HOMO - Journal of Comparative Human Biology 66 (2015) 477–491

Contents lists available at ScienceDirect

HOMO - Journal of Comparative Human Biology

journal homepage: www.elsevier.com/locate/jchb

Forearm articular proportions and the antebrachial index in *Homo sapiens*, *Australopithecus afarensis* and the great apes

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ARTICLE INFO

Article history:
Received 30 May 2014
Accepted 15 February 2015

ABSTRACT

When hominin bipedality evolved, the forearms were free to adopt nonlocomotor tasks which may have resulted in changes to the articular surfaces of the ulna and the relative lengths of the forearm bones. Similarly, sex differences in forearm proportions may be more likely to emerge in bipeds than in the great apes given the locomotor constraints in *Gorilla*, *Pan* and *Pongo*. To test these assumptions, ulnar articular proportions and the antebrachial index (radius length/ulna length) in *Homo sapiens* ($n = 51$), *Gorilla gorilla* ($n = 88$), *Pan troglodytes* ($n = 49$), *Pongo pygmaeus* ($n = 36$) and *Australopithecus afarensis* A.L. 288-1 and A.L. 438-1 are compared. Intercept-adjusted ratios are used to control for size and minimize the effects of allometry. Canonical scores axes show that the proximally broad and elongated trochlear notch with respect to size in *H. sapiens* and *A. afarensis* is largely distinct from *G. gorilla*, *P. troglodytes* and *P. pygmaeus*. A cluster analysis of scaled ulnar articular dimensions groups *H. sapiens* males with A.L. 438-1 ulna length estimates, while one A.L. 288-1 ulna length estimate groups with *Pan* and another clusters most closely with *H. sapiens*, *G. gorilla* and A.L. 438-1. The relatively low antebrachial index characterizing

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http://dx.doi.org/10.1016/j.jchb.2015.07.001

H. sapiens and non-outlier estimates of A.L. 288-1 and A.L. 438-1 differs from those of the great apes. Unique sex differences in *H. sapiens* suggest a link between bipedality and forearm functional morphology.

Introduction

Humans have relatively short forearms compared to those in the great apes. Several explanations have been advanced to explain the evolution of short forearms in humans, including long-distance running (Bramble and Lieberman, 2004), carrying food (Hewes, 1961; Lovejoy, 1981; Sinclair, 1986; Videan and McGrew, 2002) and carrying infants (Williams et al., 2010). Hominin upper limbs became available for nonlocomotor uses at the advent of bipedality, freeing them for tasks that in turn shaped their morphology (Tocheri et al., 2007). Humanlike brachial proportions are observed in *Australopithecus afarensis* (Richmond et al., 2002), and the upper limb proportions for *A. afarensis* appear to be within the range of humans albeit with a slightly longer ulna (Drapeau and Ward, 2007). Specimen A.L. 288-1 exhibits a marginally longer humerus than typical for a human of small body size (Holliday and Franciscus, 2012). The continued use of the forelimbs for locomotion in arboreal habitats would have necessitated the maintenance of some adaptations related to joint mobility and stability. However, if nonlocomotor tasks became the dominant function of the forearms, changes in the relationship between the ulna and radius and joint stress may have occurred, consequently affecting articular surface morphology (Pal and Routal, 1991).

Forearm carrying

Although the forearm is also recruited during throwing, climbing, signaling, foraging and social activities, one of the primary nonlocomotor uses of the forearm among humans is carrying. Forearm carrying results in flexion of the elbow which functions as a third class lever system (Amis, 2002). The three muscles that serve to stabilize and flex the elbow are biceps brachii, brachialis and brachioradialis. Brachialis is the primary flexor of the elbow, along with biceps brachii which also serves to supinate the forearm. Brachioradialis is recruited to increase the rapidness and power of elbow flexion, as well as to stabilize the flexed forearm (Aiello and Dean, 1990). During flexed forearm carrying, the amount of force or resistance exerted by the flexor muscles is predicated by the distance between the fixed point of the fulcrum, or the ulnar trochlear notch, and the load arm, where weight bearing occurs.

Nonlocomotor tasks also involve the rotation of the wrist during pronation and supination. These actions involve the ulnar radial notch and carpal head of the ulna as the proximal and distal rotation surfaces of the radius. It is reasonable to assume that only major changes related to locomotor use, body size and/or very specific behaviors would alter the dimensions of these two articular surfaces between the ulna and radius.

Additionally, the relationship between the lengths of the ulna and radius would potentially be modified during flexed forearm carrying. These changes include a modification of the angulation and size of the distal articulation of the radius, the lengths of the styloid processes of the radius and ulna as well as the projection of the olecranon process, all of which are different between apes and humans. However, the length of the ulna can also vary independent of radius length through an extension of the trochlear notch, enhancing the mechanical advantage of forearm carrying. Distal elongation of the trochlear notch results in a center of rotation that would be slightly further away from the muscle insertions.

Sex differences

The diminutive A.L. 288-1 and very large and robust A.L. 438-1 likely correspond to female and male representatives of *A. afarensis*, respectively (Drapeau et al., 2005; Kimbel et al., 1994; cf. Haeusler and Schmid, 1995). Sex differences in *A. afarensis* have been investigated by a number of researchers (Gordon, 2006; Gordon et al., 2008; Greenfield, 1992; Harmon, 2006; Kimbel and White, 1988; Lague, 2002; Lovejoy et al., 1989; McHenry, 1992; Plavcan, 2000; Plavcan et al., 2005; Plavcan and van Schaik, 1997; Reno et al., 2003, 2005; Richmond and Jungers, 1995). Some posit multiple species rather than sex differences characterize the remains (Senut et al., 2001; Senut and Tardieu, 1985).

Differences in forearm proportions could signal functional dissimilarities between hominins and the great apes and between female and male hominins. Forearm bones of *A. afarensis* can demonstrate the evolutionary significance of these differences. However, published forearm limb bone length estimates vary widely, particularly for A.L. 288-1. Given the potential for nonlocomotor function of the forearms in bipeds, we expect *Homo sapiens* and *A. afarensis* to be distinct from the great apes. Similarly, we also anticipate that forearm proportions will differ between the sexes only in *H. sapiens*.

Materials and methods

The samples include *H. sapiens* ($n = 51$), *Gorilla gorilla* ($n = 88$), *Pan troglodytes* ($n = 49$) and *Pongo pygmaeus* ($n = 36$). Measurements on wild ape and human remains were taken at the Cleveland Museum of Natural History (Cleveland, OH), the Smithsonian National Museum of Natural History (Washington, DC), the American Museum of Natural History (New York), the Museum of Comparative Zoology at Harvard University (Cambridge, MA), the Field Museum (Chicago), the University of Tennessee (Knoxville), the British Museum (London), the Anthropological Institute of Zurich and the Zoological Museum of Zurich. The human sample is from Africa and North America. The African sample is historic and includes 18 individuals from South Africa, three Nubians from Egypt and one individual each from German East Africa, the Congo and Liberia. The North American sample is prehistoric and includes 22 Arikara and five Grand Gulch individuals. Bone lengths were measured using an osteometric board while joint surface dimensions were taken with digital calipers (Table 1; Fig. 1).

Articular surface dimensions on the original A.L. 288-1 and A.L. 438-1 were measured at the National Museum of Ethiopia (Addis Ababa). There is temporal variation between these two fossils as A.L. 288-1 is dated to 3.18 Ma and A.L. 438-1, one of the geologically youngest specimens attributed to *A. afarensis*, is dated to 3.0 Ma (Drapeau et al., 2005; Johanson et al., 1982; Johanson and Taieb, 1976; Kimbel et al., 1994, 2004).

When flexed forearm carrying occurs, three ulnar articular surfaces are recruited, including (1) the trochlear notch, where the ulna accommodates the distal humerus, (2) the radial notch, where the ulna articulates with the proximal radius, and (3) the ulnar head, where the ulna accommodates the distal

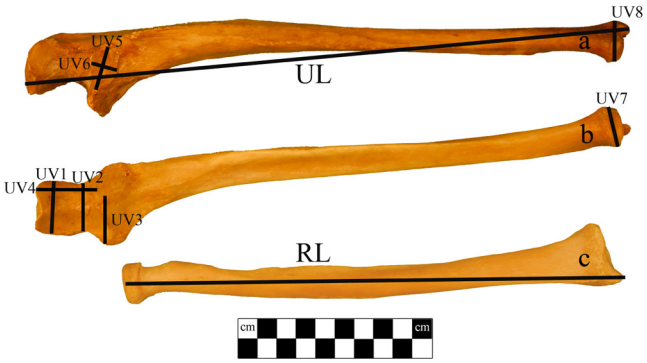

Fig. 1. Ulnar articular surface dimensions (UV1–UV8) are shown on lateral (a) and anterior (b) views of this left ulna. The antebrachial index (RU) is calculated using radius length (RL), shown on a right radius, anterior view (c), and ulna length (UL) shown in (a).

Table 1
Description of measurements and indices. Measurements taken in mm.

Code	Name	Description
UV1	Ulnar trochlear notch ML[a] breadth, proximal	Proximal portion of the articular surface at its maximum mediolateral breadth[b]
UV2	Ulnar trochlear notch ML breadth, middle	Middle portion of the articular surface at its narrowest waist[c]
UV3	Ulnar trochlear notch ML breadth, distal	Midpoint of the most medial line of the radial notch to the most medial point on the articular surface
UV4	Ulnar trochlear notch length, lateral	Midpoint of the proximal line of the radial notch to the most proximally projecting point on the olecranon process
UV5	Ulnar radial notch anteroposterior length	Anteroposterior midline length[d]
UV6	Ulnar radial notch proximodistal length	Proximodistal midline length, taken perpendicular to the radial notch anteroposterior length[e]
UV7	Ulnar head ML breadth	Maximum mediolateral ulnar head breadth, calipers held perpendicular to long axis of bone[f]
UV8	Ulnar maximum anteroposterior head length	Length of the ulnar head including the styloid process taken perpendicular to long axis of bone[g]
UL	Maximum ulna length	Proximal aspect of the olecranon process to the distal terminus of the ulnar styloid process[h]
RL	Maximum radius length	Proximal surface of the radial head to the most proximal point on the radial styloid process[i]
RU	Antebrachial index	Maximum radius length (RL)/maximum ulna length (UL)

[a] ML = mediolateral.
[b] Approximates number 32 (Knussmann, 1967).
[c] Approximates number 26 (Knussmann, 1967).
[d] Number 34 (Knussmann, 1967).
[e] Number 35 (Knussmann, 1967).
[f] Number 40 (Knussmann, 1967).
[g] Number 39 (Knussmann, 1967).
[h] Number 21 (Knussmann, 1967).
[i] Number 48 (Knussmann, 1967).

radius. Articular surfaces define the range of movement and joint stability during recruitment. It has been shown that the surface area of a limb bone joint can be accurately approximated by a standard linear dimension (Ruff, 2002). One advantage of using standard linear dimensions is that they can be scaled to limit the effects of size. This is a particularly important consideration when comparing A.L. 288-1 to extant hominoids. The three ulnar articular surfaces are approximated by eight linear dimensions (Cunningham, 2005; Ruff, 2002) (Fig. 1). Three of these serve as proxies for the breadth of the trochlear notch given its variable widths, whereas one dimension captures the proximodistal length of this joint surface; the radial notch is approximated by its anteroposterior and proximodistal lengths; and the ulnar head by its mediolateral and anteroposterior dimensions. All of these are divided by ulna length to control for size differences. Ulna length is used to scale for size in order to directly compare various competing hypotheses regarding the absolute dimensions of this forearm bone in the fossils (Table 2).

We develop an "antebrachial index" (radius length/ulna length) to compare hominins and the great apes and to identify potential differences between the sexes. The index also allows for the direct comparison of radius–ulna composites from estimates of A.L. 288-1 and A.L. 438-1 forearm limb bone lengths (Table 2).

Fossil long bone length estimates

An estimate of the maximum ulna length for A.L. 288-1 of 220 mm is provided by Kimbel et al. (1994) while Haeusler and McHenry (2004) report a minimum ulna length of 191 mm for AL 288-1 (Table 2).

Table 2
Fossil forearm bone length estimates for A.L. 288-1 and A.L. 438-1.

Radius		Ulna	
A.L. 288-1	174 mm[a]	A.L. 288-1	220 mm[d]
A.L. 288-1	203 mm[b]	A.L. 288-1	191 mm[e]
A.L. 288-1	215 mm[b]	A.L. 438-1	268 mm[d]
A.L. 438-1	259.3 mm[c]	A.L. 438-1	278 mm[f]

[a] Schmid (1983).
[b] Asfaw et al. (1999).
[c] Derived from a linear regression of radius and ulna from the extant samples used in this study ($n = 244$).
[d] Kimbel et al. (1994).
[e] Haeusler and McHenry (2004).
[f] Drapeau et al. (2005).

For the radius of A.L. 288-1, there are three length estimates published. The smallest is 174 mm [Schmid (1983) as cited in Hartwig-Scherer and Martin (1991) and Richmond et al. (2002)]; intermediate is 203 mm (Asfaw et al., 1999); and the largest is 215 mm (Asfaw et al., 1999). According to Richmond et al. (2002: p. 533) and Hartwig-Scherer and Martin (1991: p. 440), the short Schmid (1983) estimate is "humanlike" although how this was determined was not properly published (Schmid, 1983). The long radius estimate of 215 mm was based on a regression using a sample of *Pan. troglodytes* and *P. paniscus* (Asfaw et al., 1999). These authors originally used a sex- and species-balanced sample of *Pan*, *Gorilla* and *Homo* that resulted in a shorter radius length of 203 mm for A.L. 288-1. However, Asfaw et al. (1999) claim that this length (203 mm) is improbable given the missing pieces of the radial shaft, and they prefer the long estimate of 215 mm based on the *Pan* regression. Haeusler and McHenry (2007) disagree with this long estimate of radius length (215 mm), arguing that longitudinal cracks in the fossils explain the discrepancy in shaft thickness between the fragments that influenced Asfaw et al. (1999), and suggest that there is no independent reason why a chimpanzee regression model should be preferred for A.L. 288-1. We compare all combinations of radius and ulna length estimates for A.L. 288-1. These include (a) long radius length from Asfaw et al. (1999) with ulna length from Haeusler and McHenry (2004); (b) long radius length from Asfaw et al. (1999) with ulna length from Kimbel et al. (1994); (c) short radius length from Asfaw et al. (1999) with ulna length from Haeusler and McHenry (2004); (d) short radius length from Asfaw et al. (1999) with ulna length from Kimbel et al. (1994); (e) radius length from Schmid (1983) with ulna length from Haeusler and McHenry (2004); and (f) radius length from Schmid (1983) with ulna length from Kimbel et al. (1994).

The A.L. 438-1 partial skeleton includes a complete ulna that provides a maximum length reported as 278 mm by Drapeau et al. (2005) and as 268 mm by Kimbel et al. (1994) (Table 2). This 10 mm discrepancy is likely the result of the exclusion of the styloid process in the maximum length measurement of A.L. 438-1 (Kimbel et al., 1994). The A.L. 438-1 partial skeleton only preserves a small portion of the proximal radial diaphysis (Drapeau et al., 2005). To further compare ulna length estimates for A.L. 438-1 from Drapeau et al. (2005) and Kimbel et al. (1994), radius length was estimated using linear regression. Specifically, radius length was regressed against ulna length using all extant hominoids included in this study ($n = 224$). The resulting radius length estimate of 258.9 mm for A.L. 438-1 was compared to the ulna length reconstructions from Drapeau et al. (2005) and from Kimbel et al. (1994) in calculations of the antebrachial index. Although circularity is inherent in comparing an estimate to the sample from which it is drawn, given fossil preservation it may not be possible to use an entirely independent estimate of antebrachial proportions for any *A. afarensis* specimen.

Controlling for size and allometry

The small size of A.L. 288-1 compared to all other individuals in the study is problematic with respect to scaling. There are many ways to control for size (Albrecht et al., 1993; Corruccini, 1977). We chose to scale each raw measurement (Table 1) using ulna length so that published ulna length

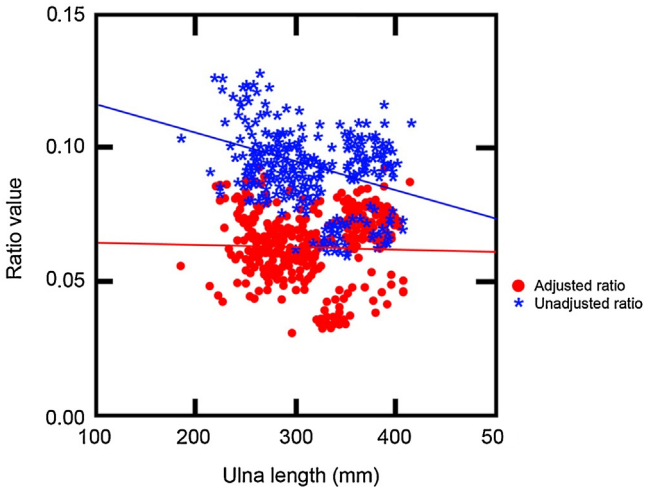

Fig. 2. Intercept-adjusted ratios control for size as well as for allometric effects. A nonzero slope or coefficient may characterize unadjusted ratios (y/x) introducing allometric artifacts into the comparison. Intercept adjusted ratios ($(y/x)adj$) are calculated by first regressing (y) by (x), then subtracting the resulting y-intercept (a) from (y), followed by division by (x), producing a flat line regression with a slope equal to zero indicative of isometry. In other words, as size (x) increases, the ratio of (y) to (x) does not increase.

estimates for A.L. 288-1 and A.L. 438-1 could be included. In this way we test multiple hypotheses of ulna length with respect to the articular surfaces associated with these fossils.

One caveat in the use of ratios to control for size is that if the relationship between an articular dimension and size is allometric rather than isometric, then ratios can produce erroneous results (Franks and Cabo, 2014). In other words, if a linear approximation of the relationship between two variables in Eq. (1) exhibits a nonzero slope, potential allometric artifacts may be inadvertently introduced into the comparison (Albrecht et al., 1993; Franks and Cabo, 2014). In Eq. (1), where raw measurement (y) is compared in a linear regression to size (x), (a) is the y-intercept and (b) is the slope or coefficient. When the relationship between (y) and (x) is linear, which is the case for our data, the exponent of size (k) = 1, resulting in a simple linear relationship between (y) and (x).

$$y = a + bx \tag{1}$$

When a nonzero slope (b) is present in the linear relationship between (y) and (x), the two variables are not independent (Franks and Cabo, 2014). Furthermore, Albrecht et al. (1993) maintain that size (x) should be uncorrelated with (y/x). In order to control for allometric distortion in the shape ratios, the original measurements were regressed against ulna length (x), and the y-intercept (a) of this relationship was subsequently subtracted from the measurement before a ratio (y/x) was constructed yielding $(y/x)adj$ (Albrecht et al., 1993). To ensure that the coefficient was zero for these intercept-adjusted ratios $(y/x)adj$ they were regressed against ulna length and the resulting slopes (b) ranged from zero to −0.001 (Fig. 2).

$$\frac{y}{x}adj = \frac{y-a}{x} \tag{2}$$

A zero coefficient produces a flat line regression between ($(y/x)adj$) and (x) indicative of isometry (Fig. 2) (Albrecht et al., 1993). Correlation coefficients for all y-intercept adjusted ratios ($(y/x)adj$) ranged from 0.038 to −0.039, thus nearly zero suggesting that the allometric effects were removed, and that these intercept-adjusted ratios ($(y/x)adj$) were virtually uncorrelated with ulna length (x), or size as demonstrated in Fig. 2 (Albrecht et al., 1993; Franks and Cabo, 2014). These intercept-adjusted ratios of ulnar articular dimensions ($(y/x)UVadj$) were used in subsequent analyses.

To calculate the antebrachial index while avoiding potential allometric effects from the creation of a ratio, radius length (y) was first regressed against ulna length (x) as shown in Eq. (1), and the resulting

Table 3
Descriptive statistics by taxon and sex[a] for all scaled ulnar articular surface dimensions ((*y*/*x*)*UVadj*) and the antebrachial index (*y*/*x*)*RUadj*) (see Table 1 and text for definitions).

Taxon and sex		UV1	UV2	UV3	UV4	UV5	UV6	UV7	UV8	RU
A. afarensis F (A.L. 288-1)[b]	Mean	0.073	0.127	0.141	0.052	0.052	0.070	0.090	0.027	101.672
	SD	0.007	0.013	0.014	0.005	0.005	0.007	0.009	0.003	12.133
A. afarensis M (A.L. 438-1)[b]	Mean	0.090	0.121	0.128	0.057	0.052	0.081	0.088	0.033	98.884
	SD	0.020	0.003	0.003	0.001	0.001	0.002	0.002	0.001	2.561
H. sapiens F (*n* = 19)	Mean	0.089	0.122	0.132	0.074	0.054	0.082	0.092	0.038	96.146
	SD	0.007	0.006	0.007	0.013	0.004	0.008	0.007	0.005	0.878
H. sapiens M (*n* = 32)	Mean	0.088	0.119	0.125	0.066	0.055	0.080	0.086	0.036	97.335
	SD	0.008	0.014	0.007	0.013	0.006	0.008	0.006	0.008	1.270
G. gorilla F (*n* = 33)	Mean	0.084	0.136	0.136	0.064	0.059	0.083	0.093	0.035	98.574
	SD	0.007	0.010	0.007	0.007	0.006	0.006	0.005	0.008	1.316
G. gorilla M (*n* = 55)	Mean	0.093	0.134	0.139	0.074	0.059	0.083	0.096	0.037	97.631
	SD	0.008	0.014	0.008	0.007	0.006	0.008	0.005	0.005	1.252
P. troglodytes F (*n* = 20)	Mean	0.074	0.105	0.119	0.055	0.052	0.696	0.089	0.028	99.640
	SD	0.007	0.006	0.006	0.009	0.006	0.010	0.005	0.004	1.448
P. troglodytes M (*n* = 29)	Mean	0.075	0.103	0.122	0.062	0.053	0.068	0.089	0.029	98.746
	SD	0.006	0.011	0.007	0.007	0.005	0.009	0.006	0.003	1.062
P. pygmaeus F (*n* = 23)	Mean	0.058	0.091	0.106	0.038	0.047	0.069	0.078	0.028	99.894
	SD	0.005	0.011	0.005	0.005	0.004	0.005	0.005	0.005	1.451
P. pygmaeus M (*n* = 13)	Mean	0.062	0.084	0.108	0.046	0.047	0.069	0.079	0.029	99.605
	SD	0.004	0.010	0.005	0.005	0.003	0.006	0.005	0.004	0.956

[a] F = female; M = male.
[b] Means and standard deviations for *A. afarensis* were calculated using four estimates for the ulna articular dimensions ((*y*/*x*)*UVadj*) and eight estimates for the antebrachial index ((*y*/*x*)*RUadj*).

y-intercept (*a*) subtracted from radius length (*y*) before dividing by ulna length (*x*) as shown in Eq. (2) resulting in an intercept-adjusted antebrachial index ((*y*/*x*)*RUadj*) (Albrecht et al., 1993; Corruccini, 1977).

Methods of analyses

Classification rates were obtained from a discriminant function analysis of scaled ulnar articular dimensions ((*y*/*x*)*UVadj*) and ulna length (UL) using four estimates of ulna length from two *A. afarensis* individuals, which were treated as a group (*n* = 4). Ulna length (UL) was included to reintroduce size on the first multivariate axis, further diminishing the effect of size-correlated shape on the second multivariate axis (Franks and Cabo, 2014). To identify whether group distinctions exist, individuals were plotted on canonical scores axes with confidence ellipses surrounding 68% of the sample for each extant taxon.

To further identify whether hominins are distinct from the great apes and whether the sexes of each taxon differ, the eight intercept-adjusted scaled articular ulna dimensions ((*y*/*x*)*UVadj*) were subjected to a cluster analysis using the mean for each female and male per taxon, and four ulna length estimates for *A. afarensis* (A.L. 288-1 and A.L. 438-1).

To address whether *H. sapiens* and the great apes show differences in the antebrachial index ((*y*/*x*)*RUadj*), each of the great ape taxa are compared to *H. sapiens* using ANOVA with Tukey's honestly significant differences post hoc test. A box and whiskers graph compares the antebrachial index in extant taxa, six A.L. 288-1 estimates and two A.L. 438-1 estimates (Table 2).

T-tests are employed to identify significant sex differences within each extant taxon in scaled ulnar articular surface dimensions ((*y*/*x*)*UVadj*) and the antebrachial index ((*y*/*x*)*RUadj*).

Results

Descriptive statistics of each of the scaled ulnar articular dimensions ((*y*/*x*)*UVadj*) and the antebrachial index ((*y*/*x*)*RUadj*) demonstrate differences exist across the taxa and between the sexes within each taxon (Table 3).

Table 4
Classification rates derived from a discriminant function analysis.[a]

Taxon	Classification rates	Jack-knifed Classification rates
A. afarensis	50%	50%
H. sapiens F	72%	67%
H. sapiens M	81%	65%
G. gorilla F	100%	100%
G. gorilla M	100%	100%
P. troglodytes F	68%	47%
P. troglodytes M	69%	59%
P. pygmaeus F	100%	96%
P. pygmaeus M	100%	100%

[a] F = female; M = male.

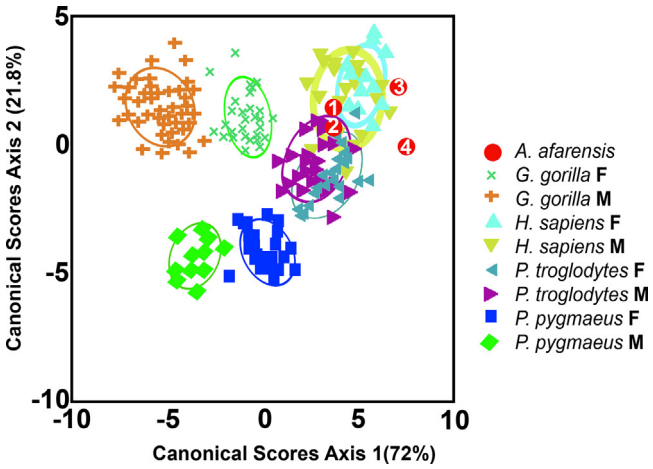

Fig. 3. Canonical Scores axes of scaled ulnar articular dimensions ((*y*/*x*)*UVadj*) and UL account for 93.8% of the variance. Each extant taxon is shown with 68% sample confidence ellipses. Four estimates for *A. afarensis* are shown using (1) ulna length for A.L. 438-1 from Drapeau et al. (2005); (2) ulna length for A.L. 438-1 from Kimbel et al. (1994); (3) ulna length for A.L. 288-1 from Haeusler and McHenry (2004); and (4) ulna length for A.L. 288-1 from Kimbel et al. (1994).

Distinctions in ulnar proportions

A discriminant function analysis yields classification rates which are highest for *G. gorilla* and *P. pygmaeus* (100%), followed by *H. sapiens* males (81%) and females (72%) (Table 4). The lowest classification rates are for *P. troglodytes* females (68%) and males (69%) and *A. afarenesis* (50%). The two estimates for A.L. 438-1 are misclassified as *H. sapiens* males. Misclassifications among *H. sapiens* and *P. troglodytes* also exist, but individuals are misclassified as the opposite sex within the same taxon suggesting distinctions between females and males are minor compared to species-specific differences. For jack-knifed classification rates, *A. afarensis* remains at 50% since the two A.L. 438-1 estimates are again misclassified as *H. sapiens* males (Table 4).

Two canonical scores axes with eigenvalues greater than one, generated from the discriminant function analysis of scaled ulnar articular dimensions ((*y*/*x*)*UVadj*) and ulna length (UL) collectively account for 93.8% of the variance (Fig. 3). The first axis represents 72% of the variance and separates *G. gorilla* males and to a lesser extent, *P. pygmaeus* males, from *H. sapiens* and *A. afarensis*. Females of *G. gorilla* and *P. pygmaeus*, as well as *P. troglodytes*, are projected between these two extremes. The fossil estimate for A.L. 288-1 using the Haeusler and McHenry (2004) ulna length falls close to the distribution for *H. sapiens*. In contrast, the fossil estimate for the ulna length of A.L. 288-1 from Kimbel et al. (1994) is an outlier, being comparatively distant from *H. sapiens* and indeed from all other extant taxa. The ulna length estimate from Drapeau et al. (2005) falls within the 68% sample confidence ellipse

Table 5
Canonical scores (CS) structure matrix for ((*y*/*x*)*UVadj*) and ulna length (UL).

Variable	CS axis 1	CS axis 2
UV1	0.212	0.457
UV2	−0.182	0.250
UV3	−0.548	0.285
UV4	0.222	0.476
UV5	−0.271	0.228
UV6	−0.195	0.036
UV7	−0.322	−0.314
UV8	−0.008	0.001
UL	−1.258	−0.207

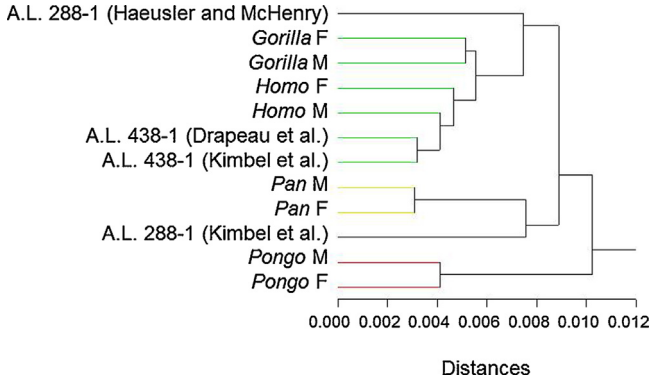

Fig. 4. Cluster analysis of scaled ulnar articular dimensions ((*y*/*x*)*UVadj*) shows A.L. 438-1 joins most closely with male *H. sapiens*. The Haeusler and McHenry (2004) A.L. 288-1 estimate for ulna length joins to *H. sapiens*, *G. gorilla* and A.L. 438-1 while that from Kimbel et al. (1994) groups with *Pan*.

for *H. sapiens* males. The estimate for A.L. 438-1 ulna length from Kimbel et al. (1994) falls within the 68% sample confidence ellipse for *H. sapiens* males, but on the periphery of the confidence ellipse for *P. troglodytes* males (Fig. 3).

On the first axis, high positive values characterize the canonical discriminant functions standardized by within-group variances for scaled trochlear notch height ((*y*/*x*)*UV*4*adj*) and scaled proximal width of the trochlear notch ((*y*/*x*)*UV*1*adj*). These contrast with ulna length (UL), scaled distal width of the trochlear notch ((*y*/*x*)*UV*3*adj*), and scaled mediolateral width of the ulnar head ((*y*/*x*)*UV*7*adj*) with high negative values on the first axis (Table 5). *Homo sapiens* and *A. afarensis* have relatively elongated and distally wide trochlear notches compared to the great apes. The mediolateral breadth of the ulnar head ((*y*/*x*)*UV*7*adj*) is smaller with respect to size in humans, but less so in *A. afarensis* while ulna length is reduced in hominins compared to the great apes, particularly in A.L. 288-1. On the second axis, a mediolaterally enlarged distal ulna ((*y*/*x*)*UV*7*adj*) and relatively long ulna length (UL) explain the negative projection of *P. pygmaeus* while the relatively expanded proximal trochlear notch width with respect to size ((*y*/*x*)*UV*1*adj*) and pronounced length of the trochlear notch ((*y*/*x*)*UV*4*adj*) in *G. gorilla*, *H. sapiens* and *A. afarensis* largely accounts for their positive projection (Table 5), as well as the separation of *P. troglodytes* and *H. sapiens*.

A cluster analysis of scaled ulnar articular dimensions ((*y*/*x*)*UVadj*) shows that some of the shortest distances are between the sexes of great ape taxa, particularly *P. troglodytes* and *P. pygmaeus*. In *H. sapiens*, the sexes are less similar to each other (Fig. 4). *Pongo pygmaeus* is clearly distinct from the other taxa followed by *P. troglodytes*. *Gorilla gorilla*, *H. sapiens* and *A. afarensis* are clustered together with the Haeusler and McHenry (2004) ulna length estimate for A.L. 288-1, while the Kimbel et al. (1994) ulna length estimate for A. L. 288-1 clusters with *Pan* by a relatively long branch. The shortest

Table 6
Tukey's post hoc test results from an ANOVA of the antebrachial index ((*y*/*x*)*RUadj*).

Taxon comparisons	*P* value
G. gorilla–H. sapiens	<0.001
G. gorilla–P. troglodytes	<0.001
G. gorilla–P. pygmaeus	<0.001
H. sapiens–P. troglodytes	<0.001
H. sapiens–P. pygmaeus	<0.001
P. troglodytes–P. pygmaeus	0.096

Table 7
T-test results between females and males for each extant taxon for scaled ulna articular dimensions ((*y*/*x*)*UVadj*) and antebrachial index ((*y*/*x*)*RUadj*).[a]

Taxon	UV1	UV2	UV3	UV4	UV5	UV6	UV7	UV8	RU
H. sapiens	0.516	0.242	**<0.001**	**0.038**	0.300	0.280	**0.002**	0.221	**<0.001**
G. gorilla	**<0.001**	0.489	0.153	**<0.001**	0.912	0.940	**0.032**	0.261	**0.001**
P. troglodytes	0.064	0.394	0.133	**0.005**	0.514	0.628	0.997	0.522	**0.025**
P. pygmaeus	**0.013**	0.062	0.412	**<0.001**	0.688	0.986	0.375	0.241	0.489

[a] Significant results are in bold.

distances are between the A.L. 438-1 estimates from Drapeau et al. (2005) and Kimbel et al. (1994) which are clustered with *H. sapiens* males followed by *H. sapiens* females.

Distinctions in the antebrachial index

An ANOVA of the intercept-adjusted antebrachial index ((*y*/*x*)*RUadj*) yields a significant difference among the taxa ($F = 40.874$; $p < 0.001$). The results of Tukey's post hoc test demonstrate that all of the great ape taxa are significantly different from *H. sapiens* (Table 6). Among the great apes, all are significantly different from one another with the exception of *P. troglodytes* and *P. pygmaeus* (Table 6).

Sex differences within humans and the great apes

Significant sex differences are pronounced in *H. sapiens* and *G. gorilla* (Table 7). All taxa exhibit significant differences in scaled length of the trochlear notch of the ulna ((*y*/*x*)*UV4adj*), and all except *P. pygmaeus* show significant distinctions in the intercept-adjusted antebrachial index ((*y*/*x*)*RUadj*). Furthermore, both *H. sapiens* and *G. gorilla* exhibit significant sex differences in scaled mediolateral breadth of the distal ulna ((*y*/*x*)*UV7adj*). In *H. sapiens*, the sexes significantly differ in scaled distal breadth of the trochlear notch ((*y*/*x*)*UV3adj*). For the scaled proximal breadth of the trochlear notch ((*y*/*x*)*UV1adj*), the sexes are significantly different in *G. gorilla* and *P. pygmaeus*. However, for the great apes, males are larger than females in all of these significant differences ((*y*/*x*)*UVadj*). In contrast, for the three articular variables which show significant sex differences in *H. sapiens* (Table 7), it is females who are relatively larger. Specifically, in the ulna, human females exhibit relatively longer but distally broader trochlear notches, with respect to size, as well as proportionally wider mediolateral breadths of the ulna head compared to males (Tables 3 and 7). For the antebrachial index ((*y*/*x*)*RUadj*) the opposite pattern prevails such that *H. sapiens* females show a significantly shorter radius with respect to ulna length compared to *H. sapiens* males, whereas in the African apes, it is females which show a significantly longer radius length with respect to ulna length (Tables 3 and 7; Fig. 5).

Forearm limb bone lengths for A.L. 288-1 and A.L. 438-1

A number of competing hypotheses have been published concerning the length of the radius and ulna in A.L. 288-1, and the ulna in A.L. 438-1. For the scaled ulna articular dimensions ((*y*/*x*)*UVadj*) of A.L. 288-1, the Haeusler and McHenry (2004) ulna length estimate of 191 mm falls within the range of *H. sapiens* females and males on PC Axis 2 suggesting fundamental similarities in ulna articular

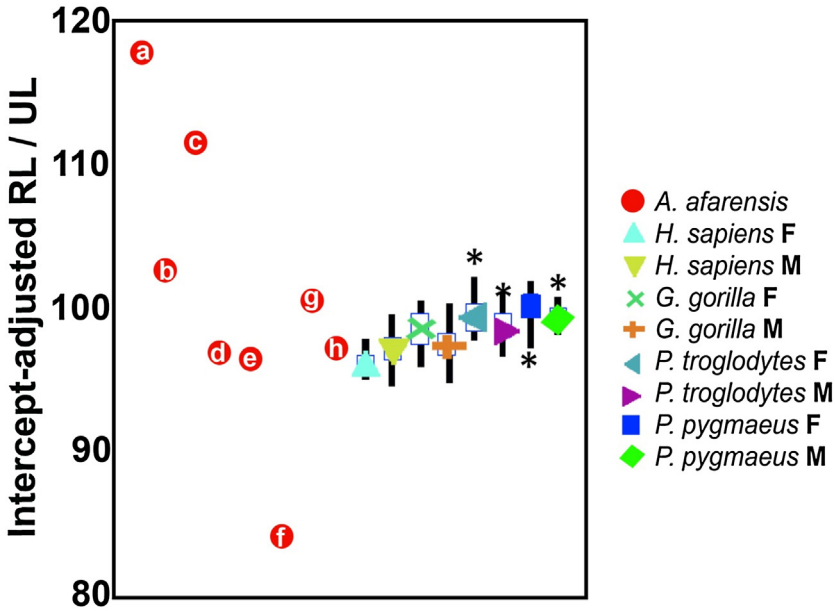

Fig. 5. A comparison of the intercept-adjusted antebrachial index ((*y*/*x*)*RUadj*) across taxa demonstrates the relatively low values for *H. sapiens* and *A. afarensis* estimates (d), (e) and (h). Fossil composites for A.L. 288-1 include (a) long radius length from Asfaw et al. (1999) with ulna length from Haeusler and McHenry (2004); (b) long radius length from Asfaw et al. (1999) with ulna length from Kimbel et al. (1994); (c) short radius length from Asfaw et al. (1999) with ulna length from Haeusler and McHenry (2004); (d) short radius length from Asfaw et al. (1999) with ulna length from Kimbel et al. (1994); (e) radius length from Schmid (1983) with ulna length from Haeusler and McHenry (2004); and (f) radius length from Schmid (1983) with ulna length from Kimbel et al. (1994). Two combinations for A.L. 438-1 include (g) radius length from this study with ulna length from Kimbel et al. (1994); and (h) radius length from this study with ulna length from Drapeau et al. (2005). Taxon identifiers are positioned on the medians. Boxes represent 50% of the observations. Whiskers demarcate the terminus of the 95% confidence intervals. Outliers are denoted by asterisks.

shape, while the ulna length estimate of 220 mm from Kimbel et al. (1994) is an outlier on PC Axis 2 suggesting an ulna that differs from the other fossil estimates (Fig. 3). The A.L. 438-1 ulna length estimate of 278 mm provided by Drapeau et al. (2005) is similar to that of *H. sapiens* males, while that of 268 mm from Kimbel et al. (1994) falls into the ranges of both *H. sapiens* and *P. troglodytes* males (Fig. 3).

For the intercept-adjusted antebrachial index ((*y*/*x*)*RUadj*), eight pairs of fossil radius and ulna length estimates are examined. The long radius length estimate from Asfaw et al. (1999) appears to be too large for either ulna length reconstructions of A.L. 288-1 as shown in (a) and (b) (Fig. 5). In contrast, the short radius length of 203 mm from Asfaw et al. (1999) falls within the range of extant hominoids if paired with the ulna length of 220 mm from Kimbel et al. (1994) as shown in (d) (Fig. 5). Similarly the Schmid (1983) estimate of radius length for A.L. 288-1 of 174 mm falls within the range of extant hominoids if paired with the Haeusler and McHenry (2004) ulna length of 191 mm as shown in (e) (Fig. 5). Both (d) and (e) fall within the range of *H. sapiens*, whereas the Schmid (1983) radius length paired with the ulna length of Kimbel et al. (1994) (f) is unrealistically low (Fig. 5).

With respect to A.L. 438-1, the radius estimate from this study, 259.3 mm, paired with the ulna length of 268 mm from Kimbel et al. (1994) falls nearly outside the range of extant hominoids as shown in (g) (Fig. 5). However, the radius estimate from this study combined with ulna length of 278 mm from Drapeau et al. (2005) falls within the range of *H. sapiens* males as shown in (h) (Fig. 5).

Discussion

Australopithecus afarensis exhibits substantial size differences in ulnar dimensions as demonstrated by the variation between A.L. 288-1 and A.L. 438-1 (Drapeau et al., 2005). However, shape variation is not extreme in *A. afarensis* (Table 3). Multivariate analyses of scaled ulnar articular dimensions ((*y*/*x*)*UVadj*) of A.L. 288-1 and A.L. 438-1 are similar to one another, particularly on canonical scores axis 2 (Fig. 3) and are similar to *H. sapiens* (Figs. 3 and 4). These observations agree with Drapeau et al. (2005) who suggest A.L. 288-1 and A.L. 438-1 ulnae exhibit similar functional capabilities, and that differences exist in size but not in indices of shape.

When the antebrachial index ((*y*/*x*)*RUadj*) is considered, valid estimates for *A. afarensis* are similar to *H. sapiens* and largely distinct from the great apes (Fig. 5). *Homo sapiens* females are significantly smaller than males in the antebrachial index ((*y*/*x*)*RUadj*) whereas the reverse is true for the African apes such that males are significantly smaller than females (Tables 3 and 7; Fig. 5). This pattern suggests that distinct sex differences in antebrachial proportions exist, and that habitual bipeds are largely distinct from the African apes (Fig. 5).

Additionally, three out of eight variables ((*y*/*x*)*UV3adj*), ((*y*/*x*)*UV4adj*) and ((*y*/*x*)*UV7adj*) show significant differences in humans. Females of *H. sapiens* exhibit relatively elongated and distally broad trochlear notches, and relatively wide mediolateral dimensions of the distal ulna with respect to size. In contrast, great ape males are significantly larger than females for several scaled ulna articular dimensions (Table 7). Lague and Jungers (1999), in an analysis of the distal humerus among hominoids, also found significant sexual dimorphism in the elbow joint of western lowland gorillas (*G. g. gorilla*) which they attribute to greater load-bearing behavior of males compared to females. In contrast, the differences in scaled ulnar articular dimensions between female and male *H. sapiens* are not due to locomotor requirements, suggesting other factors must be responsible for these sex distinctions.

The forearms of early hominins

The forearms became increasingly available for nonlocomotor functions during the transition to bipedality and this could have contributed to sex differences in forearm use since locomotor constraints were removed. This would occur only if nonlocomotor functions of the forearms were more important than locomotor ones and if these adaptations for new functions had become essential for survival (cf. Jungers, 1982; Latimer, 1991; Latimer et al., 1987; Ohman et al., 1997; Stern, 2000; Stern and Susman, 1983; Ward, 2003; Ward et al., 2011). The argument can be made that these new functions required morphological changes at the expense of adaptations to arboreality. The intermediate form of the trochlear notch in *A. afarensis* indicates both terrestrial and arboreal substrates may have been exploited (Drapeau, 2008). Drapeau and Ward (2007) conclude that *A. afarensis* was under selection to reduce the length of its upper limb segments, perhaps related to a relaxation of selection for arboreality combined with positive selection for an activity that favored shorter forelimbs. This activity may have been carrying behavior. Although energetically costly for early australopiths (Wang et al., 2003), carrying was still possible, and perhaps one of the most important functions, among many others (Alba et al., 2003), of the freed hands (Darwin, 1871; Hewes, 1961; Videan and McGrew, 2002).

Humanlike antebrachial proportions and short forelimbs may have adaptive value for habitual bipedalism and carrying behavior in terrestrial environments. Although sex-specific differences in foraging and feeding behavior may explain some of the differences in extant apes, it is also apparent that gorillas and humans are similar in the antebrachial index. Perhaps it is the terrestriality of *H. sapiens* and *G. gorilla* which explains some of the similarities in the forearm bones (Knussmann, 1967), although for the antebrachial index ((*y*/*x*)*RUadj*), females exhibit shorter radii in *H. sapiens*, whereas the African apes exhibit the reverse configuration. Additionally, in scaled articular dimensions of the ulna, females are larger than males for several traits, whereas for the great apes, where significant differences are present, it is males which exhibit the larger values suggesting sex differences in behavior.

Sex-specific patterns of foraging and feeding behavior may explain some of the differences in extant apes and humans. The sexes of *G. gorilla* are reported to exhibit differences in foraging and positional behavior with silverback males showing more terrestrial postures during feeding than females (Remis, 1995, 1999). Foraging differences between the sexes are known to exist in *P. pygmaeus* where

ecological selection has resulted in two very different body sizes and diets (Cant, 1987; Sugardjito and Hooff, 1986). Sex-specific foraging differences have been reported in *P. troglodytes* including a relatively greater amount of time devoted to foraging for insects in females and a greater consumption of mammalian meat in males (McGrew, 1992; Stanford, 1998). However, it is *H. sapiens* which stands out as exhibiting the most unique sex differences in forearm proportions. A variety of behaviors may have influenced sex differences in hominins including forearm carrying of infants, tool use and cultural modification, manipulative activities, social signaling, foraging differences, occupational stress, and other behaviors (Amaral, 2008; Hewes, 1961; Williams et al., 2010).

Competing hypotheses of radius length for A.L. 288-1 suggest that the long estimate from Asfaw et al. (1999) may overestimate this forearm bone, whereas the short estimate of 203 mm from Asfaw et al. (1999), if paired with the ulna length of 220 mm from Kimbel et al. (1994), results in an individual which falls within the range of extant hominoids in the antebrachial index (Fig. 5). However, when used alone, the Kimbel et al. (1994) ulna length estimate for A.L. 220 mm is an outlier (Fig. 3). The ulna length estimate of 191 mm from Haeusler and McHenry (2004) results in a much more humanlike ulna articular surface (Fig. 3). Additionally, the Haeusler and McHenry (2004) ulna length estimate for A.L. 288-1, when coupled with the radius length of 174 mm originally from Schmid (1983), falls within the range of *H. sapiens* (Fig. 5). The ulna length estimate for A.L. 438-1 from Drapeau et al. (2005) resembles *H. sapiens* males to a greater extent than the one from Kimbel et al. (1994) (Fig. 3). These findings indicate a relatively short humanlike forearm in both A.L. 288-1 and A.L. 438-1 (Haeusler and McHenry, 2004, 2007; Schmid, 1983).

Acknowledgments

Data collection (DLC) was supported by NSF BCS-0234193, P.E.O., Sigma Xi and the American Museum of Natural History. DLC thanks the curators of the Cleveland Museum of Natural History, American Museum of Natural History, Smithsonian National Museum of Natural History, the Museum of Comparative Zoology, the Field Museum, the University of Tennessee, the British Museum, the Anthropological Institute of Zurich, the Zoological Museum of Zurich, and the National Museum of Ethiopia. LQA thanks Drs. Marcos Duarte and Viviana Gianpaoli for discussions on, respectively, biomechanics and statistics. The authors thank Daniel Wescott for valuable comments and Monique McGee for assistance with Figs. 2, 3 and 5.

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