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# THE HUMERUS VERSUS THE FEMUR: CHANGING PATTERNS OF DIAPHYSEAL ROBUSTICITY ACROSS THE LATE ARCHAIC TO EARLY MODERN HUMAN TRANSITION

*ABSTRACT: A decrease in robusticity has been said to characterize the emergence of modern humans. Analysis of humeral and femoral diaphyses, using a biomechanical cross-sectional geometry methodology, shows that there is a mosaic pattern of changes in robusticity. There is a decrease in humeral robusticity, especially in the Near East. Once body proportions are taken into account, there is only a suggestion of a decrease in lower limb robusticity.*

*KEY WORDS: Human Palaeontology – Postcrania – Robusticity – Neanderthals – Early Modern Humans*

## INTRODUCTION

The postcranial skeleton of late archaic humans such as the Neanderthals of Europe and the Near East has been consistently contrasted with those of early and recent modern humans in terms of its perceived robusticity. In this, robusticity has been seen in terms of articular size, diaphyseal enlargement, the rugosity and size of musculo-ligamentous attachment areas, and the development of processes (vertebral, carpal, etc.) which enhance the mechanical advantages of muscles (e.g. Schaaffhausen 1858, Boule 1911-13, Twiesselmann 1961, Trinkaus 1983, Vandermeersch 1991). In particular, the level of this robusticity has been seen to contrast primarily with the comparatively reduced robusticity of early modern humans from the Middle Palaeolithic of the Near East (from the sites of Qafzeh and Skhul) and the Early Upper Palaeolithic (primarily Aurignacian and Gravettian) of Europe and the Near East (e.g. Vandermeersch 1981, Trinkaus 1983). This led one reviewer (Isaac 1984) to refer to the emergence of modern humans as the "loss of robusticity transition".

More recently, however, the nature and degree of this robusticity shift has come under increased scrutiny, as palaeontological sample sizes have increased, more thorough comparisons to recent (Holocene) humans have been undertaken, and refined analytical techniques are (in some cases) applied to the issue at hand. From this is emerging a mosaic perspective, in which it is recognized that not all of the elements associated (however indirectly) with human postcranial robusticity changed significantly across this Late Pleistocene transition, that the degree of change was variable depending upon the element involved, and that recent humans are, in some cases, as robust as even the Neanderthals and other archaic members of the genus *Homo* (e.g. Churchill 1994, Hambücken 1995, Trinkaus 1996, Bridges 1996, Trinkaus, Hilton 1996).

From this, it has become increasingly necessary to be specific about what is meant by *robusticity* and to employ measures of it which are biologically meaningful. In the context of this, there is an ongoing analysis of the diaphyseal cross-sectional geometry of Late (and earlier) Pleistocene genus *Homo* appendicular remains (e.g. Ruff

et al. 1993, 1994, Churchill 1994, Trinkaus *et al.* 1994, n.d., Churchill *et al.* n.d.) designed to assess the patterns of change in both robusticity and loading patterns in anatomically relevant regions of the appendicular skeleton. This paper is a contribution to that research program.

## ROBUSTICITY

Skeletal *robusticity* is best defined as the structural strengthening of a skeletal element, usually through the selective addition of bone tissue, so as to increase the ability of that element to resist physiologically normal biomechanical loads placed upon it. Consequently, since normal physiological loads are determined by: 1) the size of the individual, 2) the lengths of the moment arms which determine the actual force applied to a specific skeletal region, and 3) the activity level of the individual, robusticity combines the absolute amount of mechanically relevant bone tissue in the skeletal element with appropriate measures of body mass and/or regional anatomical proportions. In this, body mass and/or regional proportions are essential for the appropriate scaling of the structural integrity of the skeletal element of concern. Thus, robusticity is a special case of shape, a biomechanically relevant case. It cannot be quantified merely by any absolute measure of size, but it must compare the structural properties of the element of concern to a relevant measure of body or body segment dimensions.

For human upper limbs, which are normally non-weight-bearing, it is primarily the dimensions of the appendicular skeletal elements which are relevant. For the human lower limbs, which are normally weight-bearing, some combination of body mass and appendicular element dimensions is necessary.

## DIAPHYSEAL CROSS-SECTIONAL GEOMETRY

Since the diaphyses of long bones (as well as of metapodials and phalanges) are elongated tubular structures which are mechanically loaded by muscle contraction and body mass and momentum, transferred to the shafts by direct musculo-ligamentous attachments and through joint reaction forces, the diaphyses can be modeled as hollow beams subjected to bending and torsion and to axial compressive loadings. Since cortical bone is a moderately homogeneous structural material which responds mechanically (as well as biologically) to such loads and the induced strains, it is possible to use measures of the quantity and distribution of bone in the diaphyses, at constant percentages of relevant bone length and perpendicular to the diaphyseal axis, to assess its resistance to habitual mechanical loads on the limbs.

Resistance to axial compressive loads is best assessed by the quantity of cortical bone in the cross section, or its *cortical area* (CA). This can be assessed relative to measures

of body or limb element size or other cross-sectional measures. Of the latter measures, the full subperiosteal area, or *total area* (TA), is most appropriate. The cross-sectional area of the medullary cavity, *medullary area* (MA), is the product primarily of differential endosteal resorption during development, is in effect an empty space, and is normally closely associated with the mechanical neutral axis of the diaphysis (where bending and torsion equal zero); it is therefore of less mechanical relevance. Resistance to bending strains is best quantified by *second moments of area* ($I_i$), which combine the quantity of bone in the cross section with its distance from the mechanical neutral axis of the diaphysis. They are the products of units of cross-sectional cortical bone area times each unit's squared distance to an axis of the section, integrated across the cross section. These can be measured around the medio-lateral (x) and antero-posterior (y) axes ($I_x$ and $I_y$ respectively), which measure rigidity against antero-posterior and medio-lateral bending loads respectively. In addition, they can be measured along the major axis of the section, the plane of maximum bending rigidity ($I_{max}$) and the plane perpendicular to the major axis ($I_{min}$). Resistance to torsional loads is quantified by the *polar moment of area* (J, also abbreviated as $I_p$), which is the sum of any two perpendicular second moments of area, usually calculated as $I_{max} + I_{min}$ (or $I_x + I_y$).

The polar moment of area is employed here as an overall measure of diaphyseal strength, since it both measures torsional rigidity and sums perpendicular measures of bending rigidity (for more complete discussions of diaphyseal cross-sectional geometry, see: Lovejoy *et al.* 1976, Ruff 1989, Kimura, Takahashi 1992).

There are two distinct advantages of cross-sectional geometry analysis relative to traditional osteometric approaches (e.g. Bräuer 1988) for assessing robusticity. First, it provides a complete measure of the quantity and distribution of bone in a diaphysis rather than merely a linear approximation of its external dimensions. Secondly, since it measures the bone in mechanical terms, it is possible to formulate and test predictable theoretical scaling relationships between cross-sectional measures and bone lengths (Ruff *et al.* 1993, Churchill 1995). The disadvantage is that it requires either detailed radiographic imaging of the diaphysis (through biplanar radiography or computerized tomography) or fortuitous natural breaks at appropriate proximo-distal locations.

## MATERIALS AND METHODS

Given these considerations, what follows is a comparison of humeral and femoral diaphyseal robusticity for late archaic and early modern humans from the northwestern Old World. As the skeletal elements of the proximal limb segments, the diaphyses of these two bones provide the best reflections of habitual load levels on the upper and lower limbs [given the high level of plasticity of diaphyseal

cortical bone to load levels and patterns (see Trinkaus *et al.* 1994 and references therein)]. As such, they provide general reflections of levels of robusticity as they relate to manipulative and locomotor behaviour respectively.

The analysis is concerned with four samples. The first two consist of Near Eastern and European late archaic humans, most of which can be included within the Neanderthals (*sensu lato*). They include, for Europe, La Chapelle-aux-Saints 1, La Ferrassie 1 & 2, Fond-de-Forêt 1, Krapina 159, 160, 163 to 165, 172 & 173, Lezetxiki 1, Neanderthal 1, La Quina 5, Régourdou 1, Saint-Césaire 1, and Spy 1 & 2, and for the Near East, Amud 1, Kebara 2, Shanidar 1 & 3 to 6, and Tabun 1 & 3. The third sample consists of Near Eastern Middle Palaeolithic early modern humans from the sites of Qafzeh and Skhul (Qafzeh 3, 8 & 9 and Skhul 2 to 7). The fourth sample includes Early Upper Palaeolithic individuals from Europe and the Near East, including Crô-Magnon 4293, 4294, 4296, 4323 to 4325, Dolní Věstonice 3 & 35, Ein Gev 1, Grotte des Enfants 4 & 5, Mladeč 27, Nahal Ein Gev 1, Paglicci 3, Paid-non-Pair 2, Pataud 26.230 & 26.231, Paviland 1, and Stetten 1.

Cross-sectional properties were compared across these samples for two locations, the mid-distal humeral diaphysis (35% section) and the femoral mid-shaft (50% section). Most of the sections were reconstructed. This was done by: 1) transcribing the external contour at the diaphyseal location using silicone dental putty, 2) determining cortical thicknesses using biplanar radiography, and 3) interpolating the endosteal (medullary cavity) contours within the cortical thickness rectangle, following limitations of the external contour. The reconstructed cross-sections, along with a few scaled photographs of natural breaks, were digitized using SLICE (Nagurka, Hayes 1980, Eschman 1992), which computes cross-sectional areas and second moments of area. For a few humeri, the cross-sectional properties were computed using ellipse formulae (Runestad *et al.* 1993) from radiographically determined cortical thicknesses and external diameters.

To assess robusticity, three comparisons were employed. First, cortical area was compared to total (subperiosteal) area, a frequent measure of cortical bone expansion as well as relative medullary size. However, most diaphyseal properties are best scaled to beam length combined, for the lower limb, with a measure of body mass. Therefore, for both the humerus and the femur, cortical area and the polar moment of area were compared to biomechanical bone length. For the femur, since Neanderthals and early modern humans contrast in relative body shape and particularly with respect to body breadth (Trinkaus 1981, Ruff 1991, 1994, Holliday 1995), CA and J were also compared to appropriate powers of femur length adjusted for body breadth.

In this, it is assumed that CA reflects primarily structural resistance to axial loading, which is proportional to body mass. J, on the other hand, combines structural resistance

to loading from both body mass and beam characteristics of the femoral diaphysis. Consequently, for CA, this adjustment is: $(1+k)^2 \times (FL')^3 / 10^6$, in which $k$ is the percent difference in bi-iliac breadth [as a measure of body breadth (Ruff 1991)] relative to a recent Amerindian reference sample (see below), and $FL'$ is femur biomechanical length [distal condyles to proximo-lateral neck (Ruff, Hayes 1983)]. For J, this correction is: $(((1+k)^2 \times (FL')^3) \times ((1+k/2) \times (FL')^1))^{4/3}) / 10^{12} \Rightarrow ((1+k)^{2.67} \times (1+k/2)^{1.33} \times (FL')^{5.33}) / 10^{12}$. In this adjustment for J, $(1+k)^2 \times (FL')^3$ adjusts for relative body mass, $(1+k/2) \times FL'$ accounts for beam length, and raising it to the 4/3 power incorporates beam characteristics (see Ruff *et al.* 1993 for explanation and justification). Dividing by $10^6$ and $10^{12}$ is done to reduce the number of digits in the comparisons.

Bi-iliac breadth is rarely preserved on fossil specimens but is relatively constant within human ecogeographical body proportion groups (Ruff 1991), with an average slope versus femoral length of 0.237 within populations (Ruff, pers. comm.). As a result, bi-iliac breadth (BIB) was estimated for each specimen using either the available reference specimen [Kebara 2 (and La Chapelle-aux-Saints 1 – see Ruff *et al.* 1993) for the Neanderthals, Skhul 4 for the Qafzeh-Skhul humans, and Ohalo 2 for Near Eastern Upper Palaeolithic humans] or the mean of the available specimens (N = 6 for European Early Upper Palaeolithic humans). In this, $BIB_{est} = BIB_{ref} + ((FML_{est} - FML_{ref}) \times 0.237)$, in which the "est" values are for the specimen without a measurable BIB, "ref" are for the reference specimen or sample mean, and FML is femur maximum length. From this, $k$ was computed as: $(BIB / FML) - 0.63$, in which 0.63 is the BIB / FML ratio for the reference Amerindian sample (see Ruff *et al.* 1993).

Since the values are in mm (bone lengths), mm$^2$ (cross-sectional areas) and mm$^4$ (second moments of area), the non-adjusted comparisons are done using plots of the logged ($\ln_e$) values. For the body shape adjusted femoral comparisons, since bone length has been raised to appropriate powers, the raw CA and J values are compared to the adjusted femur length values. For all of the comparisons, males and females are pooled. For the femur, right and left sides are included, averaged when data for both femora are available. For the humerus, the frequently marked level of bilateral asymmetry among Pleistocene *Homo* humeral diaphyses (Churchill 1994, Trinkaus *et al.* 1994) makes it inappropriate to average sides; the right and left humeri are therefore considered separately.

To test for degree of similarity between the late archaic and early modern samples, standard (raw) residuals were computed relative to the pooled regression line. The resultant residuals for each sample were then compared using a t-test assuming unequal variances. However, since the samples are too small (all < 20) to test for normality, a Mann-Whitney U (Wilcoxon rank-sum) non-parametric test was also used, even though it has less power than the parametric t-test. The p-values are provided for both, and they are indicated as $p_t$ and $p_u$.
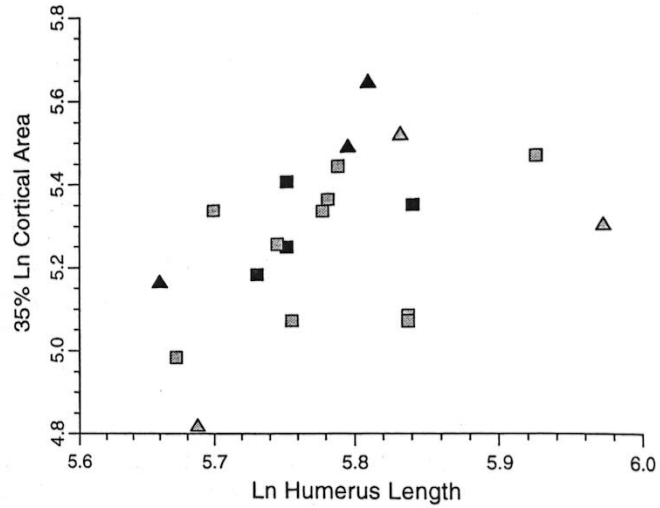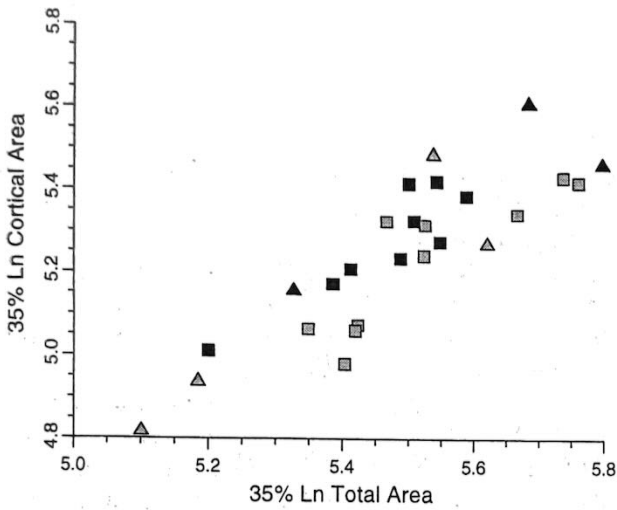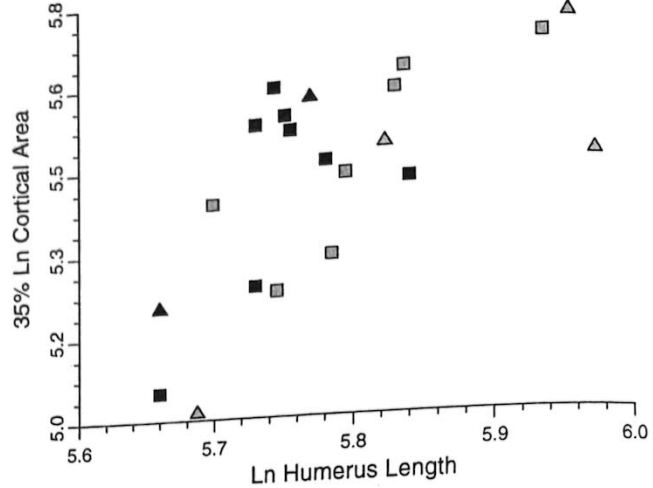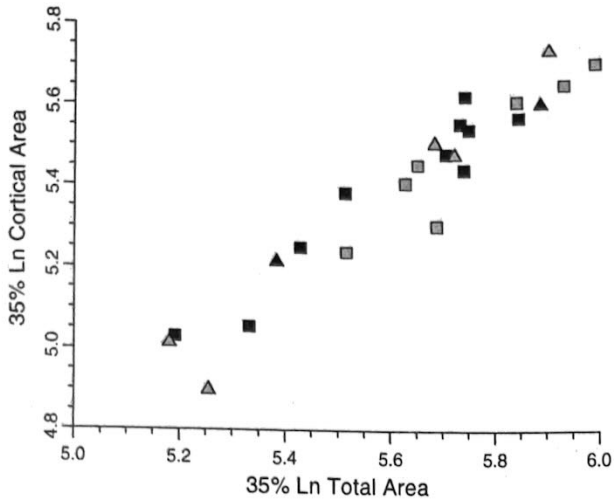
FIGURE 1. Bivariate plots of mid-distal (35%) ln cortical area versus ln total area for the right (above) and left (below) humeri. Solid squares: European late archaic humans. Solid triangles: Near Eastern late archaic humans. Shaded triangles: Qafzeh-Skhul humans. Shaded squares: Early Upper Palaeolithic early modern humans.

FIGURE 2. Bivariate plots of mid-distal (35%) ln cortical area versus ln length for the right (above) and left (below) humeri. Symbols as in *Figure 1*.

## RESULTS

### Humerus

Comparisons of humeral mid-distal shaft cortical area to total area show some differences between the late archaic and early modern human samples *(Figure 1)*. In the right humerus, there is little variation around the respective sample lines with a tendency for the late archaic sample having higher cortical areas for a given total area. This is reflected in a $p_t = 0.172$ and a $p_u = 0.248$ between the two samples. There is more scatter in the left humeral comparison, with a higher cortical area for a given total area for the left late archaic humeri relative to those for the early modern human. The difference in the left humerus is highly significant, with $p_t = 0.011$ and $p_u = 0.008$ between the two samples. However, there is still complete overlap between the late archaic and early modern humans,

with high values being provided especially by Krapina 159, 160 and 165, Shanidar 1, Skhul 4 and Tabun 1, whereas Kebara 2 plus Crô-Magnon 4294, Skhul 5, and Grotte-des-Enfants 4 and 5 have low values.

The comparisons of cortical area to humeral length *(Figure 2)* similarly show considerable overlap between the late archaic and early modern human samples, with the late archaic specimens nonetheless largely exhibiting elevated cortical area for a given bone length. Yet, there are still several early modern human humeri, especially in the left humeral comparison, who fall near the upper limits of the late archaic distribution. This overall pattern is reflected in $p_t$-values of 0.170 and 0.049 and $p_u$-values of 0.121 and 0.166 for the right and left humeri respectively. Therefore, even though only the left $p_t$-value reaches significance at the $p < 0.05$ level, all indicate a consistent difference between the samples. Interestingly,
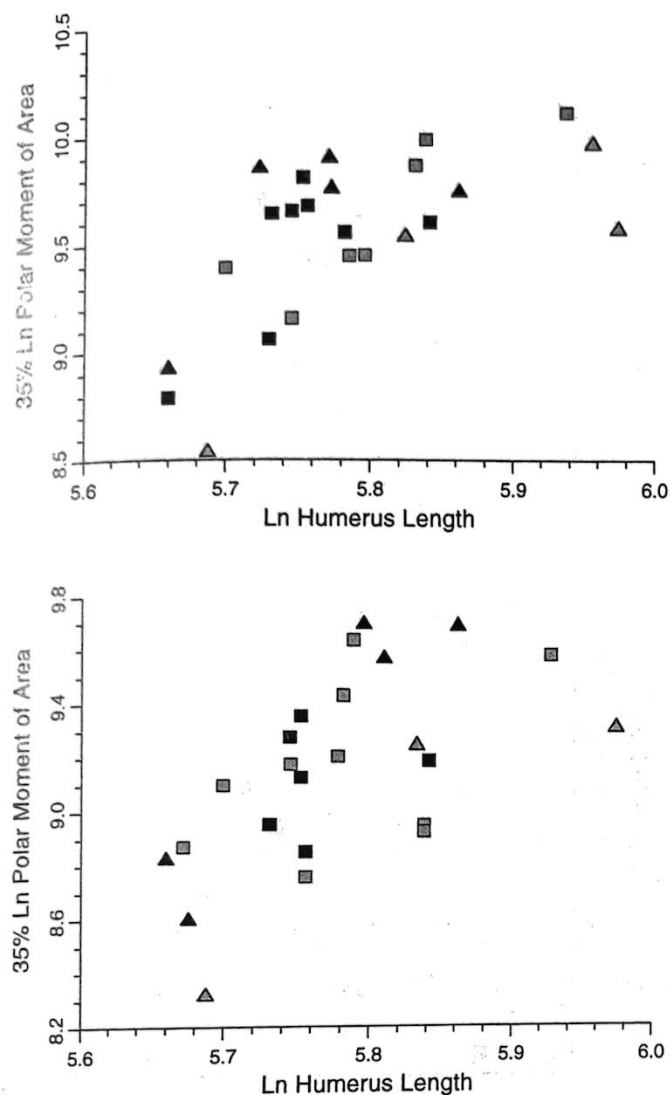
FIGURE 3. Bivariate plots of mid-distal (35%) ln polar moment of area versus ln length for the right (above) and left (below) humeri. Symbols as in *Figure 1*.

humerus (Qafzeh 8 and 9) have values near or below the next highest values, and only the Skhul 4 left humerus is within, although on the low side of, the main distribution. This results in no overlap between the Near Eastern Middle Palaeolithic late archaic and early modern humeri in relative polar moment of area values, despite substantial overlap between the two European samples. As a result, the geographically pooled late archaic versus early modern human samples have low but non-significant $p_t$-values of 0.109 and 0.171 and $p_u$-values of 0.111 and 0.192 for the right and left humeri respectively.

Consequently, there appears to be a pattern of a moderate to strong difference in measures of humeral diaphyseal robusticity between these late archaic and early modern humans, with the strongest difference occurring within the Near Eastern Middle Palaeolithic. The difference is also slightly greater for the right arm in comparisons to bone length but more pronounced for the left humerus in the cortical area to total area comparison.

**Femur**
Comparisons of late archaic and early modern human femoral cortical area to total area parallel to those for the humeri *(Figure 4)*. On average the late archaic humans have higher relative cortical areas, but the distributions for the two samples overlap completely. As a result $p_t = 0.121$ and $p_u = 0.223$, reflecting the clear but modest difference. In this, the only outlier is the low cortical area value for Dolní Věstonice 35.

When log cortical area is compared to log femoral length *(Figure 5a)*, there is a clear tendency for the late archaic humans to have higher relative cortical areas, with all of the high values being those of late archaic humans, all of the low values being from early modern humans, and an overlap in the middle of the distribution. This is reflected in highly significant $p_t = 0.0003$ and $p_u = 0.0009$ between the two samples.
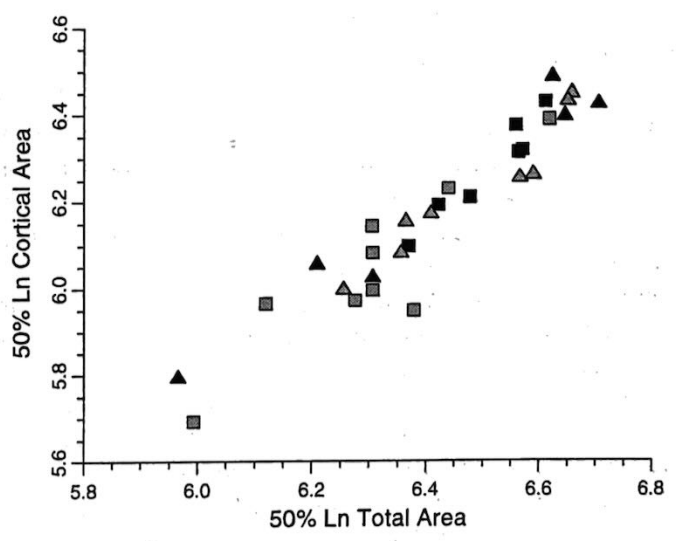
in both arms Skhul 7a and 5 have among the lowest values for relative cortical area, matched in the left arm only by Crô-Magnon 4293 and Paviland 1.

A similar pattern is evident in the comparison of the polar moment of area to humeral length *(Figure 3)*. In this, the left humeri exhibit largely complete overlap between the two samples, but there is less overlap in the right humeri, with several high values for the late archaic sample and two rather low values for the early modern humans. Nonetheless, even in the left humeral comparison, the late archaic humeri are toward the middle or upper portion of the distribution, whereas the early modern humans have a wider distribution with specimens falling in the middle or lower portion of the combined distribution. Relatively low values are especially evident for Skhul 5 and 7a, whereas the other two Near Eastern Middle Palaeolithic early modern humans preserving the right



FIGURE 4. Bivariate plots of femoral mid-shaft (50%) ln cortical area versus ln total area. Symbols as in *Figure 1*.
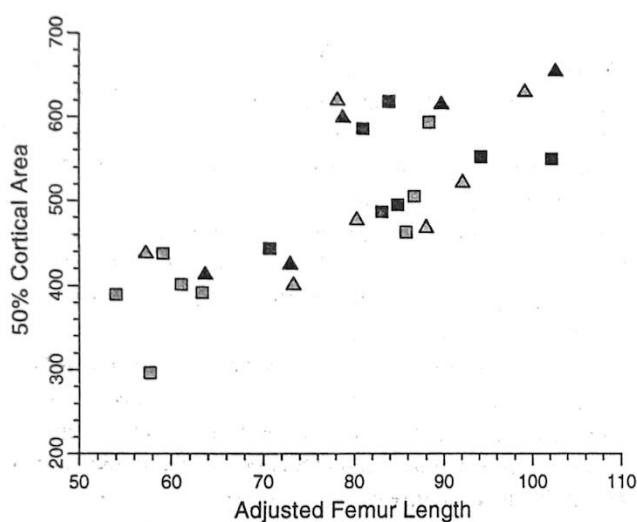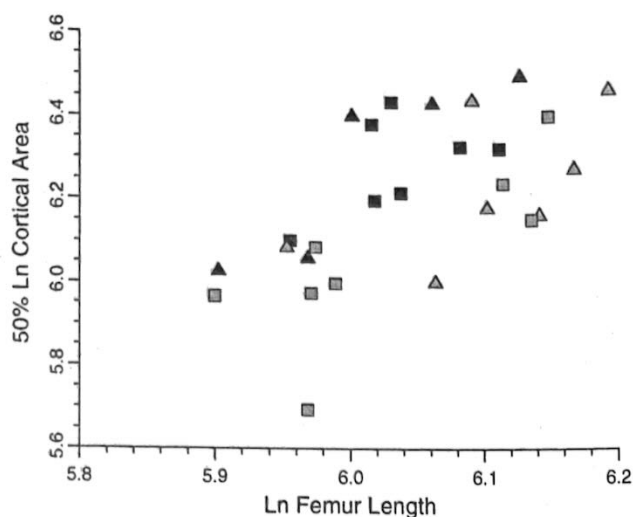
FIGURE 5. Bivariate plots of femoral mid-shaft (50%) ln cortical area versus ln length (above) and cortical area versus adjusted femoral length (see text) (below). Symbols as in *Figure 1*.
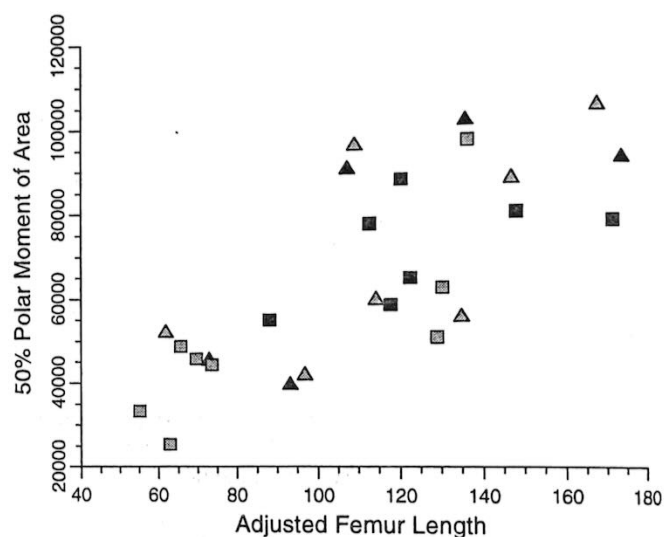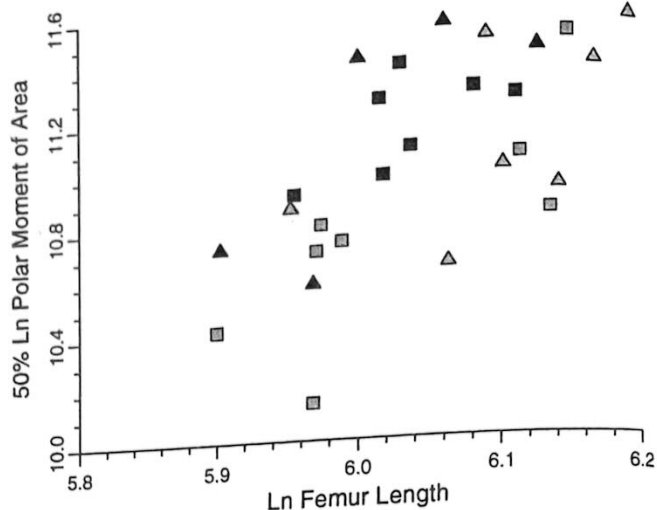
FIGURE 6. Bivariate plots of femoral mid-shaft (50%) ln polar moment of area versus ln length (above) and polar moment of area versus adjusted femoral length (see text) (below). Symbols as in *Figure 1*.

However, when cortical area is compared to adjusted femoral length *(Figure 5b)*, the difference between the samples largely disappears. In the resultant distribution, there is complete overlap between the two samples, with the late archaic humans having on average higher relative femoral midshaft cortical areas ($p_t = 0.345$ and $p_u = 0.329$). Consequently, the difference in relative body breadth, with the Neanderthals having hyperarctic body proportions, the Qafzeh-Skhul humans having highly tropical ones and the Early Upper Palaeolithic humans having warm temperate proportions (Ruff 1994, Holliday 1995), largely accounts for the contrasts in relative femoral cortical area.

A similar pattern is evident in comparisons of the polar moment of area to femoral length and adjusted femoral length *(Figure 6)*. When the log polar moment is plotted against log femoral length, most of the late archaic humans are above most of the early modern humans, producing highly significant $p_t = 0.002$ and $p_u = 0.003$. Yet, when the polar moment of area is plotted against adjusted femoral length, the late archaic humans remain more robust on average, but the difference is non-significant, with $p_t$ and $p_u$ equal to only 0.592 and 0.626 respectively.

In all of these femoral midshaft comparisons, there is little difference between the scatters for the Near Eastern Middle Palaeolithic and Early Upper Palaeolithic early modern human samples, or between the Near Eastern and early European late archaic humans. Regardless of geographical region or associated lithic assemblages, there appears to be a slight but non-significant decrease in femoral diaphyseal robusticity between the late archaic and early modern humans, once relative body breadth is taken into account.

## DISCUSSION

These comparisons of diaphyseal robusticity for the humerus and femur largely, but not entirely, parallel other indications of upper versus lower limb robusticity in these Late Pleistocene hominids. They also raise questions regarding the sources of the apparent similarities and differences in habitual load levels on the humeral and femoral diaphyses, as reflected in their relative cortical areas and polar moments of area.

### Upper Limb Robusticity

The humeral diaphyseal comparisons show a consistent trend in which the late archaic humans are more robust than the early modern humans, although the degree of difference is marked only within the Near East and in the left humeral cortical to total area comparison. At the same time, there is a suite of contrasts between late archaic and early modern humans in upper limb skeletal functional morphology, primarily related to the development of muscle attachment areas and muscular moment arm lengths (or relative mechanical advantages). The former include: a) the breadth of the scapula, b) the *M. pectoralis major*, *M. latissimus dorsi* and *M. teres major* insertions on the proximal humerus, c) the *M. pronator quadratus* crest on the distal ulna, d) the *M. opponens pollicis* and *M. opponens digiti minimi* insertions on the metacarpals, and e) the *M. flexor pollicis longus* tendon on the pollical distal phalanx (Trinkaus 1983, Churchill 1994). The latter include: a) clavicular length and scapular breadth as they affect shoulder rotation, b) the medial rotation of the radial tuberosity, c) the lateral bowing of the radial diaphysis, d) the pronounced development of the scaphoid, trapezial and hamate palmar tubercles, and e) the relative lengths of the pollical phalanges (Trinkaus 1983, Trinkaus, Villemeur 1991, Churchill 1994, Vandermeersch, Trinkaus 1995). All of these involve decreases in the relative mechanical advantages of muscles involved primarily in flexion and rotation among early modern humans relative to late archaic humans. These changes are combined with evidence of a shift in habitual grip strength in the marked decrease in the size of the distal phalangeal apical tufts (Trinkaus 1983, Vandermeersch 1991).

In terms of the relative levels of biomechanical loads that would be placed upon the humeral and other upper limb diaphyses between these two human groups, these two kinds of morphological differences provide interesting implications. The smaller muscle attachment areas among the early modern humans imply that the habitual forces on the diaphyses would have been decreased relative to those of late archaic humans, assuming that the smaller attachment areas imply reduced muscle bodies and hence less use. This would agree with the modest decrease in humeral diaphyseal robusticity, even though the magnitude of the change implied by the muscular origin/insertion areas is greater than that indicated by the diaphyseal robusticity.

At the same time, the decreased mechanical advantages for many of the upper limb muscles indicate that early modern humans would have needed to exert greater muscular contractile force than late archaic humans to generate the same manipulative force. At first glance, this appears to contradict the implications of the muscular attachment areas, since the early modern humans show consistently smaller and/or less rugose insertions, implying less use of muscular force. However, it may well be that the late archaic humans used greater muscular force on a regular basis (hence the larger and more rugose origins/ insertions), and that this was enhanced through their greater muscular mechanical advantages. At the same time, the resultant loads on their diaphyses may have been reduced from what they would otherwise have been by their greater muscular mechanical advantages, possibly diminishing the degree of contrast in humeral diaphyseal robusticity between the late archaic humans.

All of this must nonetheless be seen in the context of a probable reduction in the habitual level of manipulative force utilized by early modern humans relative to late archaic humans. This is supported by the decrease in phalangeal apical tuft dimensions, the one sure contact point between their upper limbs and the environment they were manipulating.

Between the predominantly Middle Palaeolithic late archaic humans and the Upper Palaeolithic early modern humans, this pattern of diminishing manipulative force corresponds to changes in technology, in which the increased frequency of composite and standardized tools must have increased the mechanical efficiency of the technology and reduced the habitual level of upper limb force generated during manipulative behaviors. However, only subtle differences in technology have been discerned between the Middle Palaeolithic Qafzeh-Skhul sample and the technology of late archaic humans. Yet, the greatest contrasts in humeral diaphyseal robusticity are between these Levantine early modern humans and late archaic humans generally. Given the plethora of functionally important contrasts in the upper limb between the Qafzeh-Skhul and late archaic humans, including the highly plastic diaphyseal robusticity, it is likely that there are technological behavioural contrasts between these hominid groups which are not readily apparent in the associated lithic assemblages.

### Lower Limb Robusticity

The traditionally recognized contrasts in lower limb robusticity between the Neanderthals and early modern humans (Twiesselmann 1961, Trinkaus 1983) are, in light of the analysis presented here, more apparent than real. Given that the lower limb diaphyses respond to both body weight and activity levels, and given that the effects of both weight and activity are influenced by ecogeographically determined body proportions, it is necessary to factor the influence of body proportions into any consideration of lower limb robusticity. Once this is done, the differences in femoral robusticity between late

archaic and early modern humans largely disappear. There remains some difference between the two samples in femoral diaphyseal robusticity, with the late archaic humans tending to be more robust. Furthermore, there are several other indicators of robusticity, including gluteal tuberosity size, patellar thickness, talar trochlear expansion and pedal diaphyseal breadth, in which the early modern humans are consistently modestly less robust than the late archaic humans. All of these lower limb features suggest a slight decrease in habitual levels of loading of the lower limb through locomotion, with all of them remaining at the upper limits of recent human ranges of variation (Trinkaus 1983, Ruff *et al.* 1993, Trinkaus, Hilton 1996). Apparently levels of use of the landscape, at least among adolescents and adults, decreased only slightly with the emergence of early modern humans.

## CONCLUSION

These considerations of appropriately measured humeral and diaphyseal robusticity among European and Near Eastern late archaic and early modern humans point to a mosaic pattern. In the upper limb, there is a clear decrease in habitual load levels, especially within the Near Eastern Middle Palaeolithic. In the lower limb, there is only a modest shift in robusticity, suggesting little change in landscape use and/or burden carrying with the emergence of modern humans. Moreover, it is increasingly apparent that changes in robusticity, as well as in other aspects of human functional biology, were mosaic across the late archaic to early modern human transition.

## ACKNOWLEDGMENTS

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