# Limb lengths in *Australopithecus* and the origin of the genus *Homo*

*The recent discovery of fossil limbs of* Australopithecus africanus,[1] *including a partial skeleton, makes it possible to compare body proportions of this 3–2.3-million-year-old species with those of* A. afarensis *(3.9–3 Myr),* Homo habilis *(2–1.6 Myr), and* H. ergaster/erectus *(1.9–0.4 Myr).* Australopithecus africanus *is more similar to* H. habilis *in having larger forelimbs and smaller hindlimbs than expected from proportions seen in later* Homo. *Curiously, the earlier and craniodentally more primitive* A. afarensis *is more similar to later* Homo *in fore-to-hindlimb proportions. This implies that limb proportions changed back and forth in the hominid lineage or our present view of hominid relationships is too simplified.*

Recent discoveries have sparked renewed interest in the origin of the genus *Homo*. Formal cladistic analyses using traits of the skull and teeth show that *Australopithecus africanus* is more closely related to *Homo habilis* than is the earlier and craniodentally more primitive species, *A. afarensis*.[2–5] But partial skeletons discovered since 'Lucy' (A.L. 288-1, *A. afarensis*) reveal an unexpected complication: some of the body proportions of *A. afarensis* appear to be more like later *Homo* (i.e. *H. ergaster/erectus*) than are those of *A. africanus* or *H. habilis*.[1] Particularly noticeable are the more human-like forelimb joint-sizes relative to hindlimb size in *A. afarensis*. The later species, *A. africanus* and *H. habilis*, appear to have more primitive fore-to-hindlimb joint proportions.

This study seeks to determine if the same unexpected pattern is true of limb lengths. Did *A. africanus* and *H. habilis* have the more ape-like pattern of long forelimbs and short hindlimbs? The small morph of *Australopithecus afarensis* had a short thigh compared to what is expected in modern human proportions, but the humerus was not exceptionally elongated relative to trunk dimensions.[6,7] A newly discovered partial skeleton of a large-bodied *A. africanus*, Stw 431, from Sterkfontein makes it possible to compare that species with *A. afarensis* and early *Homo*.

## Materials and methods

*Australopithecus afarensis* is represented by the beautifully preserved partial skeleton of A.L. 288-1 that has a nearly complete humerus and femur.[8] Other specimens attributed to *A. afarensis* show that the species had a high level of sexual dimorphism.[9–12] There are several large humeri and femora that have been recovered from the same deposits (locality A.L. 333) that probably represent the male of that species.[12,13] Among the largest of these is a proximal humerus, A.L. 333-107, and a proximal femur, A.L. 333-3, that may be from the same individual. Until better samples are recovered, it is reasonable to take these specimens as representing the male of *A. afarensis*. The two *H. habilis* specimens, O.H. 62[14] and KNM-ER 3735,[15] are more fragmentary, but enough is preserved to show that forelimb shafts were larger than expected from hindlimb size when compared to *A. afarensis* or later *Homo*. The newly discovered partial skeleton of *A. africanus*, Stw 431, has the distal third of the humerus and proximal thirds of the radius and ulna. Its hindlimb is represented by a partial pelvic girdle including most of the left acetabulum. Both humeral and femoral lengths of *A. africanus* must be reconstructed in order to compare with *A. afarensis*.

The reconstruction of humeral and femoral lengths is based on reduced major-axis formulae derived from samples of 116 modern humans and 140 African apes. The human sample includes individuals as small as 28 kg and as large as 87 kg. The ape sample consists of 45 *Pan troglodytes*, 16 *P. paniscus* and 74 *Gorilla gorilla* specimens. The measurements are total length of the humerus and femur (measures #12 and 32, defined in ref. 16), width of the proximal and distal articular surfaces of the humerus (#1b & e), and diameter of the femoral head (#3c).

## Results

Figure 1*a* plots the relationship between distal humeral size and humeral length. Table 1 presents the least squares and reduced major axis slopes and intercepts with the correlation coefficients and the predicted lengths for the fossils. The Stw 431 humerus is predicted to be 302 mm long by the human formula and 283 mm long by the African ape formula. It is worth noting that the size of the distal articular surface of Stw 431 almost exactly matches what would be expected from the size of the proximal articular surface of Sts 7 based on comparisons with the modern human sample. The length of the Sts 7 humerus is predicted to be 304 mm using the human sample or 302 mm using the African ape sample. The A.L. 333-107 specimen is predicted to be 273 mm and 272 mm long by the human and ape formulae, respectively.

Figure 1*b* shows the relationship between femoral head size and length. The femoral head size of Stw 431 is estimated following the procedure described in a previous study. The predicted length for Stw 431 (Table 1) is 363 mm (human sample) or 303 mm (ape sample). Note that the actual length of A.L.

288-1 femur after reconstruction of the crushed distal end is 286 mm, which is between the estimates of 293 mm (human) and 268 mm (ape). The A.L. 333-3 femoral length is 403 mm by the human prediction or 324 mm by the ape formula.

The relationship between humeral and femoral lengths appears in Fig. 2. Human and ape specimens are widely separated. Using the ape-based predictions from Stw 431, the fossil projects very close to the ape sample, but using the human-based predictions, it is intermediate. A.L. 288-1 falls between the ape and human lines. The composite *A. afarensis* male (A.L. 333-107/333-3) is placed either intermediate (using ape-based formulae) or among the humans (using human-based formulae).

Table 1. Regression formulae and length predictions.[1]

| Bone | Sample | LS slope | LS intercept | *r* | s.e. | RMA slope | RMA intercept | Fossil | Measure | *H. sapiens* L (mm) | Ape L (mm) |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Humeral head | Human | 5.65 | 79.38 | 0.84 | 15.54 | 6.69 | 37.94 | A.L. 288-1r | 27.3 | 221 | 221 |
| | Ape | 6.15 | 60.72 | 0.95 | 20.47 | 6.46 | 44.86 | A.L. 333-107 | 35.1 | 273 | 272 |
| | | | | | | | | Sts 7 | 39.7 | 304 | 302 |
| | | | | | | | | Stw 328 | 34.2[2] | 267 | 266 |
| | | | | | | | | Stw 517 | 35.3 | 274 | 273 |
| | | | | | | | | ARA-VP-7/2 | 34.6 | 269 | 269 |
| | | | | | | | | KNM-BC 1745 | 32.0 | 252 | 252 |
| | | | | | | | | OMO 119-2718 | 35.5 | 275 | 274 |
| | | | | | | | | KNM-ER 1473 | 44.0 | 332 | 329 |
| Humeralart | Human | 4.83 | 106.47 | 0.86 | 14.83 | 5.65 | 73.33 | A.L. 137-48a | 36.0 | 277 | 256 |
| | Ape | 5.82 | 51.57 | 0.95 | 21.25 | 6.16 | 33.72 | A.L. 288-1m | 29.3 | 239 | 214 |
| | | | | | | | | A.L. 322-1 | 32.7 | 258 | 235 |
| | | | | | | | | Stw 431 | 40.5 | 302 | 283 |
| | | | | | | | | KNM-KP 271 | 44.8 | 326 | 310 |
| | | | | | | | | KNM-ER 3735A | 32.3 | 256 | 233 |
| | | | | | | | | KNM-ER 1504 | 39.5 | 296 | 277 |
| | | | | | | | | KNM-ER 6020 | 44.7 | 326 | 309 |
| | | | | | | | | KNM-WT 15000 | 39.0 | 294 | 274 |
| | | | | | | | | KNM-ER 739 | 43.6 | 320 | 302 |
| | | | | | | | | TM 1517 | 40.1 | 300 | 281 |
| Femoral head | Human | 7.46 | 107.28 | 0.79 | 25.68 | 9.44 | 23.21 | A.L 288-1ap | 28.6 | 293.1 | 267.7 |
| | Ape | 4.50 | 142.61 | 0.93 | 13.35 | 4.82 | 129.91 | A.L. 333-3 | 40.2 | 402.6 | 323.6 |
| | | | | | | | | Sts 14 | 30.0[2] | 306.3 | 274.5 |
| | | | | | | | | Stw 25 | 32.4 | 390.0 | 286.0 |
| | | | | | | | | Stw 99 | 38.0[2] | 381.8 | 313.0 |
| | | | | | | | | Stw 311 | 35.7 | 360.1 | 301.9 |
| | | | | | | | | Stw 392 | 31.5 | 320.5 | 281.7 |
| | | | | | | | | Stw 431 | 36.0[2] | 363.0 | 303.4 |
| | | | | | | | | Stw 501 | 33.2[2] | 336.5 | 289.9 |
| | | | | | | | | Stw 522 | 32.1 | 3 26.2 | 284.6 |
| | | | | | | | | MLD 46 | 36.6[2] | 368.6 | 306.3 |
| | | | | | | | | KNM-ER 1472 | 40.0[2] | 400.7 | 322.6 |
| | | | | | | | | KNM-ER 1481 | 43.8 | 436.6 | 340.9 |
| | | | | | | | | KNM-ER 3228 | 45.4[2] | 451.7 | 348.7 |
| | | | | | | | | KNM-ER 738 | 33.8 | 342.2 | 292.8 |
| | | | | | | | | KNM-ER 1503 | 35.1 | 354.5 | 299.0 |
| | | | | | | | | ER-WT 15000 | 45.9 | 431.0 | 351.0 |
| | | | | | | | | SK 82 | 34.0 | 344.1 | 293.7 |
| | | | | | | | | SK 92 | 36.8 | 370.5 | 307.2 |
| | | | | | | | | SK 3155 | 30.0[2] | 306.3 | 274.4 |

[1]These lengths are not intended to be equally valid estimates of the actual limb lengths of the fossil hominids. They are meant to be used to compare fore- and hindlimb sizes. [2]Estimated.

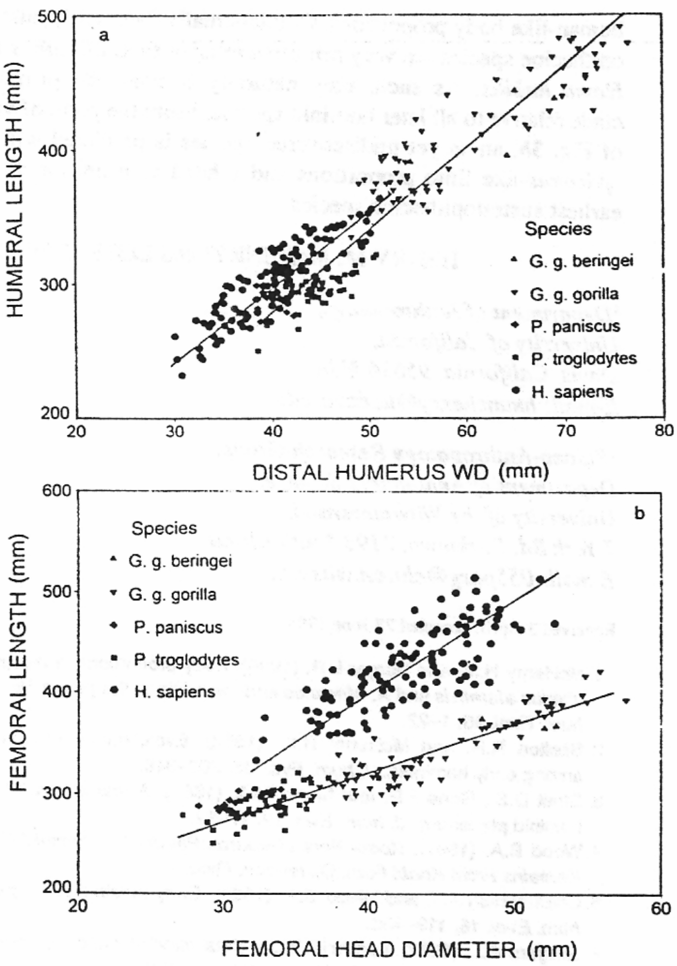


Fig. 1. *a*, Scatter plot and reduced major axis lines of the width of the distal articular surface of the humerus (horizontal axis) versus the length of the humerus in modern specimens of humans and African apes. Note that the slopes of the human line (above) is similar to that of the African ape line (below) but the two lines have slightly different *y*-intercepts, so that predictions from the human and ape reduced major axis formulae are slightly different (Table 1). *b*, Scatter plot and reduced major axis lines of the width of the femoral head versus the length of the femur in modern specimens of humans and African apes. Note that the slope of the human line (9.44) is much steeper than that of the African ape line (4.82) and the two lines have different *y*-intercepts, so that predictions from the human and ape reduced major axis formulae are very different (Table 1).

## Discussion

The incompleteness of the fossil sample makes it necessary to reconstruct parts of the anatomy, but these results are not unexpected from previous analyses of joint-size.[1] When all of the greatly expanded sample of limb-joints are compared, *A. africanus* appears to have relatively larger forelimbs and smaller hindlimbs than does *A. afarensis*. Although the small morph of *A. afarensis* (A.L. 288-1, considered female by most but not all) has relatively shorter thighs than does later *Homo*, *A. africanus* appears to be even more short-legged. This contrast between species is particularly noticeable at larger sizes: the large morph of *A. afarensis* is intermediate to human-like in fore-to-hindlimb lengths, whereas the large morph of *A. africanus* is intermediate to ape-like in these proportions. Although limb-lengths cannot be securely determined for *H. habilis*, forelimb size appears to be larger than expected from hindlimb size relative to modern humans or *A. afarensis*.[17]

Joint morphology is generally a better guide to positional and locomotor behaviour than is relative limb lengths, but the apparent disparity in limb lengths between *A. afarensis*, on the one hand, and *A. africanus* and *H. habilis* on the other, probably has behavioural implications. Perhaps the differences reflect divergent patterns of habitat use with the earlier species, *A. afarensis*, more suited to terrestrial life and the later species, *A. africanus* and *H. habilis*, more adapted to greater use of trees.

What is difficult to reconcile, however, is the apparent fact that the earlier and craniodentally more primitive species, *A. afarensis*, has fore-to-hindlimb proportions more like those of later *Homo* (*H. ergaster/erectus* and *sapiens*). The later species, *A. africanus* and *H. habilis*, share numerous unique craniodental traits with later *Homo* that are not present in *A. afarensis*.

Figures 3*a* and *b* represent two attempts at reconciliation. Figure 3*a* implies that the fore-to-hindlimb proportions were evolutionarily labile and altered from hindlimb dominance (in *A. afarensis*) to forelimb dominance (in *A. africanus* and *H. habilis*) back to the extreme hindlimb dominance of later *Homo*. This view might explain the larger-than-expected forelimbs of *A. africanus* and *H. habilis* as secondary adaptations that superficially mimic the primitive limb proportions. The remarkably small sacral and lower lumbar bodies of *A. africanus* might be a relatively simple alteration in embryogenesis where growth in that region switches off sooner than parts of the appendicular regions. Perhaps the larger forelimb of *A. africanus* and *H. habilis* do represent a reversal to a more primitive pattern. Either explanation implies homoplasy. Homoplasy is prevalent in both plant and animal evolution and hominids are no exception.[18]

Figure 3*b* implies that the resemblance of fore-and-hindlimb proportions between *A. afarensis* and later *Homo* is due to parallel evolution. By this view, *A. afarensis* evolved its relatively smaller forelimbs independent of *H. ergaster/erectus*. If the

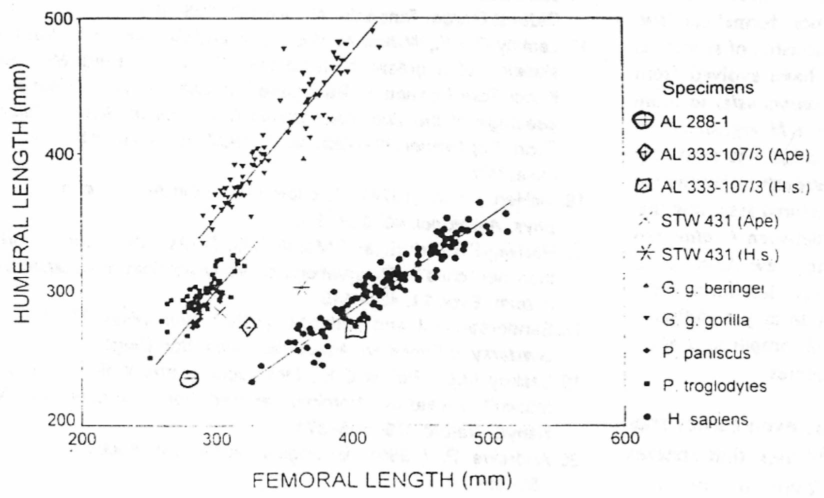


Fig. 2. Scatter plot of the femoral and humeral lengths of modern humans and African apes with the fossils included. The values for the *A. afarensis* specimen, A.L. 288-1, are reliably reconstructed from nearly complete bones, but the values of the other fossils are predicted using the reduced major axis formulae given in Table 1. Two values are plotted for A.L. 333-107/A.L. 333-3 (*A. afarensis*) and Stw 431(*A. africanus*): The 'ape' value refers to that derived from the formulae based on the African ape sample, and the 'H.s.' values are derived from the formulae based on the human sample. Note that most of the fossils fall intermediate between the ape and human lines except for *A. africanus*, when lengths are estimated using the African ape formulae and *A. afarensis* when lengths are estimated using the human formulae. This difference between the two species is what would be expected from a previous study of fore-to-hindlimb joint proportions.[1]

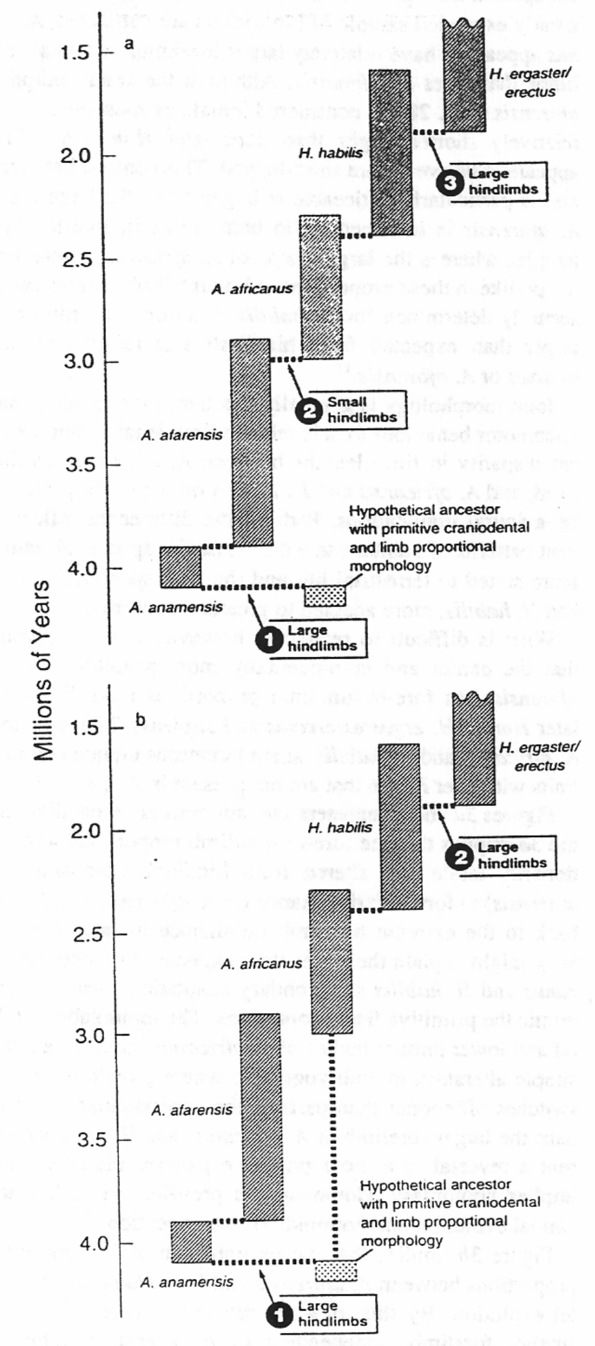


Fig. 3. *a*, A possible phylogeny of the better-known species of *Australopithecus* and early *Homo* that is supported by most formal cladistic analyses of the craniodental material.[2–5] If this relationship of species is true, then fore-to-hindlimb proportions appear to have evolved from near-human-like in *A. afarensis* (and probably *A. anamensis*) to more ape-like in *A. africanus* and *H. habilis* to human-like in *H. ergaster/erectus*. This would imply that these proportions are subject to relatively rapid change back and forth. *b*, The possible relationships among the better-known species of *Australopithecus* and early *Homo* assuming that the resemblance of fore-and-hindlimb proportions between *A. afarensis* and *H. ergaster/erectus* is due to homoplasy. By this view, *A. afarensis* (and probably *A. anamensis*) evolved relatively larger hindlimbs independent of *H. ergaster/erectus*. If this is true, then an as yet undiscovered species is predicted with *A. africanus*-like limb proportions and a head as primitive as the earliest australopithecine species.

attribution of the tibia, KNM-KP 29285, to the even earlier species of *A. anamensis* proves to be correct,[19,20] then that species could be part of this early and independent evolution of more human-like body proportions. Craniodentally these early australopithecine species are very primitive relative to *A. africanus* and *Homo habilis*. As such, they naturally become the primitive clade relative to all later hominid species. From the point of view of Fig. 3*b*, an as yet undiscovered species is predicted with *A. africanus*-like limb proportions and a head as primitive as the earliest australopithecine species.

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