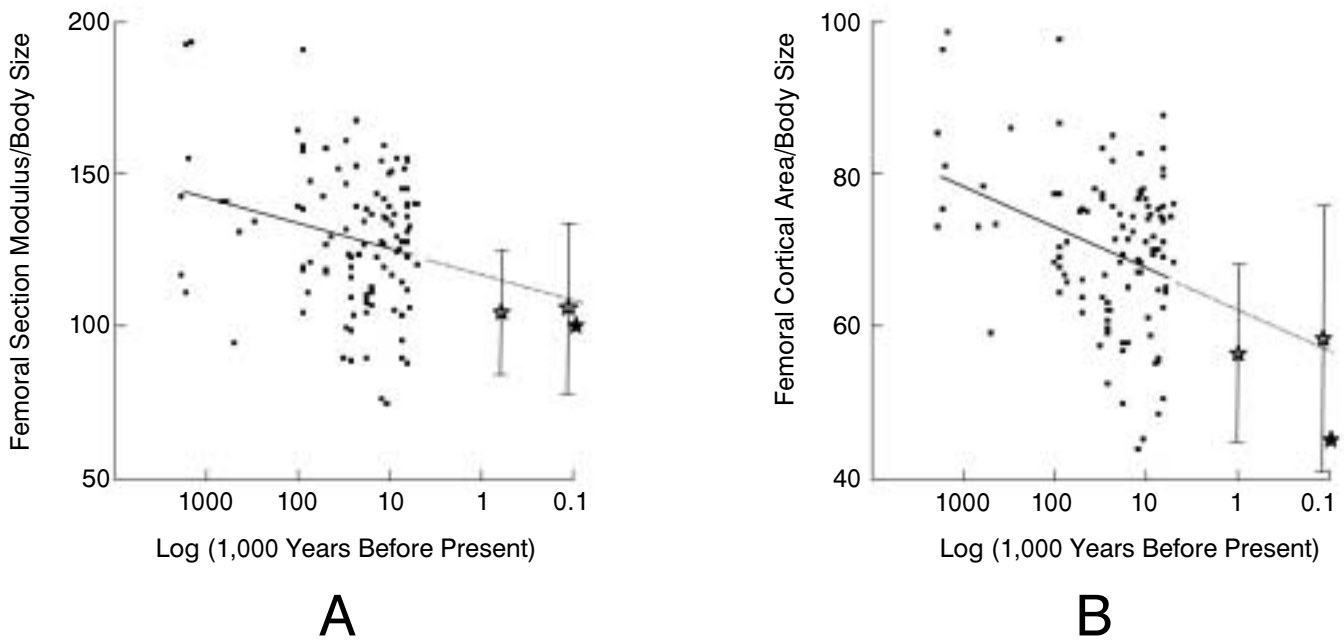


Figure 1. Temporal changes in femoral mid-shaft strength in early prehistoric *Homo* (small squares) and means for three modern human samples (open stars: Pecos archaeological and modern East African sample means \pm 2 SD; filled star: modern US white sample mean). All data standardized by body size (see text). A. Polar section modulus (average bending/torsional strength). B. Cortical area (compressive strength). Solid line is least squares regression fit through prehistoric data; dotted line is theoretical extrapolation to twentieth century. Prehistoric data from references 2 and 14; modern data from references 4 and 10.

tional variation in both genetics and environment in earlier human populations was almost certainly smaller than in most modern populations (at least modern industrial populations), allowing clearer definition of associations between skeletal structure and function, such as those arising from sexual dimorphism in body shape or behavior⁸.

I review here several studies of past populations that have attempted to relate structural variation in limb bones to their *in vivo* mechanical roles. Long bones are particularly amenable to this type of analysis because their diaphyses can be relatively simply modeled as engineering beams⁹. Long bone diaphyses are also often preserved in the archaeological/paleontological record, increasing the available sample sizes. The lower limb is emphasized, in part because its more stereotypical loading during gait facilitates interpretations of structural differences. Several recent studies of upper limb bone structural adaptation are reviewed in the last section.

Temporal changes in relative femoral strength

Figure 1 shows temporal trends in mid-shaft femoral strength over the past two million years within the genus *Homo* (our immediate ancestors, originating about 2-2.5 million years ago and extending through the present as *Homo sapiens*). Femoral strength is assessed as the polar section modulus, a measure of average bending and torsional

strength^{1,10}, and cortical area, a measure of compressive strength. Because lower limb bone loadings are dependent in part on body mass, and because body mass varied systematically among earlier *Homo*¹¹, femoral strength is expressed relative to body size. For bending/torsional strength, body size is the product of body mass and femoral length, and for compressive strength simply body mass¹⁰. Body mass was estimated from either femoral head size or reconstructed stature and pelvic breadth^{11,12}. Cross-sectional properties of the femora were obtained through CT, multiplane radiography, or photography of fortuitous breaks, with section outlines processed using customized image analysis software^{2,13,14}.

Data in Figure 1 are plotted on a logarithmic time scale, because temporal changes in relative bone strength have been shown to be approximately log-linear². There is a significant exponential decline of about 15% in both bending/torsional ($r = 0.23$; $p < 0.02$) and compressive ($r = 0.33$; $p < 0.001$) femoral strength from the earliest specimens, dated to between 1.5 and 1.9 million years ago, to the most recent specimens, dated to about 5 thousand years ago. Three modern population means are also shown, including one from a late prehistoric/protohistoric archaeological site (Pecos Pueblo, New Mexico)¹⁰ and two samples derived from anatomy teaching collections from East Africa¹⁰ and US whites⁸. Body mass was estimated from reconstructed stature and measured pelvic breadth in the Pecos and East African

samples¹⁰, and from mean estimated stature (from mean femoral length) together with mean weight for height in an appropriate reference sample¹⁵ for the modern US whites. Because individual body size data were not available for the US white sample, only the means for this sample are given in Figure 1. The three modern data points all lie close to or below an extrapolation of the regression line through the early prehistoric sample, showing that the exponential decline in bone strength has not leveled off, but if anything has increased at an even faster pace over the past few thousand years. The modern US sample is especially low, particularly in cortical area. (Only individuals under 60 years of age were included in this sample, to avoid the most extreme effects of age-related bone loss. The mean age of this sample is 43 years, which is not too different from some Paleolithic human samples, e.g., the adult Neanderthal sample from Shanidar, which has an average age at death of about 35 years¹⁶. The Pecos Pueblo sample had an average age of 34 years. The East African sample was not precisely aged, but apparently included individuals spanning an age range from early adulthood to advanced age.) The total change in relative bone strength through the modern data points is about 30%. Interestingly, articulations show little, if any, temporal change in size relative to body mass².

The ever-increasing decline in relative bone strength over the past two million years is most likely explained by advances in technology that have increasingly protected our bodies from physical demands⁷. This is especially true over the last several thousand years, during which the pace of technological change has also been the most rapid. Lack of activity-induced bone deposition during life may contribute to the increase in osteoporotic fractures late in life in modern industrialized countries: more active recent populations appear to maintain more optimum bone structure⁴. There are indications that even earlier human ancestors than those shown in Figure 1 had even stronger bones relative to body size⁵, as do living great apes¹⁰. Thus, it would seem that human cultural achievement has not all been positive, resulting in a more fragile skeleton that is more injury-prone in later life. Such results argue strongly for the benefits of physical activity throughout life¹⁷.

Age effects on bone structure

Well-preserved prehistoric juvenile remains are much rarer than adult remains, although those that have been measured show a similar increase in relative bone strength compared to modern juveniles of similar ages¹⁸. However, at least one famous early *Homo* juvenile – an 11-year-old male skeleton from about 1.5 million years ago (the "Nariokotome boy" from West Lake Turkana in Kenya) – has unusually thin cortices compared to adult early *Homo* specimens from the same general time period, more similar to those of a modern human adult (Figure 2). It can be shown that these thinner than expected cortices are probably a product of his age: modern human children have relatively thin cortices until

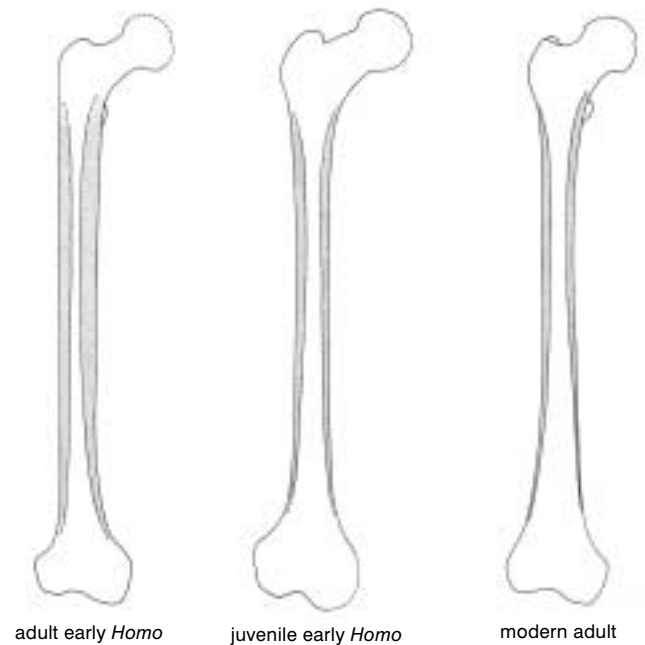


Figure 2. Tracings from A-P radiographs of three femora: an adult early *Homo* (KNM-ER 1472), a juvenile early *Homo* (KNM-WT 15000) and a modern human (32 year-old female). All specimens scaled to about the same length (KNM-ER 1472 is actually about 7% shorter than the other two specimens). There is some distortion in the distal end of KNM-WT 15000 due to postmortem crushing. Dotted lines on external surfaces indicate reconstructed contours.



Figure 3. Tracings of sections from the proximal femur (about 1/3 of femoral length from the hip joint) in two early *Homo* femora (KNM-ER 1481a, from 1.9 million years ago [left] and KNM-ER 737, from 1.6 million years ago [center]) and a modern human femur (from Pecos Pueblo) (right). Medial is to the left, anterior is up. All sections have been standardized to the same anteroposterior or external diameter to better illustrate shape differences.

mid-adolescence, when the endosteal surface changes from a state of net resorption to one of net deposition^{18,19}. Increased mechanical loading leads to greater subperiosteal expansion of long bone cortices prior to mid-adolescence, and greater endosteal contraction thereafter^{18,20,21} (although this effect has been demonstrated most convincingly in the upper limb in females). Early human adults have both expanded subperiosteal dimensions and contracted medullary cavities relative to modern adults (Figure 2)², consistent with a life-long

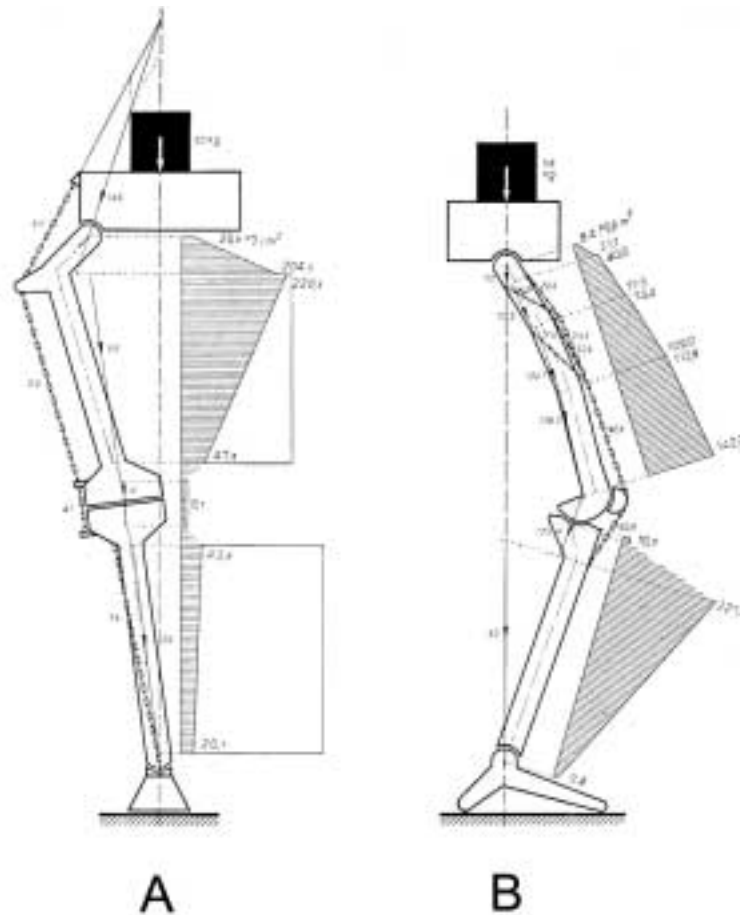


Figure 4. Predicted stresses in the femur and tibia during the stance phase of gait, as calculated by Pauwels. A: mediolateral stresses; B: anteroposterior stresses. Chains represent muscle/ligamentous tensile forces. Hatching indicates maximum stresses (bending plus compressive). (Figures 17 and 18, p. 204, in *Principles of Construction of the Lower Extremity*. Their significance for the stressing of the skeleton of the leg. F. Pauwels, *Biomechanics of the Locomotor Apparatus*. Springer-Verlag, Berlin: 1980. Used with permission of Springer Publishers.)

increase in mechanical loading. The early human juvenile shown in Figure 2 has less robust cortices, and in particular shows no evidence of a small medullary cavity, which is consistent with his pre-pubertal age (he still exhibits increased overall bone strength relative to modern children of his age range¹⁸). Interestingly, his articulations appear large relative to his diaphyseal cortical dimensions, which is also the case in modern children: articulations follow a different growth trajectory, more similar to that in bone length and stature (they "grow ahead" of current body mass)¹⁸. Bone cortices have a growth pattern more similar to that in body mass, especially in the weight-bearing lower limb, with a later age of peak adolescent growth velocity²².

Thus, long bone proportions change constantly during growth, both externally and internally, in part due to differential sensitivity to mechanical stimulation. Diaphyseal cross-sectional strength appears to be much more responsive to changes in mechanical loads (and thus tracks body mass, especially in the lower limb), while bone length and articular

size are less environmentally modifiable²²⁻²⁵. These observations have implications regarding growth tracking, the prediction of adult skeletal strength from childhood measurements, and the expected effects of environmental modification (e.g., exercise intervention programs) on bone morphology during different periods of growth²⁶.

Femoral cross-sectional shape and pelvic morphology

Overall strength is not the only structural feature of long bones to change systematically throughout human evolution. As can be seen in Figure 2, femoral neck length is relatively long in early *Homo* compared to modern humans (this is characteristic of all early human ancestors, including those prior to the origin of *Homo*). There is also a complex of traits in the pelvis and femur that distinguishes early *Homo* from more modern humans that has long been recognized^{27,28} but that remained unexplained until recently⁶. These include a femoral

shaft that is greatly expanded mediolaterally, especially proximally (nearer the hip joint) (Figure 3) and a number of pelvic traits, all of which are consistent with a relatively mediolaterally wide pelvis⁶ (although no complete early *Homo* pelvis or even os coxa has yet been discovered from this time period, prior to 300,000 years ago). In order to understand the relationship between these traits, it is necessary to first consider the pattern of mechanical loading and resultant stresses of the human lower limb during weight support.

Figure 4 is taken from Pauwels' classic study, reprinted in English in 1980²⁹. It shows the predicted stresses in the femur and tibia (modeled as columns of constant cross-sectional dimensions) under simulated *in vivo* loadings during the stance phase of gait. Because of its more mediolateral position, and the need to stabilize the trunk over the hip joint during single-legged support through the gluteal abductor mechanism (the tension band connecting the greater trochanter of the femur with the pelvis), the proximal femur exhibits large predicted stresses in the mediolateral (M-L) plane (Figure 4A). In contrast, the distal femur and tibia undergo their largest predicted stresses in the anteroposterior (A-P) plane, due to the A-P displacement of the knee joint (Figure 4B). As Pauwels recognized, these models are by necessity greatly simplified. It is also impossible to directly test all of these predictions *in vivo*, e.g., using strain gauges, although those *in vivo* strain data that have been collected are consistent with the models^{30,31}. For general comparative purposes the models probably adequately represent some of the critical features of lower limb mechanical loading during weight support.

Using a similar approach, it can be demonstrated theoretically that increasing femoral neck length should lead to an increase in M-L bending of the femoral shaft, a prediction borne out by empirical comparisons of femoral shaft morphology among modern humans⁶. Since all early human femora have relatively long necks (Figure 2), this may in part explain the mediolateral buttressing of the proximal shaft in these specimens (Figure 3). The long femoral neck itself may be explained by the need to provide additional leverage around the hip joint for the gluteal abductors, because of the wider pelvis (specifically, the wider distance between the hip joints). There is other evidence from the skeletal material itself that the gluteal abductors were in fact very strong in early *Homo*^{6,27,32}, supporting this model. This, too, should have increased M-L bending of the femoral shaft⁶.

The increased M-L distance between the hip joints in early *Homo* may be related to a different birth mechanism whereby the neonate's head was maintained in a transverse (M-L) orientation rather than undergoing an M-L to A-P rotation during birth as occurs in modern humans^{6,33}. This in turn may have limited increases in neonatal head size, necessitating birth of a relatively immature (secondarily altricial) infant³⁴ and constraining increases in relative brain size (encephalization). In fact, relative to body size, brain size did not increase significantly between at least 1.5 and 0.5 million years ago¹¹. After this, relative brain size increased rapidly, and at the

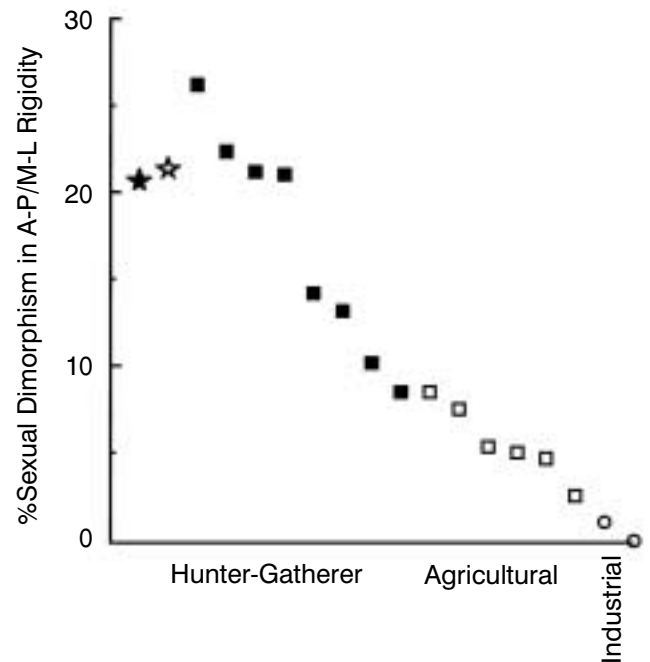


Figure 5. Sexual dimorphism in anteroposterior to mediolateral bending rigidity in the midshaft femur, measured using sex/sample means as [(male-female)/female] * 100. Filled star: Neanderthals; open star: Upper Paleolithic humans; filled squares: recent archaeological hunter-gatherers; open squares: recent archaeological agriculturalists; open circles: industrial. Samples described in references 8 and 38-40.

same time the early *Homo* pelvic-femoral structural complex disappeared⁶. These important but seemingly disparate evolutionary events can be tied together by taking a mechanical approach to human lower limb structural variation.

Sexual dimorphism in lower limb bone cross-sectional shape

Males and females are sexually dimorphic in pelvic structure, so, given the above results, it is reasonable to expect sexual dimorphism in femoral cross-sectional shape as well. In fact, comparisons among a number of modern human populations show this to be the case, with females having slightly more M-L strengthened proximal femoral shafts, corresponding to the increased M-L distance between their hip joints (again related to obstetrics)⁸. However, the same comparisons also demonstrate significant sexual dimorphism in cross-sectional bone shape more distally in the lower limb, peaking in the region about the knee. Furthermore, this dimorphism varies systematically depending upon subsistence strategy⁸.

This latter finding appears to be explained by variation in A-P (rather than M-L) stresses, the dominant mechanical factor in the region near the knee joint (Figure 4B).

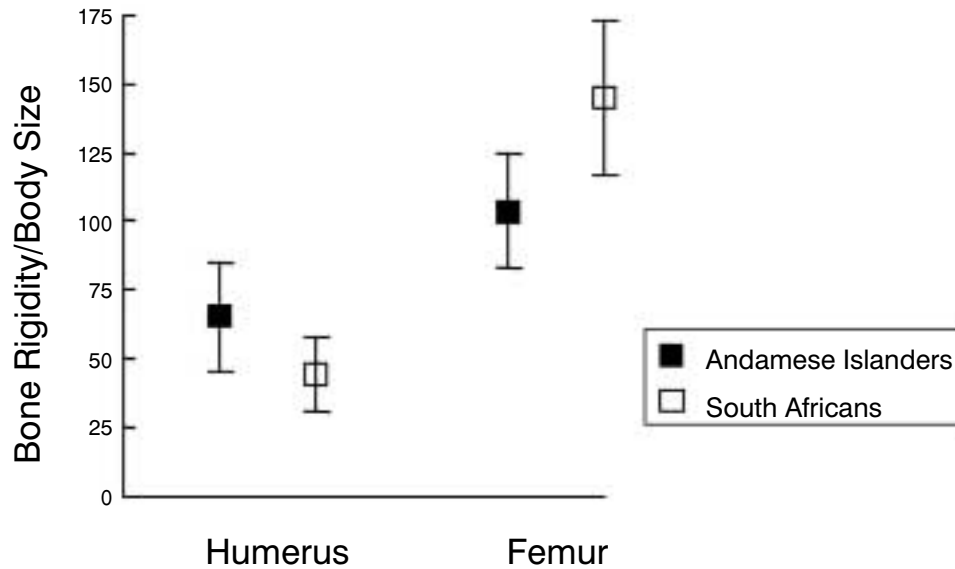


Figure 6. Polar second moments of area in the midshaft humerus and femur, standardized for body size, in Andamese Islanders and later Stone Age South Africans (Mean \pm 1 SD)⁴⁷. "Body size" is humeral length^{5,33} for the humerus, and body mass (estimated from femoral head size) \cdot femoral length for the femur. Humeral values multiplied by 10^{11} , femoral values by 10^2 . Original reference⁴⁷ reported data by sex, with all differences between populations significant at $p < 0.01$; data combined across sexes here for simplicity.

Anteroposterior bending of the distal femur and proximal tibia would be expected to increase greatly with increased flexion of the knee joint²⁹. Running also greatly increases A-P bending of the tibial diaphysis³¹ (also see results of animal strain gauge studies, where maximum strains in the femur and tibia become more A-P oriented in running versus walking^{35,36}). Thus, activities that involve running and movement over rough terrain, e.g., climbing hills, would be expected to preferentially increase A-P bending loads in the region near the knee joint. Sexual dimorphism in activity patterns varies systematically with subsistence strategy, with males engaging in more long-distance travel among hunter-gatherers, the sexes performing more equivalent tasks among agriculturalists, and very little dimorphism in locomotor behavior among industrialized populations^{8,37}.

Figure 5 shows average male-female differences in A-P relative to M-L bending rigidity (ratio of A-P/M-L second moments of area) of the midshaft femur in a number of human archaeological (and two cadaveric) samples^{8,38-40}. The midshaft femur is used for comparison here because it is a commonly measured site and thus more data are available; however, patterns of variation in the midshaft femur are representative of the entire midshaft femur to midshaft tibia region, i.e., the region about the knee⁸. It is clear that hunter-gatherers show more sexual dimorphism in cross-sectional shape than agriculturalists (all Native Americans), and industrial samples (one US white, one Japanese) show essentially no sexual dimorphism. Interestingly, two paleontological samples – Neanderthals ("archaic" humans from about 36,000 to 100,000 years ago) and Upper Paleolithic

humans ("early anatomically modern" humans from about 10,000 to 33,000 years ago) show levels of sexual dimorphism that are similar to those of modern hunter-gatherers, suggesting a similar division of labor. This is despite the fact that there are substantial differences in overall morphology of the body and lower limb bones between Neanderthals as a whole and modern humans⁴¹⁻⁴⁵. Also, there is no such subsistence (or temporal) effect on sexual dimorphism in *proximal* femoral cross-sectional shape⁸, as would be expected since there is no evidence that sexual dimorphism in pelvic shape varied systematically between any of these groups. Thus, patterns of variation in long bone cross-sectional structure may provide fairly specific information regarding mechanical loading patterns in the past, provided that the same mechanical model (Figure 4) can be applied to all groups in such comparisons⁴⁶, which is very likely true here.

Structural adaptation in the upper limb

The upper limb bones are more difficult to model mechanically than the lower limb bones, because of the multi-functional nature of the human upper limb and thus the variety of mechanical loadings that it may encounter. Also, body size standardization is more difficult for the upper limb^{10,26}, because it is not a weight-supporting organ. However, several recent studies have examined patterns of variation in bone structure in earlier humans in relation to repetitive, stereotypical use of the upper limb. These studies are useful in defining some of the limits of bone adaptation to very mechanically stressful environments.

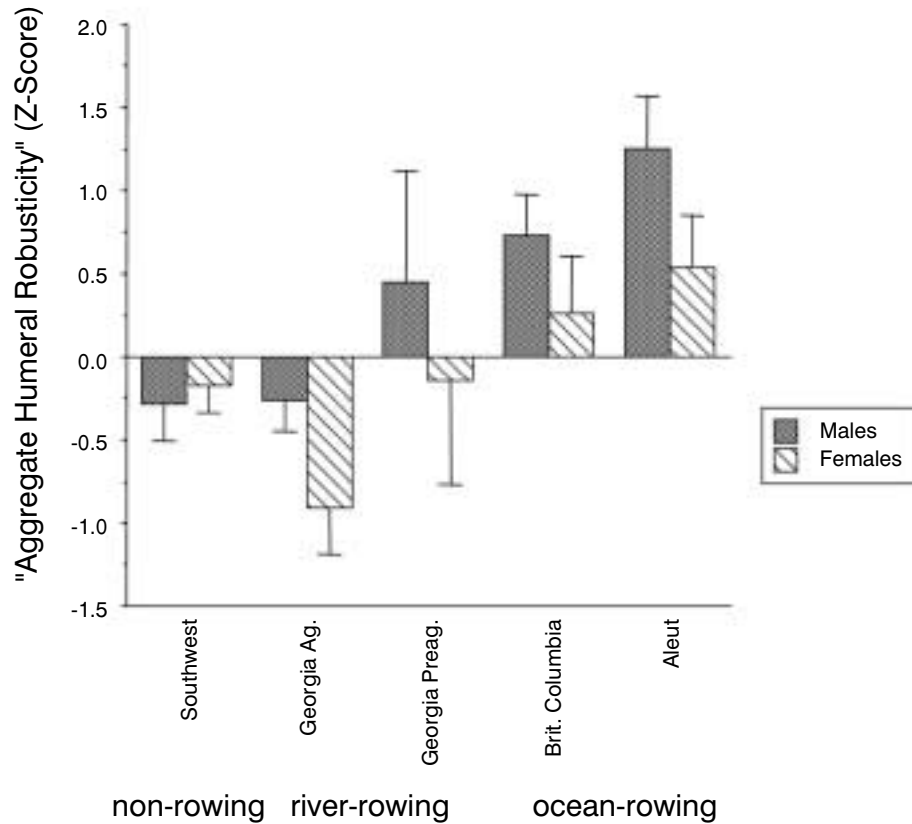


Figure 7. Humeral strength indices in five archaeological Native American samples: Southwestern Puebloans, Georgia Coast agriculturalists and pre-agriculturalists, British Columbians and Alaskan Aleuts⁴⁸. "Aggregate Robusticity" is the average z-score (calculated over all samples) for total subperiosteal and cortical areas, and second moments of area in the A-P and M-L planes and the polar second moment of area, of a section 35% of bone length from the distal end (means \pm 1 SE.). Z-scores standardized over bone length^{5,33}.

Two studies have compared limb bone strengths in recent archaeological samples that varied in the extent to which the upper limbs were used for rowing or paddling. Stock and Pfeiffer⁴⁷ examined cross-sectional diaphyseal properties of upper and lower limb bones in Later Stone Age (2,000-11,000 years ago) South African foragers who inhabited a rugged terrestrial environment, and protohistoric (19th century) Andamanese Islanders who had limited terrestrial but high marine mobility, i.e., through canoe paddling. Figure 6 shows the mean midshaft humeral and femoral rigidities (polar second moments of area) in each group, standardized for body size. ("Body size" was factored in using powers of bone length for the humerus² and the product of estimated body mass and bone length for the femur¹⁰). The marine-adapted Andamese Islanders have significantly greater relative humeral strength than the South African sample, while the terrestrial South Africans have relatively stronger femora. Thus, resource use (marine versus terrestrial) is reflected in differences in upper to lower limb bone strength proportions.

Weiss⁴⁸ compared measures of humeral diaphyseal strength in a series of Native American archaeological samples that varied in the extent to which they used their upper

limbs for paddling or rowing over water: not at all (Southwestern Puebloans), on rivers (Georgia coast), or on the open ocean (British Columbian and Alaskan Aleuts). Figure 7 shows the relative humeral strengths, by sex, for each group. With increasing use of the arms in water transport, the humeral strength index increases. The highest indices are found among the ocean-rowing groups, which, based on ethnohistoric accounts, faced the most difficult and strenuous environmental challenge. Within the Georgia coast groups, the agriculturalists probably paddled on rivers less frequently than the more mobile pre-agricultural foragers, and they exhibit correspondingly lower humeral strength. Weiss notes, however, that females, who probably paddled or rowed much less than males, also show a similar pattern of variation between groups, raising the possibility that factors other than water transport are involved in determining upper limb bone strength (e.g., in the case of the marine-adapted groups, food processing of large marine mammals). Some of these results could also be biased by systematic differences in body shape between groups (more northern groups tend to have relatively shorter limbs), since humeral length was used to standardize strength for body

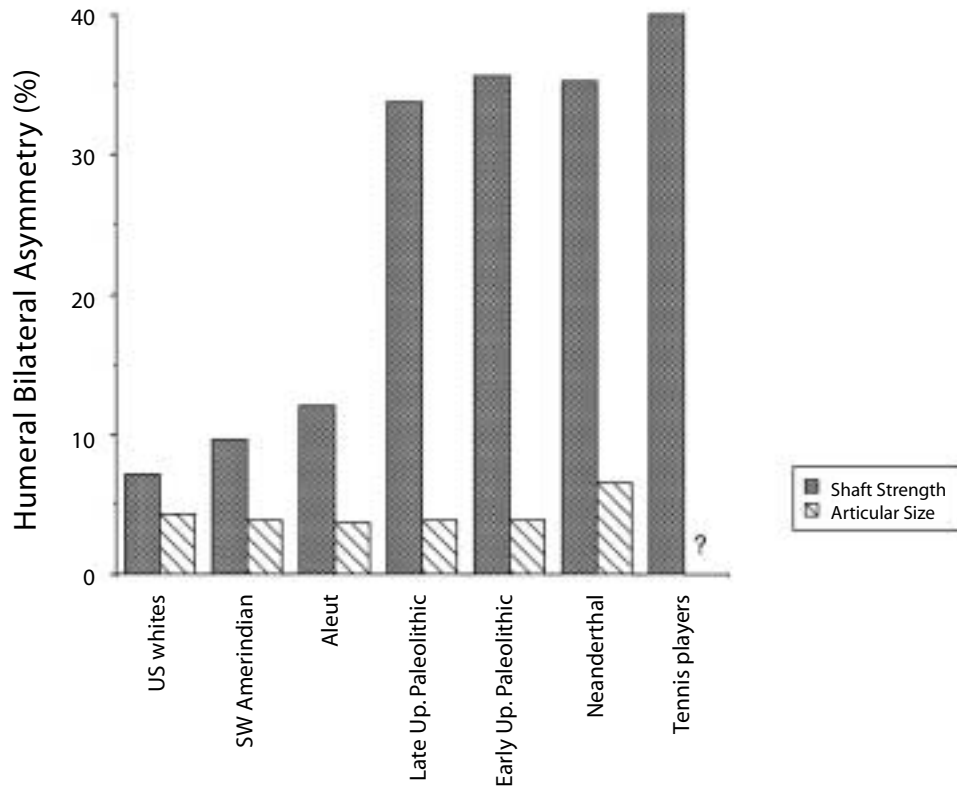


Figure 8. Median percent bilateral asymmetry in the humerus, measured as $[(\text{maximum}-\text{minimum})/\text{minimum}] \cdot 100$, in three recent skeletal and archaeological samples – US whites, Southwestern Puebloans, and Alaskan Aleuts; three Paleolithic samples – Late Upper Paleolithic (20,000-30,000 years ago), Early Upper Paleolithic (9,000-19,000 years ago), and Neanderthals (36,000-100,000 years ago)⁵²; and a modern professional tennis player sample²⁴. Shaft strength is the polar section modulus, measured at 35% of bone length. Articular size is the square of the distal humeral articular surface breadth (see reference 39 for explanation and justification).

size. In a further analysis that attempted to factor in body mass in addition to bone length, differences between groups were generally much more marked among males than among females, better corresponding to cultural/behavioral expectations, although Aleut females still had relatively strong arms.

Bilateral asymmetry in upper limb bone strength is another way to assess bone structural responses to mechanical loading, since most humans strongly favor one upper limb (usually the right) over the other during behavioral use. This method has the advantage of inherently controlling for systemic factors such as body size and nutrition. Comparison of the playing and non-playing arms of racquetball players has been particularly popular, given the expected large and repetitive stresses imposed by such activities on the upper limb bones^{18,20,21,24,49}. Such studies have repeatedly demonstrated significantly increased bone strength in the playing arm over the non-playing arm, and where non-playing controls have been included, increased bilateral asymmetry in the players (although controls also show some bilateral asymmetry). Age dependency of bone mechanical adaptation has also been studied using this design, documenting

differences in responsiveness of the periosteal and endosteal surfaces at different ages, as noted above, as well as differences in overall response between age groups (children and adolescents show more response than adults).

Bilateral asymmetry of the upper limb bones has also been studied in skeletal remains, with some interesting results. In terms of length, weight, muscle scar development, and strength, "right dominance" of the upper limb bones has been present for at least 100,000 years^{24,50}, and possibly much longer⁵¹. Bilateral asymmetry in bone strength is greater in earlier, Paleolithic samples than in more recent samples. Figure 8 shows the average (median) asymmetry present in humeral diaphyseal strength in three recent skeletal samples and three earlier samples⁵², as well as in a sample of living professional tennis players²⁴ originally measured by Jones et al.⁴⁹. Among the recent skeletal samples, asymmetry in strength is greatest among Aleuts, as might be expected given their very rigorous lifestyle (see above). Strength asymmetry in the Paleolithic samples is much higher, almost equal to that found in living professional tennis players, who have extraordinarily high levels of asymmetry (about 40% difference between arms). Possible explanations for this

include stereotypical behavioral patterns that involved greater use of one limb (normally the right) in strenuous activities such as spear thrusting⁵³.

Figure 8 also shows average asymmetry in distal articular "area" (breadth squared) of the humerus in the same samples, except for the tennis players, where such data were not available. Unlike diaphyseal asymmetry, articular asymmetry is equivalent in all the groups (perhaps slightly higher in Neanderthals), and is smaller than diaphyseal strength asymmetry. Thus, there is no systematic increase in articular asymmetry in populations with more rigorous lifestyles. This is in accord with other evidence that indicates lower responsiveness of articulations – at least externally – to mechanical loadings during life^{24,25}.

Conclusions

Research involving human skeletal remains forms an important complement to experimental and observational studies of living humans and/or animal models. The vast majority of humans lived in the past, and an appreciation of the range of variation present among such populations leads to a deeper understanding of modern skeletal morphology and functional adaptation. One of the clearest messages from such an analysis is the extraordinary degree to which the skeleton can adapt to differences in mechanical loading, both positive and negative. A temporal decline in average bone strength, increasing exponentially, has led to a 30% decrease in average femoral strength relative to body size over the past two million years, with half of that decrease occurring over the past several thousand years alone. While a genetic component to this decline can not be discounted, it is perhaps revealing that modern athletes can increase their bone strength by at least this amount through increased mechanical loading, as documented by bilateral comparisons of the playing and non-playing arms of professional racquetball players. This same degree of upper limb bilateral asymmetry can be observed in paleontological specimens as well, indicating a similar range of adaptive bone modeling/remodeling. This suggests similar cellular mechanisms at work, which is not surprising given the similar response of various animal models to mechanical loading/unloading⁵⁴⁻⁵⁶. Thus, one lesson to be learned from comparisons with earlier humans is that we are not necessarily preordained to have weaker bones – our skeletons were once stronger, and they still retain the ability to add bone during life, given the appropriate mechanical stimulus.

Another implication of the results presented here is that both body shape and behavior may influence mechanical loadings on the limbs, and thus bone shape. Both kinds of effects appear to be specific to the mechanically most relevant regions; for example, differences in pelvic structure primarily affect the structure of the proximal femur, while differences in activities involving flexion/extension of the knee have their greatest effect around the knee. This is consistent with experimental studies demonstrating localized skeletal

adaptation to changes in mechanical loading^{17,57}. The results shown here also argue for the inclusion of body shape (as well as body size) parameters in mechanical models¹⁰. With respect to body "size", body mass rather than stature is the mechanically most appropriate dimension, at least for weight-bearing elements²².

Finally, discovery of several important juvenile skeletons in the paleontological record⁵⁸⁻⁶⁰ has played a part in stimulating new investigations of skeletal ontogeny, in particular, patterns of development of long bone cortices and their relationship to mechanical factors^{18,22,23,61,62}. These studies have amply demonstrated the dynamic nature of bone modeling and remodeling during development, and the consequent changes in skeletal proportions that are part of normal human growth, past and present. These and other studies also underscore the critical importance of mechanical factors during skeletal growth and development⁶³⁻⁶⁶. Again, the skeletal studies form a complement to more experimental and observational studies of skeletal growth in living humans and other animals.

Thus, much can be learned from examination of the human archaeological and paleontological record. Living humans represent only a small fraction of the total record of human evolution. Deciphering this record can lead to important insights into the adaptive potential of the modern human skeleton.

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