

# CHAPTER 12

## Robusticity of Bone and Muscle

*“General massiveness apparently is a primitive hominid character”*  
[Weidenreich, 1943, p. 175].

*“All of the postcranial elements [of *A. afarensis*] indicate high levels of skeletal robustness with regard to muscular and tendinous insertions”*  
[Johanson and White, 1979, p. 324].

*“The presence of increased cortical [bone] tissue in the early hominines, while widely recognized, has elicited very few explanatory models”*  
[Kennedy, 1985].

**Introduction.** Increased robusticity of the skeleton refers to strengthening by addition of compact bone tissue to the outer (cortical) layer that forms the main component of most bones. Robusticity of the muscular system denotes increased muscular mass, typified by modern body-builders. Bone robusticity in fossil hominins can be determined by measurements of the bones themselves, but statements about muscular robusticity are based on evaluation of rugosities on the surface of bones where muscles were attached.

Some authors have based their assessment of skeletal robusticity on visual inspection of bones. Others have used quantitative methods, such as determinations of the percent of cortical area in cross sections at specific sites on bone shafts [e.g., Ruff, 2009; Berger, et al., 2010b]. The general conclusion that can be drawn from these reports is that bones of most if not all extinct hominin species were very robust compared to ours. Such generalized, thickened, cortical bone is found in very few animals [Kennedy, 1985]. Apparently the musculature was also massive in fossil hominins, although the evidence for this is more limited.

Why were our early hominin ancestors so robust? The evidence will first be presented, followed by the explanations that have been proposed to explain it. The discussion will be focused on the postcranial part of the body; that is, everything from the neck to the feet.

**Paleontological evidence.** The earliest hominin postcranial specimens are from *Orrorin tugenensis*, dated at 6 Mya, represented by three fossil femora discovered in Kenya by Senut, Pickford and colleagues [Senut, et al., 2001]. In

one (BAR 1002'00) the femoral neck is complete. The cortex of the neck is thickest inferiorly and thinnest superiorly (a condition linked to bipedalism). However, superiorly, anteriorly and posteriorly the cortex is relatively thicker than it is in modern humans, although thinner than in African apes. Another of the specimens (BAR 1003'00) is larger and more robust [Pickford, et al., 2002]. Richmond and Jungers [2008] concluded that the width of the shaft of BAR 1002'00 is similar to early hominin femora in general, all of which have mediolaterally broad shafts. The robusticity exhibited by this ancient *Orrorin* femur appeared near the time of origin of the hominin lineage and persisted for more than 4 million years.

The degree of postcranial bone robusticity has not been reported for *Ardipithecus ramidus*. The bony remains are poorly fossilized and all large limb bones are variably crushed. Some of the smaller, better preserved bones of the hand and foot are described as robust [White, et al., 2009; Lovejoy, et al., 2009j].

*Australopithecus* had robust bones. A femur shaft of *A. anamensis* (from Kenya; 4.2-3.9 Mya) is notable for its thick cortex [White, et al., 2006]. The humerus also had an extremely thick cortex with a cortical area of about 86%—more robust than in tree-climbing African apes [Ward, et al., 2001].

*A. afarensis* (~3.9 to 3.0 Mya) maintained a robust post-cranial skeleton during the nearly one million years of its existence. The proximal ends of a radius and ulna from Sterkfontein, South Africa (3.3 Mya) are robustly structured, as are the first metacarpal and proximal phalanx of the thumb [Clarke, 1999, 2002]. In a partial *A. afarensis* skeleton from Hadar, Ethiopia, dated at 3 Mya, the ulna is large and robust. Muscle markings on the humerus are “quite dramatic” as are those on other bones. Even the hand is robust. The metacarpal shafts are thicker for their length than those of chimpanzees [Drapeau, et al., 2005] and some of the foot bones are described as having markedly thick cortical bone [Latimer, et al., 1982]. *Australopithecus africanus* was also very robust, similar to *A. afarensis* [McHenry, 1986].

The femora of *Paranthropus* (*A. robustus* ~1.8-1.0 Mya) [Klein, 1999] have large transverse shaft diameters, as do all non-*Homo* femora and other postcranial elements in hominins from the Pliocene and Pleistocene eras [McHenry 1991a, b].

**Robusticity continued during the transition to *Homo*.** Three hominin species associated with the transition from *Australopithecus* to *Homo* about 2 Mya (Chapters 6, 7) show a high degree of postcranial robusticity. In *A./H. habilis*, this is well documented in the femur and humerus; the phalanges of the hands are also exceptionally robust, with thick mid-shaft diameters with thick walls and features indicating powerful musculature [Susman and Creel, 1979; Susman and Stern, 1982; Trinkaus, 1984]. The relative cortical thickness (% CA) of the OH 62 femur (83.2%) is similar to other early *Homo* femora near mid-diaphysis (about 80-85%) and is elevated relative to modern humans (71.5%)

[Ruff, 2009]. The humerus in OH 62 also has relatively thick cortices (% CA, 79.7%), similar to the KNM-ER 1808 mid-distal humerus (81.7%) and again elevated relative to modern humans (59.8%). “Both the humerus and femur of OH 62 have relatively thick cortices...although they are not unusually thick when compared to other early *Homo* adult specimens” [Ruff, 2009, p. 96].

*Australopithecus sediba* from the Malapa site in South Africa (2.0 Mya) [Berger, et al., 2010a; Woodhead, et al., 2011] had a robust skeleton, including the humerus, femur and phalanges of the hand, which had strong attachment sites for the flexor digitorum superficialis muscle [Berger, et al., 2010b, Table S2]. Based on the percentage of cortical area (% CA) in cross-sections at or near midshaft in specimen MH1 (a juvenile), the humerus had a % CA of 75, which exceeded that of *A. africanus* (63-74%) and was somewhat less than in *A./H. habilis* (80%) and *H. erectus* (82%). (The latter two estimates are from Ruff [2009]). The % CA of the femur was 84% for the *A. sediba* juvenile; 80% for *A. africanus*, and (from Ruff [2009]) 83% for *A./H. habilis*. By this measure, the *A. sediba* femoral shaft was near the top of the *H. erectus* range.

Metatarsals found at the Dmanisi hominin site (1.8 Mya) have elevated robusticity indices based on body mass estimates. A complete adult femur shaft is markedly robust, with a narrow medullary canal. A less-robust tibia has mid-shaft proportions like those of early *Homo* [Lordkipanidze, et al., 2007].

Early African *Homo erectus* femora have very thick shafts [Walker and Leakey, 1993]. Robusticity also characterized the femur of *H. erectus* in China, exceeding that in any other living primate [Weidenreich, 1947]. The same is true of the humerus. *Homo heidelbergensis* ~500 kya had massively robust bones [Roberts, et al., 1994; Stringer, et al., 1998; Wood, 2010; Stringer, 2012]. In fact, all premodern people were characterized by extraordinary muscularity and robust bones, including hominins from Atapuerca, Spain, dated at about 0.3 Mya [Klein, 1999] and *H. neanderthalensis*, who was very robust throughout the postcranial skeleton, including the hand [Trinkaus, 1983].

**Children were robust.** Robusticity also characterized the skeletons of hominin children. The femoral morphology of three *Homo* juveniles (one *H. erectus* specimen and two Neanderthals) was studied by Ruff and coworkers [1994]. The midshaft femoral cortical bone thickness in these children (ages about 4-12 years) all fell in the upper part of the range for modern humans of a similar age. Increased diaphyseal robusticity relative to modern humans was apparently a characteristic of immature as well as adult *H. erectus* and *H. neanderthalensis* [Ruff, et al., 1994]. Even *infants* were robust. Skeletal robusticity was documented in a Neanderthal child found in Ukraine whose estimated age was 5-7 months [Vlcek, 1973]. The bones display pronounced robusticity compared to a modern child of the same age, according to Vlcek, who asserted that the robusticity of ribs and long bones in the infant may be regarded as “phylogenetically ingrained”—that is, genetic, due to evolutionary selection.

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