

THE SOUTHERN AFRICAN EARLY HOMINID RECORD AND INDICATIONS OF EMERGING COMPLEXITIES IN HUMAN EVOLUTION

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Over the past thirty years the discovery of increasing numbers of well preserved postcranial elements and partial skeletons of early hominids has allowed more accurate studies of the total morphological pattern of the postcranium of early bipedal apes. East African early hominid species such as *Australopithecus afarensis* are particularly well represented in the fossil record, and until relatively recently, this species was the only Pliocene-aged hominid species with a partial skeleton that had associated upper and lower limbs and girdles. Throughout the eighties and nineties, studies of the *A. afarensis* postcranium resulted in conflicting viewpoints as to the «modernity» or relative «humanness» of the species' skeleton. The recognized presence of many individual primitive traits in the postcranium of *A. afarensis*, such as the possession of a somewhat shortened femora, a relatively small size of the cross-sectional areas of the lumbar and sacral centra (Sanders 1990), a conical-shaped thorax (Schmid 1983), and curved shafts of the proximal phalanges, metatarsals and metacarpals (Stern and Susman 1983), to name some of the most important, seemed to reflect a total morphological pattern «[...] intermediate in its postcranial anatomy between modern humans and apes» (McHenry 1991). Yet the clearly derived human-like pattern of upper-limb shortening, ilium and general pelvic shape, knee and foot

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morphology result in the unequivocal conclusion that «[...] in the key characteristics that are essential for human-like bipedality, the earliest known hominids are not at all intermediate» (McHenry 1991).

The nearly contemporaneous southern African early hominid species *A. africanus* had, until recently, a much smaller and poorly represented sample of postcranial fossils. Most studies attempting to synthesize the information derived from postcranial analyses of early hominids tended to presume that since the cranio-dental complex of *A. africanus* was more derived than that in *A. afarensis*, and because *A. africanus* appears slightly later in time in the fossil record than *A. afarensis*, the overall pattern of «humaness» in key morphological areas related to bipedalism was established in *A. afarensis* and inherited by, and carried on in, *A. africanus*. This is despite recognition by some researchers that in certain key features the *A. africanus* skeleton was even more «primitive» than the «intermediate» skeleton of *A. afarensis* (Sanders 1990, McHenry 1991, Berger and Tobias 1996).

The past decade and a half has seen numerous discoveries of early hominid postcranial fossils in southern Africa including at least one partial skeleton with associated upper and lower girdle elements preserved. This material largely derives from Sterkfontein Member 4, dated to around 2.4-2.8 mya, and has been associated with the species *A. africanus* (McHenry and Berger 1998a). This material comprises more than 60 individual adult postcranial elements and adds considerably to the number of postcranial fossils associated with this early hominid species. Evidence derived from the study of this new material seems to contradict previous assumptions that the postcranial morphology of *A. africanus* is simply a continuation of the intermediate ape-human total morphological pattern exhibited by *A. afarensis* and surprisingly demonstrates in at least two key areas of the postcranium that *A. africanus* is more primitive than *A. afarensis* (McHenry and Berger 1998a, 1998b, Berger 1998).

The recent examination of relative upper and lower limb mass (McHenry and Berger 1998a) and limb length (McHenry and Berger 1998b) in early hominids has revealed unexpected results. Specifically, *A. africanus* exhibits joint sizes and relative mass distribution between the upper and lower limbs, as well as predicted proportional limb lengths more closely resembling that observed in *Pan* and other hominoids rather than the intermediate ape-human to human-like

condition predicted for, and observed in, these same features in *A. afarensis*. Using predictive methods for estimating both body weight and limb lengths from joint sizes in order to maximize sample sizes in both *A. afarensis* and *A. africanus*, McHenry and Berger (1998a, 1998b) found that on the whole *A. afarensis* was largely human-like in its upper-lower limb mass distribution and limb proportions in large individuals (presumably males) and intermediate between apes and humans in these features in small individuals (presumably females). These results for the smaller individuals are consistent with the findings of previous studies (e.g. Jungers 1982, McHenry 1992, etcetera). The analyses of *A. africanus* specimens, large and small, resulted in a very different pattern of mass distribution and limb lengths. Small individuals in the *A. africanus* sample gave proportional mass and limb length estimates more in line with those found for apes, and more particularly *Pan*, while large individuals in the sample appear as intermediate between apes and humans in these relationships.

The result that the very small individuals have differing proportions to the larger individuals is not new. The convergence between limb-joint proportions in modern humans and African apes at small body sizes has been discussed by previous researchers (Jungers 1982, 1985, McHenry 1991, 1992, Hartwig-Scherer 1993, McHenry and Berger 1998a). Thus the intermediate status of mass and length proportions predicted from joint size in smaller *A. afarensis* specimens such as A.L. 288-1 is not surprising. This trend also accounts for the much more human-like predictions made for the larger individuals in the *A. afarensis* sample. Although there are no associated small skeletons of *A. africanus* that have both upper and lower limbs or girdles preserved, the pattern for the whole *A. africanus* assemblage is clear: There are no upper limb elements small enough relative to the small lower limb elements to give proportional relationships close to that seen in the *A. afarensis* sample (see figure 5 in McHenry and Berger 1998a). What is even more surprising is the intermediate ape-human-like proportional mass and limb lengths predicted for the large bodied specimens of *A. africanus*, predictions confirmed by the clearly intermediate status of the mass and predicted limb proportions of the only partial skeleton with upper and lower limb-girdle elements preserved, Stw 431 (see figures 2 and 4 in McHenry and Berger 1998a).

When using predictors of human body weight based on joint size, the entire *A. africanus* postcranial sample exhibits a tendency towards large body weights in the upper limb and small body weights in the lower limb, with very little overlap in the sample. *A. afarensis* produces almost the opposite results, with both large and small upper limb elements and large and small lower limb elements, a result not surprising given the intermediate human-ape-like pattern in these measures exhibited by the small bodied Lucy. This overlapping sample is what one would expect in a random assemblage of animals that are fairly human-like in their body proportions. A better overlapping distribution is achieved for *A. africanus* when an ape sample is used, indicating a closer relationship between the upper-lower limb relationships observed in apes and *A. africanus*' mass distribution and proportional limb lengths (figure 1).

Although there is one good small *A. afarensis* partial skeleton (A.L. 288-1) and one good large *A. africanus* partial skeleton (Stw 431), I must acknowledge that the sample of large *A. afarensis* specimens and likewise small associated *A. africanus* specimens is woefully incomplete and we are reliant on the use of possibly unassociated fragments to predict the limb and mass relationships in these samples. Furthermore, the use of joint size to predict body weights and limb lengths is by no means universally accepted (see Asfaw *et al.* 1999). Nevertheless, one cannot ignore the surprisingly different pattern of distribution in mass and limb length between *A. africanus* and *A. afarensis* when using the same methods to assess relative joint size, body weight and limb length. Unless early hominids violate general trends observed in other hominoids, the conclusion that must be reached from these studies is that Stw 431 makes an unlikely proportional male to Lucy's female.

Further clues that something different is going on in the postcranium of *A. africanus* may be seen when one compares the pelvis and sacrum of Sts 14, one of the smallest *A. africanus* specimens and presumably a female, to that of the presumed female *A. afarensis* A.L. 288-1. Although the Iliac and pubic area of these two pelvises are roughly equal in size (Sts 14 is only slightly smaller), the sacrum of Sts 14 is just over half the size of Lucy's, giving a body weight estimation of only around 10 kg to Lucy's 16.4 kg. A statistic that is even more surprising given the already unusually small size of this anatomical

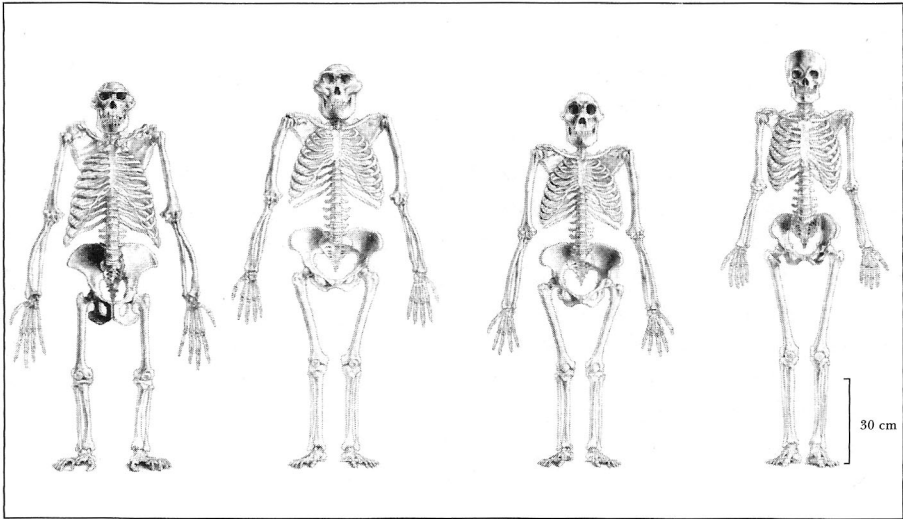


Figure 1. Artists reconstruction of male specimens of (from left to right) *Pan troglodytes*, *Australopithecus afarensis*, *Australopithecus africanus* and *Homo sapiens*, based on the reconstructions of limb lengths and mass by McHenry and Berger (1998a, 1998b). Note the wrist position against the femur for the various species (from Berger 1998). Artwork used with permission of the artist (John Gurche) and reprinted with permission of the National Geographic Society.

region in Lucy when compared to modern humans (Sanders 1990, McHenry 1991). This tendency towards an extremely small lower back in *A. africanus* is also seen in the Stw 431 skeleton. Although its upper limbs are almost two and a half times the size of Lucy's, the sacrum of Stw 431 is only some 17% larger than Lucy's and this is really on a result of greater antero-posterior and supero-inferior size of the first sacral vertebrae. The sacrum of Stw 431 is in fact medio-laterally narrower than that of Lucy. Additionally, ilium height in Stw 431 only exceeds the same measurement in Lucy by some 10 mm, a surprisingly small difference given the substantial size differences observed in every comparative measurement of the upper limb between the two skeletons.

I personally find the above mentioned morphological differences hard to attribute to simple variation. My skepticism that these results simply represent normal variation observed between similarly proportioned hominid species is heightened by Sts 14 also exhibi-

ting an unusually small sacrum. Additionally, Hausler and Schmid (1995) have demonstrated numerous other morphological differences between the pelvises of Sts 14 and A.L. 288-1 that were attributed by these authors to gender differences, but may relate to other functional differences (Schmid, personal communication). It appears to me to be more plausible to argue, even on this small amount of evidence, that a small lower back, pelvic region and in fact smaller lower limbs and longer arms are a pattern typical to *A. africanus*. If this is the case, then despite the well documented retained primitive features in the skeleton of *A. afarensis*, this species exhibits a more derived, human-like postcranium relative to that of *A. africanus*, at least where limb proportions and pelvic girdle size are concerned. Given the many well documented derived features observed in the craniodental complex of *A. africanus* relative to the same complex in *A. afarensis*, these results are indeed unexpected.

In our 1998 paper on limb-lengths my co-author Henry McHenry and I differed in our interpretation of these results. Henry suggests that the more ape-like proportions seen in *A. africanus* are the result of a reversal, possibly as a re-adaptation to an arboreal lifestyle. His adoption of this stance stems from the strong craniodental evidence that suggests a mother-daughter relationship between the more primitive *A. afarensis* and the more derived *A. africanus*. I find the idea of an evolutionary reversal towards the primitive condition unlikely and rather support the hypothesis that these postcranial differences result from separate evolutionary processes. Thus I would predict that an ancestral form with what I perceive as a primitive hominid body, such as that possessed by *A. africanus*, and a head as primitive as, or more so than that of *A. afarensis* exists but has yet to be discovered.

If no reversal has occurred, do recently discovered early Pliocene species such as *A. anamensis* fulfill the morphological role of being a good common ancestor for *A. afarensis* and *A. africanus*? Certainly cranially *A. anamensis* appears promising as a common ancestor, but based on the small sample of postcranial material attributed to this species (Leakey *et al.* 1995), the «larger hindlimb» condition we have observed in *A. afarensis* has already arisen by 4.1 mya. This suggests that if I am correct in my hypothesis that a reversal has not occurred, then the common ancestor of the *A. anamensis/afarensis* lineage and the *A. africanus* lineage is to be found even earlier than 4.1 mya.

Regardless of whether *A. africanus* and *A. afarensis* represent separate lineages or whether *A. africanus* represents a reversal within the same lineage, given the present fossil record, the evolution of later hominids becomes clearly more complex. White *et al.* (1998) have argued that only one species of hominid existed at any one time in the Pliocene of Africa. If this is true then the Pliocene evolution of hominids was punctuated by shifts in postcranial morphology from primitive to derived to primitive. *Homo habilis*, has also been suggested to have long arms and short legs based on the analyses of two different partial skeletons, KNMER 3735 and OH 62 (Leakey *et al.* 1989, Johanson *et al.* 1987). If *H. habilis* is considered to be the probable ancestor of the *H. erectus/ergaster* lineage then another reversal in postcranial morphology from the primitive to the derived must have occurred in the early Pleistocene. As complex as this scenario is, even it does not take into account the presence of at least three other hominid species in the genus *Homo* and three known in the genus *Australopithecus* during this time period. It seems far more probable to me that we still face gaps in the fossil record of the Pliocene and early Pleistocene hominid record that represent long lived lineages that possess different body proportions.

If *A. africanus* and *A. afarensis* are viewed as sister taxa, rather than having a mother-daughter relationship then either *A. afarensis* or *A. africanus* could give rise to *Homo habilis*, I would argue that in this scenario the similarity in limb proportions between *A. africanus* and *H. habilis* makes *A. africanus* the more likely ancestral form.

What then is one to make of the reportedly long legs and long forearms of the newly described species *A. garhi* from around 2.5 mya in East Africa (Asfaw *et al.* 1999)? We simply do not have the fossil evidence available at this time to sort out these complexities, but what does appear to be emerging from studies of postcranial anatomy of early hominids is that the diversity of hominid adaptations long recognized for the early Pleistocene existed also in the Pliocene.

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