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. When opposing authors hold 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, forearms for climbing should be shared with chimpanzees. Lucy preserves partial ulna and radius. We used high-resolution X-ray CT scans of Lucy for reconstructing by mirroring right and left portions, and using 3D cross-sections of humans, chimpanzees, and Australopithecus 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 sectional geometry to evaluate curvature in 3D. In chimpanzees, these flaws contribute to produce a stable primate foramen 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 may have been important for the acquisition of 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 hominids and is represented by about 25% of the skeleton by element count. Her limb bones are well preserved by long bone elements including: 1) humerus (nearly complete) and L (two fragments); 2) ulna (proximal and distal fragments) and L (proximal and distal fragments); and 3) radius (proximal, middle, and distal fragments). 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 species from the typical modern human condition” (Kibbel et al. 1994). Other researchers have instead noted that the ulna of A. afarensis “...diverges from the modern African ape condition and matches the human morphology...” (Kibbel et al. 1994, 450), in support of the view that “A. afarensis has relative upper-limb proportions that are within the range of variation in humans...” (Deurop and Ward 2007, 340). These contrasting conclusions suggest that it is worth re-examining Lucy’s upper limb.

Long bone lengths
Given the missing diaphyseal portions of Lucy’s limb elements, some compressive fracturing, and differing lengths of the same portion of R and L elements, questions remain about the long lengths of these elements. We used a combination of mCT and next- generation scans, 3D prints, and mCT scans to reconstruct and evaluate the model.

- The R humerus (A.L. 288-1m) is nearly complete and its reconstructed length has been reported between 236.8 mm (Johanson et al. 1982) and 246 mm (Haefliger, 2001). Kappelman et al. (2012) used mCT scans to reorient the 29 tiny compressive and presumably perimortem fractured bone fragments of its proximal end, and realigned the spiral fracture of the proximal end, to obtain a value of 237 mm for the length from the head to the capitulum (Figure 1a).
- The ulna and radius are more problematic (Figure 1b). The proximal radius is represented by a R fragment (A.L. 288-1p) that contains about 25% of the proximal radius, and is more complete than R (A.L. 288-1l). The cross-section of the distal portion of the right radius (A.L. 288-1p) has been catalogued as A.L. 288-1p, here called A.L. 288-1lp (Figure 1c), matches the central portion of the cross-section of the distal portion of the left radius (A.L. 288-1l) when mirrored as R. This reconstruction suggests that 8.8 mm is missing at the distal end of the bone: an unknown length is missing between the R proximal (A.L. 288-1p) and reconstructed distal portion of the shaft (A.L. 288-1lp & g).

Both ulna are missing their diaphyses, with the I proximal portion (A.L. 288-1l) more complete and longer than the R proximal portion (A.L. 288-1lp & g). Given that Lucy shares with the chimpanzee moderate curvature (see below) of both ulna and radius, and lacks the sharply keeled and prominent interosseous crest of humans (Figure 4), we used the mCT scans to estimate the ulnar and radius lengths of Lucy and obtain a value of 238.8 mm from 222-229 mm from the olecranon process to ulnar head, close to the descriptions by a number of other authors (340-345 mm) assuming an isometric correlation between the radial head with the radius, and ulnar head with ulnar notch. We estimate the 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 = 71.7, F = 62.3), chimpanzees (M = 21.8, F = 23.5), pongids (M = 20.8, F = 22.0), and Australopithecus (M = 19.4, F = 20.0). Figure 2 plots all four species, with Pan displaying a longer radius relative to the length of the humerus that is between Homo and Gorilla, and H. habilis relatively longer still. Figure 3 limits this analysis to endemic primates, with results for the central portion of the radius of 183 mm to 236 mm, with a value of 237 mm for the radius from the head to the capitulum (Figure 1a). 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 4), we use the mCT scans to estimate the ulnar and radius lengths of Lucy and obtain a value of 238.8 mm from 222-229 mm from the olecranon process to ulnar head, close to the descriptions by a number of other authors (340-345 mm) assuming an isometric correlation between the radial head with the radius, and ulnar head with ulnar notch. We estimate the length of the radius at 208-212 mm, close to the range of 203-215 mm by Asfaw et al. (1999).

What about Lucy? Deurop and Ward (2005) note that “both proximal and distal fragments are very straight” (408). They provide maximum and minimum curvature estimates (see Figure 4) and note that these estimates “…should therefore be interpreted with due caution” (408). Although their method requires more material than is available, there is enough enough preserved of Lucy’s proximal radius 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. 288-1) 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.