A new reconstruction of the forearm of A. L. 288-1 ("Lucy") and functional interpretations

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ABSTRACT. A long running debate in human evolution concerns the degree to which early hominins combined arboreal behaviors with terrestrial bipedalism. The argument in favor of obligate terrestrial bipedalism considers the arboreal-linked traits (e.g., curved phalanges) to be retained primitive features inherited from an arboreal ancestor that had no adaptive value in the descendant, whereas the opposing argument holds that these traits were adaptations for arboreal locomotion. A new approach by Ruff et al. (2016) examined long bone cross-sectional geometry, a feature that responds dynamically to loading during the life, and showed that Lucy is intermediate between humans and chimpanzees in having high humeral strength, most likely produced by frequent climbing. If Lucy climbed by using her arms to pull herself up, forearm traits for climbing should be shared with chimpanzees. Lucy preserves partial ulnae and radii. We used high-resolution X-ray CT scans of Lucy for the reconstruction by mirroring right and left portions, and using 3D cross-sections of humans, chimpanzees, and australopiths to construct and evaluate scaled models. Lucy's ulna is more similar to chimpanzees in being anteroposteriorly curved and laterally bowed proximally, and straight distally; and differs from humans in lacking a concave, deeply furrowed and sharply keeled interosseous margin, and a triangular shaft cross-section. Lucy's radius more closely resembles the chimpanzee and again differs from humans in lacking a sharply keeled interosseous margin. Unlike earlier studies that quantify curvature in 2D only, we apply measures of tortuosity to evaluate curvature in 3D. In chimpanzees, these traits combine to produce a stable pronated forearm for knuckle-walking, and powerful pronation and supination when climbing; since Lucy was not a knuckle-walker, it appears that these traits facilitated powerful pronation and supination, behaviors that align with her high humeral strength and together underscore the importance of climbing in her species.

Is Lucy human-like, ape-like, neither, or both?

The famous fossil A.L. 288-1 ("Lucy"), discovered in 1974 in the Afar of Ethiopia, is a young adult female of *Australopithecus afarensis*. It is one of the most complete Pliocene hominins and is represented by about 25% of the skeleton by element count. Her forelimbs are well-represented by long bone elements including: 1) humerus: R (nearly complete) and L (two fragments); 2) ulna: R (proximal and distal fragments) and L (proximal and distal fragments); and 3) radius: R (proximal, midshaft, and distal fragments) and L (distal fragment) (Figure 1). Detailed descriptions are given in Johanson et al. (1982) and some features, *e.g.*, those of the proximal ulna, are said to *"…strongly distinguish the specimen from the typical modern human condition"* (:420). Other researchers have instead noted that the ulna of *Au. afarensis "…diverges from the modern African ape condition and matches the human morphology…"* (Kimbel et al., 1994: 450), in support of the view that "A. afarensis *has relative upper-limb proportions that are within the range of variation observed in humans…"* (Drapeau and Ward, 2007: 340). These contrasting conclusions suggest that it is worth reexamining Lucy's upper limb.

Long bone lengths

Given the missing diaphyseal portions of Lucy's forelimb elements, some compressive fracturing, and differing lengths of the same portion of some R and L fragments, questions remain about the original lengths of these elements. We used a combination of mCT and NextEngine scans, 3D printouts, and photographs to reconstruct and evaluate the models.

The R humerus (A.L. 288-1m) is nearly complete and its reconstructed length has been estimated between 236.8 mm (Johanson *et al.*, 1982) to 246 mm (Hausler, 2001). Kappelman *et al.* (2016) used mCT scans to reorient the 29 tiny compressive and presumably perimortem fractured bone fragments of its proximal end, and realign the spiral fracture of the diaphysis, to obtain a value of 237 mm for the length from the head to the capitulum (Figure 1a).

The ulnae and radii are more problematic (Figure 1b). The proximal radius is represented by a R fragment (A.L. 288-1p) that continues distally past the radial tuberosity by about 43 mm. The distal portion of the L radius (A.L. 288-1v) is more complete than R (A.L. 288-1q). The cross-section contour of the distal portion of the R diaphyseal fragment (also catalogued as A.L. 288-1p, here called A.L. 288-1p') matches the central portion of the cross-section contour of the distal L radius (A.L. 288-1v) when mirrored as R. This reconstruction suggests that 8.8 mm is missing at the distal gap on the R side; an unknown length is missing between the R proximal (A.L. 288-1p) and reconstructed distal portion of the shaft (A.L. 288-1v/q & p').

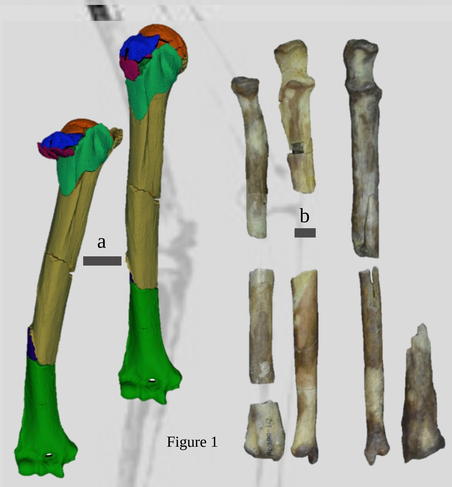


Figure 1

Both ulnae are missing their diaphyses, with the L proximal portion (A.L. 288-1t) more complete than R (A.L. 288-1n), and R distal portion (A.L. 288-1o) slightly longer and more complete than L (A.L. 288-1u). Given that Lucy shares with the chimpanzee moderate curvature (see below) of both the ulna and radius, and lacks the sharply keeled and prominent interosseous crest of humans (Figure 6), we elected to use *Pan* to estimate the length of the missing segment. We used photographs and scaling in Avizo to estimate length of the ulna and obtained values from 222-226 mm from the olecranon process to ulnar head, close to the Kimbel et al. (1994) estimate of 220 mm (presumably not including the length of the styloid process). These estimates permit us to in turn estimate the length of the radius by articulating the radial head with the radial notch, and ulnar head with ulnar notch. We estimate length of the radius at 208-212 mm, close to the range of 203-215 mm by Asfaw et al. (1999).

We use these estimates to compare the humerus to the radius. Young et al. (2010) provide values for humans (M = 71; F = 62), chimpanzees (M = 21; F = 25), gorillas (M = 42; F = 20), and gibbons (M = 32; F= 30). Figure 2 plots of all four species, with *Pan* displaying a longer radius relative to the length of the humerus than *Homo* and *Gorilla*, and *Hylobates* relatively longer still. Figure 3 limits these data to *Homo*, *Pan*, and *Hylobates*, and provides LS regressions by mixed sex.

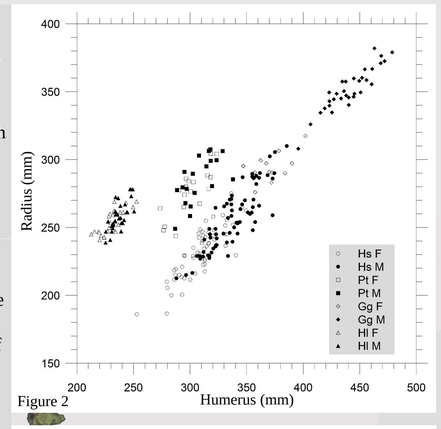


Figure 2

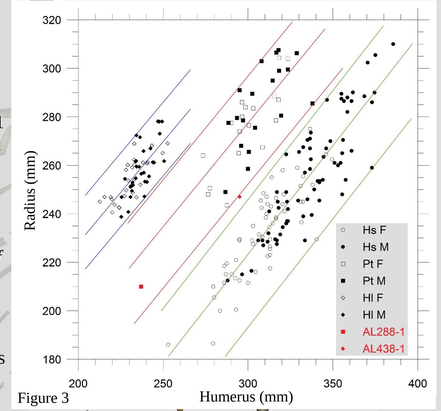


Figure 3

Figure 2 also plots our values for A.L. 288-1 (humerus = 237 mm, radius 210 mm) along with the values for A.L. 438-1, a large, presumably male *Au. afarensis* (Kimbel *et al.* 1994). The A.L. 438-1 ulna is 268 mm long, and we estimate the length of its radius at 247 mm by the method described above. Kimbel *et al.* (1994) suggest that A.L. 137-50, a large humerus with an estimated length of 295 mm, can be paired with the ulna to estimate relative forelimb proportions. The LS regression lines for each modern species are simply duplicated and translated above and below the distributions so as to fully include all specimens of that species. This plot demonstrates that A.L. 288-1 falls within the range of *Pan* while A.L. 438-1 is at the lower edge of the *Pan* distribution. We agree with the conclusion of Kimbel *et al.* (1994) that *Au. afarensis* had *"…relatively long ulnae (and, presumably, forearms)… distinctly closer to the relative ulnar length of chimpanzees than to that of modern humans"* (:450-451).

Curvature

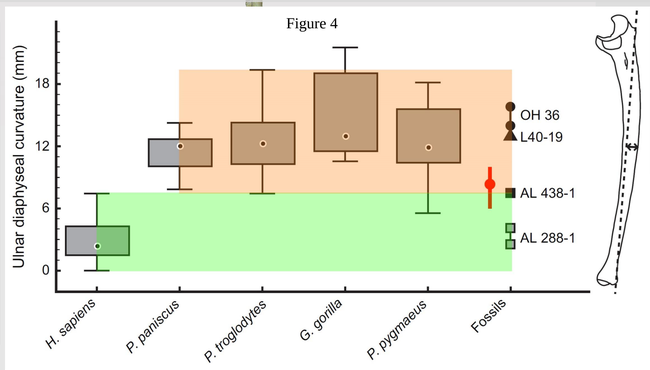
Differences in ulnar and radial curvature serve to distinguish between humans and apes, with humans exhibiting straighter shafts. The higher degree of curvature in apes is believed to enhance powerful forearm pronation (Aiello and Dean, 1990). Ulnar curvature is usually described in 2D from lateral view, and quantified by measuring the anteroposterior deviation from a straight line in the sagittal plane. Several different methods that have been used in the past (see Aiello et al., 1999). Drapeau and Ward (2005) offer a slightly different method that attempts to account for diaphyseal robusticity by rooting the proximal position of the line at the point where another line dropped posteriorly from the radial notch intersects the shaft, and placing the distal point of the line at the intersection with the smallest distal diameter of the shaft (see Figure 5). Figure 4 reproduces Drapeau and Ward (2005)'s figure 16 and illustrates the straighter shaft of humans versus the curved shaft of the apes.

All of these methods require nearly complete ulnae along with a consistent placement of the shaft in lateral view. Although this orientation appears straightforward, slight rotation of the shaft around its long axis can influence the results. For example, photographs of A.L. 438-1 in lateral view are given in Kimbel et al. (1994: fig. 3f) and Drapeau and Ward (2005: fig. 5), and in each case the medial portion of the trochlear notch is visible, showing that the element is rotated out of true lateral view; the line drawing in Drapeau and Ward (2005: fig. 2) is more difficult to interpret because it illustrates a shaft that is much straighter than that shown in the photographs even though the medial aspect of the trochlear notch is not visible.

We used a 3D printout of a NextEngine scan of A.L. 438-1 to evaluate the possible effect of shaft rotation by photographing the element in various degrees of rotation while attempting to minimize visibility of the medial portion of the trochlear notch and maximizing visibility of the longitudinal trochlear keel. We followed the method of Drapeau and Ward (2005), and our values of ulnar curvature of A.L. 438-1 range from 6-9 mm using the 3D printout, and produce a value of 10 mm for the photograph in their figure 3, for a mean of 8.25 mm (Figure 4: mean: red filled circle; range: red bar), a value close to their reported single value of 7.5 mm. This range of values isintermediate between *Homo* (green bar) and *Pan* (orange bar). We agree with Drapeau and Ward (2005) who state that A.L. 438-1 has a more curved ulna that humans (caption, their Fig. 16), a comment at odds with Kimbel et al. (1994: 450) who state that A.L. 438-1 *"…diverges from the modern African ape condition and matches the human morphology…"*

Figure 4. Boxplots of ulnar curvature in lateral view from Drapeau and Ward (2005: fig. 16). Our measurements of A.L. 438-1 (red) reflects slight rotations of the shaft around long axis. Our estimates for Lucy suggest that she falls within the range of A.L. 438-1. Green box *H.s.* range; orange box *P.t.* range. Dot = median, box interquartile range (25-75%), whiskers range excluding outliers.

Figure 4



What about Lucy? Drapeau and Ward (2005) note that *"both proximal and distal fragments are very straight"* (:608). They provide minimum and maximum curvature estimates (see Figure 4) and note that these estimates *"…should therefore be interpreted with due caution"* (:608). Although their method requires a complete element, there is enough anatomy preserved of Lucy's L proximal ulna to evaluate their observation that the element is *"very straight."* We used Avizo to produce an isosurfaced 3D rendering of Lucy's proximal ulna (A.L. 288-1t) from mCT scans, and scaled and compared it with scaled versions of A.L. 438-1, *Homo*, *Pan troglodytes*, and *Pan paniscus*. (Figure 5). The transparent overlay illustrates that Lucy can be easily accommodated within the range of A.L. 438-1.

Figure 5

Figure 5. Lateral views of left ulnae scaled to mesiodistal length of trochlear notch with the shaft oriented to curvature measurement construction following Drapeau and Ward (2005) of (a) Lucy, (b) bonobo, (c) chimpanzee, (d) A.L. 438-1, and (e) human. Transparent overlays of Lucy on the other ulnae are aligned with the posterior contour. The posterior contour of Lucy is moderately curved (yellow line) and closely matches that of A.L. 438-1, suggesting a similar degree of ulnar curvature as reflected in our range of measurements in Figure 4.

Figure 6. Anterior views of left ulnae scaled to mesiodistal length of trochlear notch and aligned to each other with the trochlear keel approximately parallel of (a) Lucy, (b) A.L. 438-1, (c) chimpanzee, (d) bonobo, and (e) human. Lucy's ulna is laterally bowed proximally (yellow line), has a deeply furrowed attachment for the m. brachialis (yellow arrow), lacks a hollow on its proximolateral aspect to accommodate rotation of radial tuberosity (red arrow), and also lacks the concave, deeply furrowed and sharply keeled interosseous margin along with a triangular shaft cross-section (white arrow); these traits or their absence are shared with A.L. 438-1 and *Pan* and distinct from humans. Humans also demonstrate a ulnar shaft with generally more lateral orientation (green arrow).

Next steps: curvature in 3D

Most studies of forearm curvature have focused on 2D ulnar curvature in the anteroposterior dimension as seen in lateral view. Figure 6 uses the same scaled elements from Figure 5 but instead shows the anterior view, illustrating that ulnar curvature is complex in three dimensions. Our next steps will involve quantifying this tortuosity by examining how the centroid of the cross-sectional areas curve in 3D through the length of the shaft (Figure 7). This work is in progress.

Figure 7

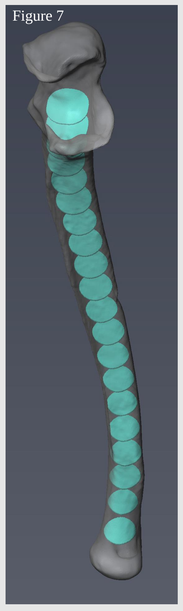


Figure 7. Angled anterior view of human left ulna with transparent cross-sections at 5% increments that illustrate the 3D path of the centroid's curvature through the proximodistal extent of the shaft.

CONCLUSION

Although Lucy's forearm elements are fragmentary, it is possible to reconstruct and estimate the lengths of the long bones. Our results agree with those of other workers on the following points: Lucy and the presumed male A.L. 438-1 have forelimb proportions more similar to *Pan* than *Homo*, and their ulnar curvature is intermediate between *Pan* and *Homo*. Sometimes an even higher degree of curvature is found in other early hominins including Omo 40-19 and OH-36. Our results along with the detailed anatomical descriptions of these elements that point to an emphasis on those muscles that aid powerful pronation, supination, and flexion and are important to climbing (*e.g.*, insertion site of m. brachialis, prominent radial tuberosity for m. biceps brachii, etc.), together suggest that climbing was an important component in the locomotor behavior of *Au. afarensis.*

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