RECONSTRUCTING AUSTRALOPITH BODIES

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Adrienne L. Zihlman[1]
azihlman@ucsc.edu

Carol E. Underwood[1]
carol_underwood@hotmail.com

Debra R. Bolter[2]
bolterd@yosemite.edu

Austin

[1]Department of Anthropology, University of California, Santa Cruz   [2]Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg, South Africa

I. INTRODUCTION

Australopith postcranial skeletal remains are numerous and morphologically distinct from *Pan* or *Homo*. Partial skeletons, as those of *Au. afarensis* (AL 288), *Au. africanus* (Sts 14), and *Au. sediba* (MH2), provide approximations of overall body size, linear dimensions and overall morphology (e.g., Robinson, 1972; Johanson & Taieb, 1978; Schmid, 1983; Haeusler, 2002; Schmid et al., 2013). Key measurements taken on these and other fossil limb, pelvic, and foot bones provide a framework for estimating values of soft tissue. We use available linear values as guides to "reconstruct" body proportions and muscle groups in a small-bodied australopith. Soft tissue values derived from *Pan* and *Homo* individuals serve as "book ends" and bracket our estimates for australopiths.

II. MATERIALS and METHODS

Data are derived from standardized dissection methods of an adult female *Pan paniscus* (n=1) and a female *Homo sapiens* (n=1) (cf. Zihlman et al., 2011; Zihlman and Underwood, 2013; Zihlman and Bolter, 2015; Zihlman and Underwood, in prep). On one side of the body, upper and lower limbs are removed, weighed, and separated by segment (arm, forearm, hand; thigh, leg, foot). Each segment is weighed then separated by muscle, bone, and skin; each tissue is weighed. Back extensors are removed by region (cervical, thoracic, lumbar, sacral) and weighed. On the other set of limbs, each individual muscle is detached and weighed.

Upper and lower limb proportions relative to total body mass, distribution of muscle mass to limbs, and regional distribution of back extensors are calculated. Muscles are grouped by function, and relative contribution of antagonists is determined. Proportion of tissues – skin, muscle, bone – is determined for the foot.

III. RESULTS - Female *Pan* and *Homo*

Limb proportions. *Pan* upper limbs and lower limbs relative to total body mass are 15.5% and 20.8% respectively. *Homo sapiens* values 7.8% and 25%, respectively.

Muscle distribution and proportions of back extensors. Muscle acting on upper and lower limbs differs. In *Pan* 36.8% of total body muscle acts on the upper limb and 42.6% on the lower limbs. In *Homo* upper limb muscle drops to 20%, and lower limb rises to 60%. Although *Homo* has less overall muscle mass than *Pan*, both species have about 80% of muscle acting on the limbs. Of back extensors, *Pan* has 23% in the lumbar region, whereas *Homo* has 41%.

Gluteals and thigh muscles. In *Pan*, *g. maximus* is equal to or lighter than the mass of *g. medius* (45/55%). In humans, *g. maximus* approaches a 2:1 value to *g. medius* (~70/30%). Thigh muscles are partitioned into three compartments: quadriceps muscles, hamstring muscles, and adductor muscles. The percent of hamstrings to total thigh musculature is in *Pan* (20%) and *H. sapiens* (22.7%). However, the adductors and quadriceps are "switched" in proportions. Adductors are heavy in *Pan* (47.3%) with lighter quadriceps (32.7%), whereas humans emphasize the quadriceps (45.2%) and have proportionally smaller adductors (32.1%).

Footprints and foot bones. Tissue composition of the foot in *Pan* and *Homo* document similar amount of bone mass (38.7% and 38%). *Pan* has more muscle at 32.4% than *Homo* at 21%. In *Homo* skin/fat comprises 41% of the foot tissues, while in *Pan* the value is 28.9%.

IV. DISCUSSION - Australopiths

Bipedal locomotion in the australopiths affected their limb mass and muscle mass distribution. Using *Pan* and *Homo* comparative data, we reconstruct these soft tissue values for the extinct group within these parameters (Zihlman and Underwood, in prep).

Limb proportions. Humeral/femoral ratio of AL 288, at 84, is intermediate between that of *Pan* at 95 and *Homo sapiens* at 75 (Johanson and Taieb, 1978). This measurement indicates australopiths (*Au. afarensis*) had shorter upper limbs compared to *Pan*, and presumably lighter ones as well. If upper limbs are intermediate in mass between *Pan* and *Homo*, as are linear proportions,

(DISCUSSION CONTINUED)

then australopith upper limb mass would be about 12% relative to total body mass. Lower limb mass would be similar to *Pan* and *Homo*, about 23% of total body mass. **FIGURE 1**.

Muscle proportions. Muscle distribution to upper limbs, if also intermediate between *Pan* (36%) and *Homo* (20%), would constitute about 28% in australopiths of total muscle mass acting on the upper limbs. In maintaining the consistent 80% of body muscle acting on the limbs in both *Pan* and *Homo*, then australopiths would maintain about 52% muscle acting on the lower limbs. **FIGURE 1**.

Australopiths with 5 lumbar vertebrae (Ward et al., 2017) likely connects to greater muscle in this region. We estimate about 34% in the lumbar region—intermediate between *Pan* (23%) and *Homo* (41%)—related to an incipient lumbar curve and lower back flexibility, and consistent with a shift to bipedalism.

Gluteals and thigh muscles. In functional muscle groups acting on the lower limbs, we estimate australopith *gluteus maximus* heavier than *g. medius* with a shift towards bipedalism. Gluteals in *Pan* (45/55%), and *Homo* (70/30%) function in extension, abduction, and rotation of the hip joint, although with varying attachments and muscle shapes (Zihlman & Brunker, 1979). Their functions were likely similar in australopiths. Bone/muscle relationships follow the shape of the australopith pelvic girdle—an intermediate state between *Pan* and *Homo* (Zihlman & Hunter, 1972). The short, expanded australopith ilium as evidenced in Sts 14 probably correlates with increased bony attachment for *g. maximus* compared to *Pan*, and a greater mass ratio of *g. maximus* at 60% to *g. medius* at 40%. **FIGURE 2**.
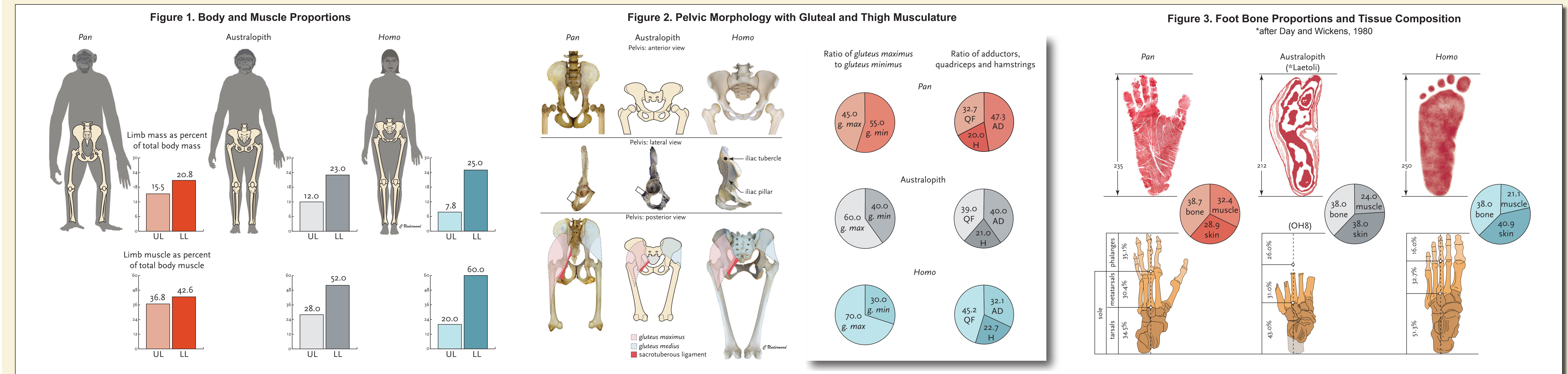
Thigh muscle ratios in australopiths probably show a shift in relative proportions of adductors and quadriceps, but not in hamstrings. We interpret this from the constant proportion of the hamstrings in *Pan* (20%) and *Homo* (23%), and we estimate 21% in australopiths. We estimate a decrease in adductors in asutralopiths at 40% compared to *Pan* (47.3%), with an increase in quadriceps at 39% compared to *Pan* (32.7%). The lighter mass of adductor estimates in australopiths like MH2, more similar to those of *Homo*, is indicative of the role that femoral torsion plays in bringing the knees and therefore feet into the midline in bipedalism. **FIGURE 2**.

Foot tissue composition and footprints. Australopith footprints at Laetoli, Tanzania, show an external form that is much like *Homo*, though the lateral border of the foot apparently carries more body weight (Day and Wickens, 1980, Schmid, 1980). The partial Olduvai fossil foot provides another line of evidence for commenting on bipedal function. OH8 (Olduvai Hominid, unknown genus/ species) retains most of the tarsus, though is missing the posterior calcaneus, the ends of the metatarsals, and all of the phalanges (Day and Napier, 1964). The metatarsals are robust, particularly I and V, aligning these features with *Homo* more than with *Pan*. The tarsus appears relatively long and more robust than in Pan and suggests more stability in the australopith foot during weight-bearing.

We estimate that the australopith foot has shifted from having less muscle at 25% compared to *Pan* (32.4%), but with similar bone composition at 38% to both *Pan* and *Homo*. We posit that the australopith foot had increase in skin/fat tissues, at 37%, a value closer to that found in *Homo* (41%), and correlated with the importance of skin and fat for support and padding when the foot serves as a bipedal platform. **FIGURE 3**.

V. SUMMARY

Comparisons of fossil bone morphology with *Pan* and *Homo*, and the soft tissues from dissections, offer an opportunity to estimate australopith skin, bone and muscle—body elements that do not fossilize. This fuller picture of australopith bodies, although speculative, is based on comparative data from two of its closest living relatives. The similarities of components between *Pan* and *Homo* lend plausibility to the tissue estimates we present, and point up how small shifts, say in adductor and quadriceps muscles, may result in functional changes in strength or refined movements. Shifts in muscle proportions need not be major to effect major functional change.

Figure 1. Body and Muscle Proportions

Figure 2. Pelvic Morphology with Gluteal and Thigh Musculature

Figure 3. Foot Bone Proportions and Tissue Composition
*after Day and Wickens, 1980

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