Henry M. McHenry
Department of Anthropology, University of California, Davis, California 95616, U.S.A. E-mail: hmmchenry@ucdavis.edu

Lee R. Berger
Department of Anatomical Sciences, University of the Witwatersrand, 7 York Rd, Parktown 2193 Johannesburg, South Africa

Body proportions in *Australopithecus afarensis* and *A. africanus* and the origin of the genus *Homo*

New discoveries of *A. africanus* fossils from Member 4 Sterkfontein reveal a body form quite unlike earlier *Australopithecus* species. The new adult material consists of over 48 fore- and hindlimb specimens and includes an associated partial skeleton, Stw 431. The forelimbs are relatively large: the average size of their joints corresponds to a modern human with body mass of 53 kg. The hindlimbs are much smaller with an average size matching a modern human of only 33 kg. Analyses of the Stw 431 partial skeleton confirm these results. In contrast, *A. afarensis* and *anamensis* more closely approximate a human pattern of forelimb to hindlimb joint size.

This is an unanticipated complication in our understanding of early human evolution. In general, craniodental morphology tracks time in species of *Australopithecus*: *A. anamensis* (3·5–4·1 Ma) is the most primitive with a strongly sloping symphysis, large canine roots, etc., *A. afarensis* (3·0–3·6 Ma) is less primitive, and *A. africanus* (2·6–3·0 Ma) shares many derived characteristics with early *Homo* (e.g., expanded brain, reduced canine, bicuspid lower third premolar, reduced prognathism, greater flexion of the cranial base, deeper TMJ). The new postcranial material, however, reveals an apparently primitive morphology of relatively large forelimb and small hindlimb joints resembling more the pongid than the human pattern. More pongid-like proportions are also present in the two known associated partial skeletons of *H. habilis* (OH 62 and KNM-ER 3735). This may imply either (1) that *A. africanus* and *H. habilis* evolved craniodental characters in parallel with the lineage leading to later *Homo*, or (2) that fore- to hindlimb proportions of *A. afarensis* (and perhaps *A. anamensis*) evolved independent of the lineage leading to *Homo* and does not imply a close phylogenetic link with *Homo*. Both of these explanations or any other phylogeny imply homoplasy.

© 1998 Academic Press

Introduction

An unexpected result from the attempt to estimate the body weight of early hominids (McHenry, 1992) is the discovery of differences in fore- to hindlimb proportions in *Australopithecus africanus* and *Australopithecus afarensis*. In that study using modern human standards, the size of the forelimb joints predicts an average weight for *A. africanus* of 51 kg, but the hindlimbs correspond to an average of only 34 kg. Using all species of Hominoidea for comparison, the forelimb estimates average 42 kg and the hindlimb,

44 kg (McHenry, 1992, Table 4). The proportions for *A. afarensis* are more human-like with an average weight using the modern human comparative sample of 42 kg from the forelimb and 38 kg from the hindlimb. The estimates based on all species of Hominoidea predict 28 kg from the forelimb and 49 kg from the hindlimb. Is it possible that *A. africanus* is more ape-like in its body proportions than the earlier and craniodentally more primitive *A. afarensis*?

The purpose of this paper is to examine this apparent twist in the evolutionary

history of our lineage. With available fossil evidence, is it true that *A. africanus* had more ape-like body proportions and *A. afarensis* had more human-like proportions? This is an interesting question because one might expect *A. africanus* to be more human-like. This expectation derives from the fact that it is later in time (McKee, 1993; McKee *et al.*, 1995; Walter, 1993), shares a long list of derived craniodental traits with *Homo* relative to the primitive *A. afarensis* (McHenry & Skelton, 1985; Skelton & McHenry, 1992; Strait *et al.*, 1997; Kimbel, 1986; White *et al.*, 1981), and has some postcranial synapomorphies with *Homo* as well (McHenry, 1994*a*; Ricklan, 1987, 1990). This is not what would be expected from progressive evolution, but corresponds more with the model that sees the pattern of phylogeny marked by contingencies, homoplasy, historical particulars, and chance (Gould, 1995). It is also interesting because the two associated partial skeletons of *H. habilis* appear to have fore- to hindlimb proportions more similar to those of *A. africanus* (Hartwig-Scherer & Martin, 1991; Leakey *et al.*, 1989).

These subjects can be addressed now with more clarity because of the wealth of new discoveries from Sterkfontein. There are more than 48 adult fore- and hindlimb fossils from Member 4 added to the sample since the last monograph on the subject (Robinson, 1972), including a partial skeleton thanks to the persistence and skill of P. V. Tobias, the late A. Hughes, R. J. Clarke, and the staff of the Sterkfontein project over the last three decades.

Materials and methods

We examine the limb proportions of *A. africanus* and *A. afarensis* by making direct comparisons of fore- to hindlimb joint-sizes in associated partial skeletons and by expanding on the analyses presented in McHenry (1992). McHenry (1992) presents predicted body weights derived from regression formulae that related various measures of skeletal size with body weight in modern species of Hominoidea. That paper presents evidence for why the formulae based on the hindlimb joint size within *H. sapiens* appeared to be the most reasonable. This becomes particularly apparent from the partial skeletons of the early hominids.

McHenry (1992) describes the comparative sample used here. It consists of 32 male and 23 female modern North American *H. sapiens*, six Khoisan *H. sapiens*, two Akaka Pygmy *H. sapiens*, six male and nine female *Pan troglodytes*, five male and seven female *P. paniscus*, eight male and four female *Gorilla gorilla*. All of these were examined and measured by one of us (H.M.M.) to eliminate possible errors introduced by interobserver differences. There are 16 measurements in this data set with 51 additional measures (of the scapula, carpals and metacarpals, tarsals and metatarsals) in seven specimens that serve as standards. These are an Akaka Pygmy skeleton reported in McHenry (1992) with an estimated body weight of 28·4 kg, a Khoisan female with an estimated weight of 41·8 kg, and two North American females weighing 54·4 and 62·1 kg, two female chimps with wild-collected body weights of 42·2 kg and 50·0 kg and a male chimp of 60·0 kg.

Table 2 lists the fossil sample. It includes only those specimens whose adult status could be assured by the presence of an epiphysis. We follow the original describers of *A. afarensis* in attributing all of the Sidi Hakoma and Denen Dora Member hominids of the Hadar Formation to one species (Johanson *et al.*, 1982) because of the strong case made for the unity of that hominid sample (Kimbel *et al.*, 1984; White, 1985; Kimbel *et al.*, 1994). We also group all Member 4 Sterkfontein hominid postcranial material into the single species, *A. africanus*. More than one species may be present

(Kimbel & Rak, 1993; Clarke, 1988), but, at present, there are no morphological reasons to separate the postcranial sample.

The variables are as follows:

(1) SCAPULA: The product of the anteriorposterior and inferosuperior diameters of the glenoid.

(2) HUMHEAD: The maximum anteroposterior diameter of the humeral head taken perpendicular to the shaft axis.

(3) ELBOW: The product of the capitular height and articular width of the distal humerus. The capitular height is the distance from the anteroproximal border of the capitulum to the distoposterior border along the midline. The articular width is taken across the anterior aspect of the articular surface from the lateral border of the capitulum to the edge of the articular surface medially.

(4) HUMCAP: The product of the mediolateral and proximodistal diameters of the capitulum. The mediolateral diameter is the distance between the lateral border of the capitulum on the anterior aspect and the groove that separates the capitulum from the trochlea. The proximodistal diameter is the distance from the anteroproximal border of the capitulum to the distoposterior border along the midline.

(5) RADTV: The mediolateral diameter of the radial head.

(6) CAPITATE: The product of the proximodistal and palmodorsal diameters of the capitate. The proximodistal diameter is taken with one arm of the calipers flat on the distal articular surface and the other on the most distant point on the head. The palmodorsal diameter is taken with one arm of the calipers flat against the dorsal surface and the other to the most palmar point.

(7) MC1: The product of the mediolateral and palmodorsal diameters of the base of metacarpal 1 plus the product of the mediolateral and palmodorsal diameters of the head of metacarpal 1.

(8) MC1BASE: The product of the mediolateral and palmodorsal diameters of the base of metacarpal 1.

(9) MC2: The product of the mediolateral and palmodorsal diameters of the base of metacarpal 2 plus the product of the mediolateral and palmodorsal diameters of the head of metacarpal 2.

(10) MC2BASE: The product of the mediolateral and palmodorsal diameters of the base of metacarpal 2.

(11) MC3: The product of the mediolateral and palmodorsal diameters of the base of metacarpal 3 plus the product of the mediolateral and palmodorsal diameters of the head of metacarpal 3.

(12) MC3BASE: The product of the mediolateral and palmodorsal diameters of the base of metacarpal 3.

(13) MC4: The product of the mediolateral and palmodorsal diameters of the base of metacarpal 4 plus the product of the mediolateral and palmodorsal diameters of the head of metacarpal 4.

(14) MC4BASE: The product of the mediolateral and palmodorsal diameters of the base of metacarpal 4.

(15) MC4HEAD: The product of the mediolateral and palmodorsal diameters of the head of metacarpal 4.

(16) MC5: The product of the mediolateral and palmodorsal diameters of the base of metacarpal 5 plus the product of the mediolateral and palmodorsal diameters of the head of metacarpal 5.

(17) MC5BASE: The product of the mediolateral and palmodorsal diameters of the base of metacarpal 5.

(18) MC5HEAD: The product of the mediolateral and palmodorsal diameters of the head of metacarpal 5.

(19) SAC: The product of the antero-posterior and transverse diameters of the superior aspect of the sacral body.

(20) ACET: The transverse diameter of the acetabulum taken between the inner walls of the rim, perpendicular to the line connecting the point where the axis of the ischium intersects the rim and the point where the anterolateral border of the ilium intersects the rim.

(21) FEMHEAD: The maximum supero-inferior diameter of the femoral head.

(22) DISTFEM: The product of the bi-epicondylar and shaft anteroposterior diameters of the distal femur (measurements 12 and 13 of McHenry & Corruccini, 1978).

(23) PROXTIB: The product of the antero-posterior and transverse diameters of the proximial tibia. The a–p diameter is taken with one arm of the calipers on the line connecting the posterior surfaces of the medial and lateral condyles and the other arm on the most distant point on the medial condyle. The transverse diameter is the distance between the most medial point on the medial condyle and the most lateral point on the lateral condyle, taken perpendicular to the a–p diameter.

(24) DISTTIB: The product of the antero-posterior and transverse diameters of the talar facet on the distal tibia. The a–p diameter is the distance between the most anterior and posterior points of the talar facet projected on the a–p plane. The transverse diameter is the distance between the point where the midline of the talar facet intersects the fibular facet (laterally) and the lateral surface of the medial malleolus at the point of greatest curvature medially.

(25) TALUS: The mediolateral diameter of the tibial facet on the talus (measurement 5a of McHenry, 1974).

(26) NAVICULAR: The product of the minimum distance from the midpoint along the border between the facets for the cuboid and the lateral cuneiform to the rim of the talar facet, and the distance from the point of intersection of intermediate and lateral cuneiform facets with the dorsal surface to the most distant point on the tuberosity, plus the product of the maximum diameter of the talar facet taken perpendicular to the maximum diameter.

(27) MEDCUN: The product of the medio-lateral breadth of the navicular facet taken perpendicular to its long axis and the dorsoplantar height of the navicular facet, plus the product of the mediolateral and dorsoplantar diameters of the MT1 facet of the medial cuneiform.

(28) LATCUN: The product of the maxi-mum dorsoplantar height of the lateral cuneiform with one arm of the caliper held parallel to the proximodistal axis flat on the dorsal surface and the other brought to the tuberosity, and the distance from the most dorsal point along the junction of the navicular and cuboid facets to the dorsolateral corner of the metatarsal III facet, plus the product of the maximum dorsoplantar height of the navicular facet and the maximum mediolateral diameter of the navicular facet of the lateral cuneiform.

(29) MT1BASE: The product of the medio-lateral and dorsoplantar diameters of the base of metatarsal 1.

(30) MT1HEAD: The product of the mediolateral and dorsoplantar diameters of the head of metatarsal 1.

(31) MT2BASE: The product of the medio-lateral and dorsoplantar diameters of the base of metatarsal 2.

(32) MT2HEAD: The product of the mediolateral and dorsoplantar diameters of the head of metatarsal 2.

Three methods for comparing the fore- to hindlimb joint proportions appear in this study. First, the size of the forelimb joints

are compared directly with those of the hindlimb in associated skeletons. This method derived reduced major axis (RMA) formulae from log transformed measurements of the human and African ape samples. The method of RMA has the advantage over least squares (LS) and major axis (MA) because the slope is independent of the correlation coefficient and it gives the best estimate of the relationship between variables in cases where the error variance is not known (Aiello, 1992). The percent prediction errors (Smith, 1980, 1984; Dagosto & Terranova, 1992; Aiello & Wood, 1994) of the fossil values from what is predicted from the human and African ape RMA formulae provide a measure of how different the fore- to hindlimb proportions are in the fossils from the comparative samples. The *A. afarensis* partial skeleton, A.L. 288-1, preserves numerous fore- and hindlimb joints, but the two attributed to *A. africanus*, Sts 14 and Stw 431, are less complete. The former has no preserved forelimb elements. Stw 431 has a well preserved elbow joint but the hindlimb is represented by only a fragmentary pelvic girdle. Fortunately, the superior surface of the body of the sacrum is intact and enough of the acetabulum remains to allow reasonable reconstruction. The joints compared in this part of the analysis are, therefore, the lumbosacral, hip, and elbow. The elbow comparisons use the size of the distal articular surface of the humerus and the transverse diameter of the radial head. The method of comparing percent deviations from predictions based on RMA formulae is superior to comparing simple ratios, because the latter can be distorted by the non-linearity of the two variables.

The second method makes use of the entire adult sample of limb elements by grouping them into approximate size categories. Table 2 presents this approach. Each fossil whose adult status can be assured by the preservation of an epiphysis is compared to the equivalent element in three modern human skeletons that serve as standards. Those fossils that range from slightly smaller than an Akaka Pygmy skeleton (with an estimated weight of 28 kg) to slightly smaller than a Khoisan skeleton (with an estimated weight of 45–50 kg) are referred to the ''small'' category. Those fossils that approximately match the size of the equivalent elements of this Khoisan skeleton are placed into the ''medium'' category. The ''large'' designation is for those fossils that are larger than the Khoisan standard and closer to that of a North American skeleton whose body weight at death was 54 kg. The comparisons involved measurements and observations with the intention of grouping only approximately. This approach had the advantage of using the entire adult sample attributed to *A. afarensis* and *A. africanus*. This method reveals the disproportionate number of small hindlimbs and large forelimbs in the *A. africanus* sample.

The third method involves prediction of body weight from joint size based on the relationship between skeletal size in modern human and ape specimens of known body weight. Within the superfamily Hominoidea, the span of body weights is large and there is a reasonably close relationship between various measures of skeletal size and body weight (Jungers, 1985), but modern humans are peculiar. The earliest and most complete partial skeleton of *Australopithecus*, A.L. 288-1, has fore- and hindlimb joints that are consistent with what is expected in a small-bodied modern human (McHenry, 1992), although this specimen has short thighs (Jungers, 1982), and exceptionally small lower vertebral centra to the extent that its sacral body is much smaller than the tiniest modern human known (McHenry, 1992). What we present here are predictions of body weight assuming human and ape proportions of fore- and hindlimb dimensions.

This third method extends that presented in McHenry (1992). In that study, body
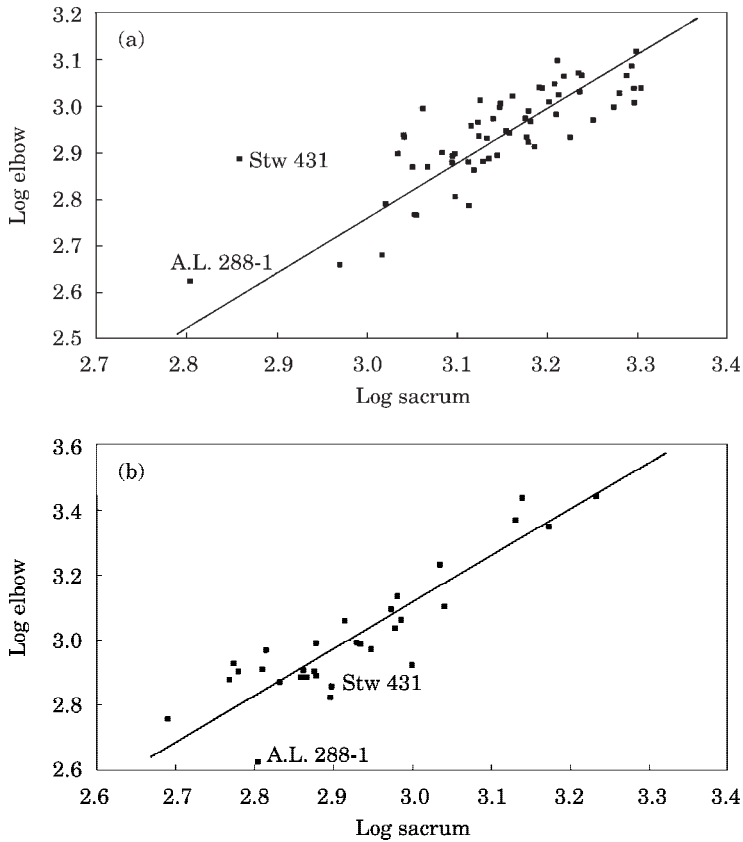
Figure 1. (a) Scatterplot and RMA of distal humeral size (ELBOW) *vs.* the size of the sacral centrum (SAC) in the human sample with Stw 431 (*A. africanus*) and A.L. 288-1 (*A. afarensis*). The RMA parameters and the percent prediction errors appear in Table 1. (b) Scatterplot and RMA of distal humeral size (ELBOW) *vs.* the size of the sacral centrum (SAC) in the African ape sample with Stw 431 (*A. africanus*) and A.L. 288-1 (*A. afarensis*). The RMA parameters and the percent prediction errors appear in Table 1.

weight is predicted from linear dimensions of skeletal size by three methods, least squares, reduced major axis, and major axis. Although the differences in assumptions among these methods are important, with high correlations, all of them produce similar results. That paper struck a compromise by averaging the estimates made by the three methods. In this study we employ reduced major axis. In practice, as long as the correlation coefficient is reasonably high (i.e. above 0·9) and the size of the fossils lies close to the range of the comparative sample, the three methods yield similar results (McHenry, 1992).

Results

Figure 1 presents a plot relating dimensions of the distal humerus (ELBOW) and sacral body (SAC) in the human sample [Figure 1(a)] and African ape sample [Figure 1(b)] with the partial skeletons of *A. afarensis* (A.L. 288-1) and *A. africanus* (Stw 431) inserted. Table 1 gives the RMA formulae and percent prediction errors of the fossils. Both fossils fall above the human line, but the percent prediction error of *A. africanus* (+94%) is much greater than that of *A. afarensis* (+23%) and is well outside the observed range in modern humans (Table

Table 1 Regression formulae and percent prediction errors relating fore- and hindlimb measures and percent prediction errors of the A.L. 288-1 and Stw 431 partial skeletons*

Meas	Sample	r	S.E.	RMA slope	RMA int	PE† A.L. 288-1	PE† Stw 431	PE‡ mean	PE S.D.§	PE obsv. range¶
ELBOW vs. SAC	Human	0·770	0·063	1·1749	− 0·7592	23%	94%	0·6%	14·7	− 23 to 43
	Ape	0·901	0·081	1·4225	− 1·1474	− 39%	− 7%	0·8%	18·5	− 36 to 35
RADTV vs. SAC	Human	0·731	0·034	0·6076	− 0·5835	14%	56%	0·3%	8·4	− 19 to 18
	Ape	0·886	0·034	0·5619	− 0·2510	− 29%	− 2%	0·4%	7·9	− 16 to 15
ELBOW vs. ACET	Human	0·841	0·047	2·5585	− 1·3924	59%	58%	0·5%	11·2	− 25 to 29
	Ape	0·966	0·051	2·1054	− 0·3710	− 28%	− 20%	0·9%	11·9	− 21 to 24
RADTV vs. ACET	Human	0·817	0·026	1·3412	− 0·9283	27%	37%	0·3%	8·4	− 19 to 18
	Ape	0·952	0·025	0·8750	− 0·0140	− 23%	− 8%	0·3%	5·8	− 10 to 12

*Figures 1–4 are scatterplots of these data around the reduced major axis.
†PE refers to the percentage prediction error which is the observed value minus the predicted value divided by the predicted value times 100 (Smith, 1980, 1984).
‡PE mean is the average percentage prediction error for the comparative sample (Dagosto & Terranova, 1992; Smith, 1980, 1984).
§PE S.D. is the standard deviation of the prediction errors in the comparative sample.
¶PE obsv. range gives the maximum prediction error in the comparative sample.
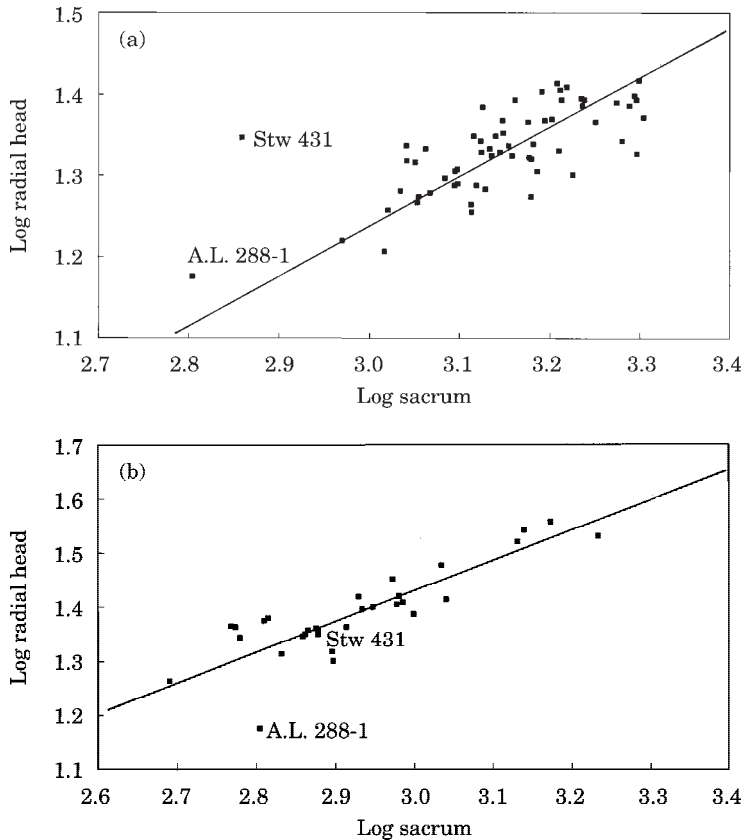
Figure 2. (a) Scatterplot and RMA of diameter of the radial head (RADTV) *vs.* the size of the sacral centrum (SAC) in the human sample with Stw 431 (*A. africanus*) and A.L. 288-1 (*A. afarensis*). The RMA parameters and the percent prediction errors appear in Table 1. (b) Scatterplot and RMA of distal humeral size (ELBOW) *vs.* the size of the sacral centrum (SAC) in the African ape sample with Stw 431 (*A. africanus*) and A.L. 288-1 (*A. afarensis*). The RMA parameters and the percent prediction errors appear in Table 1.

1). In the plot of African apes [Figure 1(b)] *A. africanus* is close to the RMA line with a percent prediction error of − 7%. *A. afarensis* is well below the African ape line (− 39%) and is outside the observed range (Table 1). In this respect, therefore, *A. afarensis* is intermediate between modern humans and African apes, but *A. africanus* is like modern apes.

A similar result appears when the size of the radial head is plotted against the size of the sacral centrum [Figure 2(a) & (b)]. *A. africanus* falls well above the human line (56%) and is far out of the observed range

in the human sample. *A. afarensis* is above the RMA but in the observed range of modern humans (14%). In this comparison, the *A. africanus* partial skeleton is very similar to that seen in the African ape sample [− 2% deviation, Figure 2(b)] and *A. afarensis* is well below the observed range (− 29%).

Since the relative size of the sacral centra in all Plio-Pleistocene hominids is exceptionally small relative to limb joints when compared to modern humans, it is important to use other hindlimb joints to compare relative forelimb size. Figure 3(a) and (b) compare the transverse diameter of the
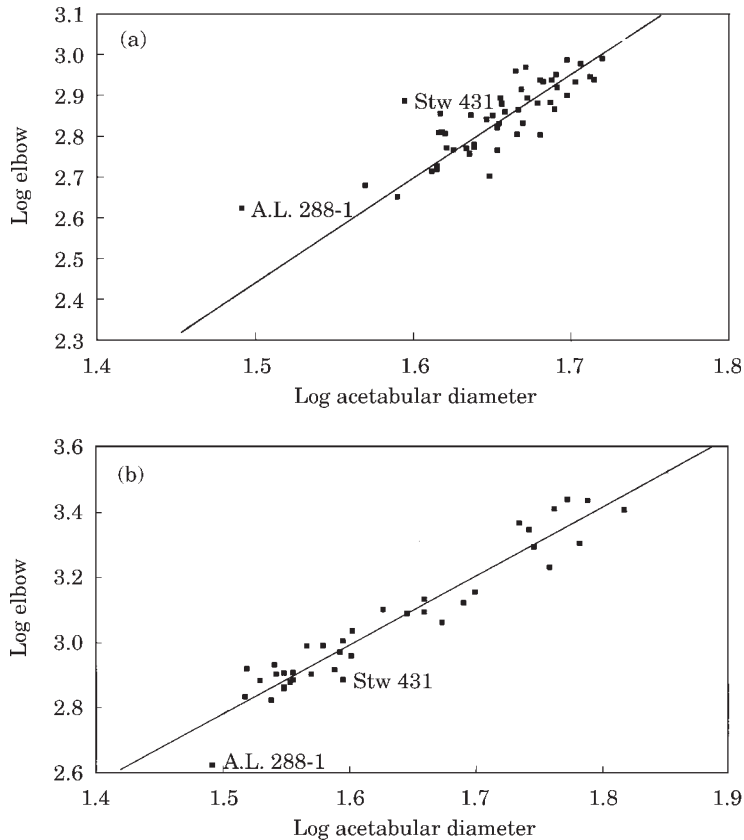
Figure 3. (a) Scatterplot and RMA of distal humeral size (ELBOW) *vs.* the transverse diameter of the acetabulum (ACET) in the human sample with Stw 431 (*A. africanus*) and A.L. 288-1 (*A. afarensis*). The RMA parameters and the percent prediction errors appear in Table 1. (b) Scatterplot and RMA of distal humeral size (ELBOW) *vs.* the transverse diameter of the acetabulum (ACET) in the African ape sample with Stw 431 (*A. africanus*) and A.L. 288-1 (*A. afarensis*). The RMA parameters and the percent prediction errors appear in Table 1.

acetabulum with the size of the distal humerus. Both *A. afarensis* and *A. africanus* fall above the human line (59 and 58% respectively) and out of the observed range in the human sample. They fall below the African ape axis (-28 and -20%). Figure 4(a) and (b) present the comparison of acetabular and radial head size in the human and African ape samples. *A. afarensis* is intermediate between human and ape in this respect (27% deviation above the human RMA and -23% deviation below the ape RMA). *A. africanus*, however, is more similar to the ape sample: Stw 431 is 37%

deviation above the human RMA and -8% below the ape RMA.

Table 2 lists all of the adult limb fossils available for study in three general size categories. Both fore- and hindlimb specimens of *A. afarensis* are well represented in all three sizes, although there is a predominance of large hands from the A.L. 333 site and no small forelimb specimens from that site. There are some small forelimb specimens from A.L. 333 such as the two clavicles, A.L. 333-94 and A.L. 333X-6/9, but they may not be adult. There is only one small forelimb specimen from Member 4 of
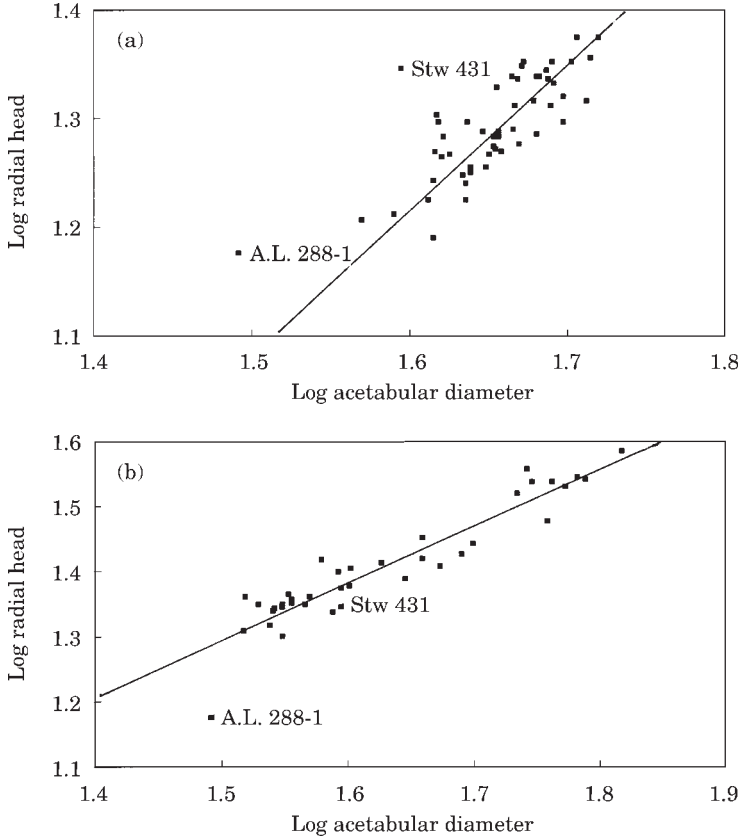
Figure 4. (a) Scatterplot and RMA of diameter of the radial head (RADTV) *vs.* the transverse diameter of the acetabulum (ACET) in the human sample with Stw 431 (*A. africanus*) and A.L. 288-1 (*A. afarensis*). The RMA parameters and the percent prediction errors appear in Table 1. (b) Scatterplot and RMA of diameter of the radial head (RADTV) *vs.* the transverse diameter of the acetabulum (ACET) in the African ape sample with Stw 431 (*A. africanus*) and A.L. 288-1 (*A. afarensis*). The RMA parameters and the percent prediction errors appear in Table 1.

Sterkfontein and that is the Stw 418 meta-carpal I. It is possible that *A. africanus* had thumbs that were relatively smaller than those expected from the size of the other metacarpals by modern human standards. Almost all of the hindlimbs of *A. africanus*, by contrast, fall into the small category and none is large.

Table 3 presents the regression formulae, fossil measurements and predicted body weights. Figure 5(a) and (b) plot predicted body weights in *A. africanus* [5(a)] and *A. afarensis* [5(b)] using the human formulae, and Figure 6(a) and (b) use the formulae

based on the African ape sample. These estimates are not intended to be viewed as equally valid approximations of the true body weight. It is inappropriate to use these figures as well-considered estimates of species body-mass. Table 4 of McHenry (1992) is to be viewed in the same light. In both cases the intention is to explore what is reasonable in the light of all the available evidence. Obviously, to approach a valid estimate of body mass in a hominid speci-men, hip, thigh, or ankle size is more likely to be closer to the real value than is, for example, wrist size and the estimates could

be improved by appropriate corrections as suggested by many (e.g., Aiello & Wood, 1994; Dagosto & Terranova, 1992; Hartwig-Scherer, 1993; Smith, 1993*a*, *b*, 1994, 1996). The intention here is to compare estimates based on fore- and hindlimb size.

Figures 5 and 6 show how remarkably different the two fossil samples are. *A. afarensis* displays a pattern similar to that seen in the modern human sample [Figure 5(b)] and a highly skewed distribution when formulae based on the African ape samples are applied [Figure 6(b)]. *A. africanus*, on the other hand, has a skewed distribution when human-based formulae are applied [Figure 5(a)] but a more even distribution of fore- and hindlimb sizes when the African apes are used as standards [Figure 6(a)].

Given the fact that both fossil species are bipedal hominids it is remarkable that unlike the sample of *A. afarensis*, the material from Sterkfontein Member 4 has no large hindlimbs to match its huge forelimbs. The *A. afarensis* sample includes many large hindlimb elements such as A.L. 333-3 and -w40 proximal femora, -4, -61, and -w56 distal femora, -42, -x26 and -7 distal tibiae, -9B, -85, and -9A distal fibulae, -8 and -55 calcaneus, -36 and -47 naviculars, -28 medial cuneiform, -79 lateral cuneiform, and -72 and -115 metatarsals. One of the largest hindlimb specimens from Member 4 of Sterkfontein is the Stw 99 femur, but this specimen may be associated with Member 5. Its stratigraphic position lies close to the boundary between Members 4 and 5.

Discussion

The results from the analyses of the partial associated skeletons show that fore- to hindlimb joint proportions of *A. afarensis*, as represented by A.L. 288-1, are more similar to modern *H. sapiens* than are those of *A. africanus* (Stw 431). This confirms the results from the analyses of the larger samples of the two species, but there is a complicating consideration. At small sizes like that of A.L. 288-1, limb-joint proportions of modern humans and African apes are more similar than at larger sizes like that of Stw 431 (Hartwig-Scherer, 1993; McHenry, 1992). Until the discovery of an associated partial skeleton of a large-bodied *A. afarensis*, uncertainty will lurk, but the A.L. 333 material probably contains fore- and hindlimb parts of single individuals. The largest forelimb specimens such as the A.L. 333-107 and -87 proximal humeri, the A.L. 333-29 distal humeri, the A.L. 333-119 and 33X-5 proximal ulnae and the A.L. 333-12 distal ulna may well belong to the same individual as the large hindlimb pieces such as the A.L. 333-40 proximal femur, the A.L. 333-61 and 333W-56 distal femora, the A.L. 333-42 proximal tibia, the A.L. 333-7 distal tibia and the A.L. 333-9B distal fibula. Another large-bodied adult might be composed of the A.L. 333W-22 and -31 distal humeri and the A.L. 333-3/4 femora, the A.L. 333X-26 proximal tibia, the A.L. 333-9A and -85 distal fibulae, and the A.L. 333-8 and -55 calcanei. Whatever the exact association, the large forelimb fragments of *A. afarensis* have equivalently large hindlimbs so that proportions appear to be more human-like than those of *A. africanus*. There are simply no large hindlimbs in the *A. africanus* collection to match the large forelimbs.

This study compares limb *joint* sizes and not limb lengths or shaft diameters. There are as yet no limbs of *A. africanus* complete enough to reconstruct limb length with the same certainty as can be done for A.L. 288-1. Compared to modern humans, A.L. 288-1 has a short femur relative to the length of the humerus (Jungers, 1982). It cannot be said, therefore, that the overall limb proportions of *A. afarensis* are human-like but only that the proportions of fore- to hindlimb joint sizes are similar to those of modern humans except for the unusually small lumbosacral joint. The proportions of

Table 2 Adult fore- and hindlimb specimens attributed to *Australopithecus afarensis* and *A. africanus* grouped according to approximate size*

	Small†	Medium‡	Large§
A. afarensis forelimb	A.L. 288-1 partial skeleton A.L. 137-48A and B humerus and ulna A.L. 322-1 humerus	A.L. 333W-36 ulna A.L. 333W-15 MC II A.L. 333W-42 MC II A.L. 333W-58 MC I	MAK-VP-1/3 humerus A.L. 333-29 humerus A.L. 333-31 humerus A.L. 333-87 humerus A.L. 333-107 humerus A.L. 333W-22 humerus A.L. 333-11 ulna A.L. 333-12 ulna A.L. 333-119 ulna A.L. 333X-5 ulna A.L. 438-1 ulna A.L. 333-130 radius A.L. 333-40 capitate A.L. 333-50 hamate A.L. 333-80 trapezium A.L. 333-91 pisiform A.L. 333-14 MC V A.L. 333-16 MC III A.L. 333-17 MC V A.L. 333-18 MV IV A.L. 333-56 MC IV A.L. 333-65 MC III A.L. 333-89 MC V A.L. 333-122 MC IV A.L. 333W-6 MC III A.L. 333-23 MC II A.L. 333W-26 MC V A.L. 333W-35 MC V A.L. 333W-39 MC I
A. afarensis hindlimb	A.L. 288-1 partial skeleton A.L. 128-1 femur A.L. 129-1 femur A.L. 129-1 femur A.L. 333-6 tibia A.L. 333-96 tibia A.L. 333-75 talus	A.L. 333W-56 femur A.L. 333-7 tibia A.L. 333-42 tibia A.L. 333-8 calcaneus A.L. 333-28 med. cuneiform A.L. 333-37 calcaneus A.L. 333-55 calcaneus A.L. 333-79 lat. cuneiform A.L. 333-13 MT V A.L. 333-21 MT I A.L. 333-54 MT I A.L. 333-78 MT V A.L. 333-115 partial foot	A.L. 211-1 femur A.L. 333-3 femur A.L. 333-4 femur A.L. 333-117 femur A.L. 333W-40 femur A.L. 333-123 femur A.L. 333-61 femur A.L. 333X-26 tibia A.L. 333-9A fibula A.L. 333-9B fibula A.L. 333-85 fibula A.L. 333W-37 fibula A.L. 333-36 navicular A.L. 333-47 navicular A.L. 333-72 MT II
A. africanus forelimb	Stw 418 MC I	Stw 328 humerus Stw 517 humerus Stw 46 radius Stw 380 ulna Stw 398 ulna Stw 399 ulna TM 1526 capitate Stw 64 MC III Stw 68 MC III Stw 330 MC IV Stw 552 MC IV	Stw 431 partial skeleton Sts 7 scapula an humerus Stw 162 scapula Stw 339 humerus Stw 516 radius Stw 26 MC IV Stw 63 MC V Stw 65 MC IV Stw 292 MC IV Stw 382 MC II Stw 394 MC IV

Table 2 (*Continued*)

	Small†	Medium‡	Large§
A. africanus hindlimb	Sts 14 os coxa and femur	Stw 431 partial skeleton	
	Sts 34 femur	Stw 99 femur	
	TM 1513 femur	Stw 435 MT II	
	Stw 25 femur		
	Stw 318 femur		
	Stw 392 femur		
	Stw 403 femur		
	Stw 501 femur		
	Stw 522 femur		
	Stw 527 femur		
	Stw 358 tibia		
	Stw 389 tibia		
	Stw 396 tibia		
	Stw 514 tibia		
	Stw 515 tibia		
	Stw 347 talus		
	Stw 352 calcaneus		
	Stw 486 talus		
	Stw 238 MT I		
	Stw 377 MT II		
	Stw 387 MT III		
	Stw 388 MT III		
	Stw 477 MT III		
	Stw 485 MT III		
	Stw 496 MT III		

*Includes only specimens whose adult status can be confirmed by the presence of a fused epiphysis.

†Range is size from slightly smaller than an Akaka Pygmy skeleton (with estimated weight of 28 kg) to slightly smaller than a female Khoisan skeleton (with an estimated weight of 45–50 kg).

‡Approximately equal in size to a female Khoisan skeleton (with an estimated weight of 45–50 kg).

§Larger than the female Khoisan skeleton (45–50 kg) and closer to a 54 kg North African skeleton.

fore- to hindlimb shaft robusticity appear to be unhuman-like in *A. afarensis* as well. Hartwig-Scherer (1993) shows that the midshaft circumference of A.L. 288-1 humerus corresponds to a modern human weighing 41 kg but that specimen's femur has a circumference matching a 34 kg human.

It may be that taphonomic processes produced the odd distribution of fore- and hindlimbs found in Member 4 of Sterkfontein and shown in Tables 2, 3 and Figures 5 and 6. Perhaps a predator destroyed the large hindlimbs, but left the large forelimbs. That appears unlikely because both hands and feet are represented, and a predator would presumably not destroy small hands and large feet in a selective manner. Nor does it seem likely that other taphonomic processes would result in only small hindlimbs being preserved in Sterkfontein Member 4.

Although the key features associated with bipedality are present in all species of *Australopithecus* (McHenry, 1994a; Latimer, 1988, 1991; Latimer & Lovejoy, 1989, 1990a,b; Latimer *et al.*, 1987; Lovejoy, 1988), the relatively large forelimb joints of *A. africanus* may imply greater arboreality in this species than in *A. afarensis*. Limb proportions were part of the evidence cited by Jungers (1982) to show that *A. afarensis* had more arboreal adaptations than modern people (Susman *et al.*, 1984; Jungers & Stern, 1983). The shoulder morphology of

Table 3   Regression formulae and weight predictions*

Bone	Sample	LS slope	LS int	r	S.E.	RMA slope	RMA int	Fossil	Meas	H.S. wt	Ape wt
Scapula	Human	1·5573	−2·6763	0·914	0·074	1·7038	−3·0839	A.L. 288-11	422·4	24·5	23·0
	Ape	1·1867	−1·7424	0·971	0·066	1·2221	−1·8471	Sts 7	690·3	57·7	41·9
								Stw 162	881·5	85·9	56·5
Humhead	Human	1·8308	−1·1930	0·944	0·057	1·9404	−1·3642	A.L. 288-1r	27·3	26·5	17·9
	Ape	1·8308	−1·1930	0·944	0·055	2·5558	−2·4184	A.L. 333-107	35·1	43·1	34·0
								Sts 7	39·7	54·7	46·5
								Stw 328	34·2	41·0	31·8
								Stw 517	35·3	42·8	34·5
Elbow	Human	0·8635	−0·7788	0·943	0·057	0·9152	−0·9257	A.L. 137-48a	525·6	36·7	23·7
	Ape	1·2870	−2·1258	0·995	0·027	1·2935	−2·1447	A.L. 288-1m	420·5	29·9	17·7
								A.L. 322-1	526·2	36·7	23·7
								Stw 431	769·5	52·0	38·8
Humcap	Human	1·8985	−3·0029	0·987	0·030	1·9235	−3·0635	A.L. 333-29	268·6	40·6	30·7
	Ape	1·4391	−2·0000	0·969	0·067	1·4851	−2·1201	A.L. 333w-22	316·2	55·6	39·1
Radtv	Human	1·9910	−0·8912	0·955	0·051	2·0859	−1·0132	A.L. 288-1p	15·0	27·5	10·7
	Ape	3·3155	−2·8619	0·985	0·046	3·3660	−2·9309	A.L. 333x-14	22·2	62·4	39·9
								Stw 431	22·2	62·4	39·9
								Stw 516	22·5	64·2	41·7
Capitate	Human	1·8792	−3·0159	0·999	0·009	1·8811	−3·0197	A.L. 288-1w	203·8	21·2	11·5
	Ape	1·6338	−2·6878	0·966	0·070	1·6913	−2·8442	A.L. 333-40	357·8	60·8	29·8
								TM 1526	294·2	42·1	21·4
MC1	Human	1·3514	−1·6502	0·915	0·059	1·4769	−1·9563	A.L. 333w-39	285·1	46·7	100·1
	Ape	1·9417	−2·8289	0·791	0·066	2·4547	4·0259	Stw 418	230·5	34·1	59·4
MC1 base	Human	1·7761	−2·2355	0·973	0·0339	1·8254	−2·3430	A.L. 333-58	144·8	40·0	64·1
	Ape	1·9829	−2·4808	0·968	0·027	2·0485	−2·6192				
MC2	Human	0·9885	−0·8098	0·990	0·021	0·9985	−0·8343	A.L. 333w-23	400·9	58·2	55·8
	Ape	1·2782	−1·5833	0·952	0·033	1·3441	−1·7519	A.L. 333w-48	300·6	43·7	37·9
								Stw 382	414·7	60·2	56·5
MC2 base	Human	1·1315	−0·9083	0·976	0·032	1·1593	−0·9708	A.L. 333w-15	169·2	41·0	43·3
	Ape	1·0353	−0·6699	0·984	0·019	1·0522	−0·7084				
MC3	Human	1·1968	−1·2933	0·990	0·021	1·2089	−1·3230	A.L. 333w-16	316·7	50·1	35·2
	Ape	0·8717	−0·6341	0·998	0·008	0·8734	−0·6381	Stw 64	326·3	52·0	36·1
								Stw 68	336·1	53·9	37·0
MC3 base	Human	1·3504	−1·3325	0·999	0·004	1·3518	−1·3352	A.L. 333w-6	200·0	59·6	44·4
	Ape	1·2853	−1·3103	0·999	0·003	1·2366	−1·3135	A.L. 333w-65	180·0	51·7	38·7

Table 3 (Continued)

Bone	Sample	LS slope	LS int	r	S.E.	RMA slope	RMA int	Fossil	Meas	H.S. wt	Ape wt
MC4	Human	0.7623	−0.1021	0.979	0.030	0.7787	−0.1392	A.L. 333-56	220.4	48.5	33.9
	Ape	0.7964	−0.3249	0.933	0.039	0.8536	−0.4697				
MC4 base	Human	0.7353	−0.1820	0.962	0.040	0.7643	−0.1243	A.L. 333-122	118.6	51.2	45.9
	Ape	0.6755	0.2674	0.830	0.060	0.8139	−0.0260	Stw 65	128.1	54.3	48.9
								Stw 330	116.6	28.5	45.3
MC4 head	Human	0.7820	−0.0871	0.992	0.019	0.7883	−0.0744	A.L. 333-18	128.6	54.6	32.1
	Ape	0.8367	−0.2539	0.976	0.024	0.8573	−0.3016	Stw 26	133.3	56.2	33.1
								Stw 292	124.3	53.2	31.2
								Stw 394	175.9	69.9	42.0
								Stw 552	115.0	50.0	29.2
MC5	Human	0.8665	−0.2900	0.997	0.012	0.8691	−0.2955	A.L. 333-14	222.6	55.6	60.8
	Ape	2.5488	−4.1994	0.9511	0.033	2.6798	−4.5028	A.L. 333-89	175.9	45.3	32.7
MC5 base	Human	0.9143	−0.1371	0.975	0.03236	0.9377	−0.1830	A.L. 333w-26	110.0	53.9	233.8
	Ape	6.6727	−11.2607	0.993	0.013	6.7197	−11.3487	A.L. 333w.35	107.9	52.9	205.4
								Stw 63	110.6	54.1	242.5
MC5 head	Human	0.7878	−0.1371	0.999	0.00718	0.7886	−0.1354	A.L. 333-17	101.5	52.2	37.8
	Ape	1.6607	−1.7447	0.922	0.042	1.7992	−2.0324	A.L. 333-27	116.6	58.2	48.5
Sac	Human	1.4991	−2.9735	0.968	0.043	1.5492	−3.1290	A.L. 288-1an	636.4	16.4	31.5
	Ape	1.8765	−3.7409	0.921	0.106	2.0375	−4.2140	Sts 14	461.7	10.0	16.4
								Stw 431	721.6	19.9	40.7
Femhead	Human	1.7125	−1.0480	0.976	0.033	1.7538	−1.1137	A.L. 288-1ap	28.6	27.6	30.4
	Ape	2.8826	−2.7130	0.988	0.041	2.9176	−2.7660	A.L. 333-3	40.2	50.1	82.1
								Sts 14	30.0	30.0	35.0
								Stw 25	32.4	34.3	43.8
								Stw 99	38.0	45.4	69.7
								Stw 311	35.7	40.7	58.1
								Stw 392	31.5	32.7	40.3
								Stw 431	36.0	41.3	59.5
								Stw 501	33.2	35.8	47.0
								Stw 522	31.1	31.9	38.8
								Stw 527	32.5	34.5	44.2
Distfem	Human	0.9600	−1.5678	0.968	0.043	0.9921	−1.6762	A.L. 129-1a	140.6	28.0	36.1
	Ape	1.4479	−1.5495	0.984	0.049	1.4714	−1.6030	A.L. 333-4	208.2	41.3	64.3
								A.L. 333w-56	202.6	40.2	61.8
								TM 1513	163.6	32.5	45.1
								Sts 34	193.3	38.4	57.7

Table 3 (Continued)

Bone	Sample	LS slope	LS int	r	S.E.	RMA slope	RMA int	Fossil	Meas	H.S. wt	Ape wt
Proxtib	Human	1·0583	−1·9537	0·991	0·023	1·0683	−1·9880	A.L. 129-1b	1595·6	27·1	31·2
	Ape	1·5066	−3·3283	0·993	0·032	1·5172	−3·3648	A.L. 288-1aq	1625·2	27·7	32·1
								A.L. 333x-26	2730·3	48·2	70·6
								A.L. 333-42	2560·0	45·0	64·0
								A.L. 333w-26	2730·3	48·2	70·6
								Stw 514	1776·7	30·4	36·8
Dist tib	Human	0·9005	−0·8790	0·974	0·039	0·9246	−0·9473	A.L. 288-1ar	329·4	24·0	25·2
	Ape	1·6314	−2·7021	0·989	0·039	1·6495	−2·7518	A.L. 333-6	470·9	33·4	45·4
								A.L. 333-7	612·5	42·6	70·1
								A.L. 333-96	441·0	31·5	40·8
								Stw 358	318·5	23·3	23·8
								Stw 389	539·7	37·9	56·9
								Stw 515	376·1	27·2	31·4
Talus	Human	1·7712	−0·7512	0·937	0·060	1·8903	−0·9148	A.L. 288-1as	17·3	26·6	44·3
	Ape	3·1699	−2·2714	0·940	0·093	3·3722	−2·5282	Stw 102	18·6	30·5	56·6
								Stw 347	17·6	27·5	47·0
								Stw 486	19·6	33·7	67·5
Navic	Human	1·1982	−1·7338	0·9016	0·0794	1·3289	−2·1033	A.L. 333-36	848·7	61·5	93·9
	Ape	1·7597	−3·1838	0·987	0·043	1·7829	−3·2490	A.L. 333-47	797·4	56·6	84·0
Med Cun	Human	1·0641	−1·2228	0·9822	0·0345	1·0833	−1·2741	A.L. 333-28	409·3	36·0	39·5
	Ape	1·8670	−3·2782	0·992	0·034	1·8821	−3·3192				
Lat Cun	Human	1·5541	−2·6113	0·9930	0·0217	1·5651	−2·6419	A.L. 333-79	594·4	50·1	101·1
	Ape	1·5467	−2·3008	0·934	0·097	1·6560	−2·5889				
MT1 base	Human	1·0264	−1·0315	0·993	0·0169	1·0336	−1·0506	A.L. 333-54	408·9	44·6	63·9
	Ape	1·2823	−1·5433	0·986	0·018	1·3005	−1·5893				
MT1 head	Human	0·86151	−0·4654	0·984	0·0264	0·8755	−0·4998	A.L. 333-21	262·4	41·5	82·1
	Ape	1·7641	−2·3887	0·834	0·060	2·1152	−3·2021	A.L. 333-115A	302·8	47·0	111·2
MT2 base	Human	0·9781	−0·6264	0·967	0·0375	1·0115	−0·7036	Stw 238	183·6	38·6	33·5
	Ape	1·5396	−1·9594	0·994	0·012	1·5489	−1·9817	Stw 377	176·9	37·2	31·7
								Stw 435	235·5	49·6	49·3
MT2 head	Human	1·9404	−2·3545	0·997	0·01125	1·9462	−2·3673	A.L. 333-72	142·3	66·6	52·6
	Ape	1·2775	−1·0305	0·982	0·020	1·3009	−1·0805	A.L. 333-115B	134·8	59·9	49·0

*These weight estimates are not intended to be equally valid estimates of the actual body mass of the fossil hominids. They are intended to be used to compare fore- and hindlimb joint sizes.
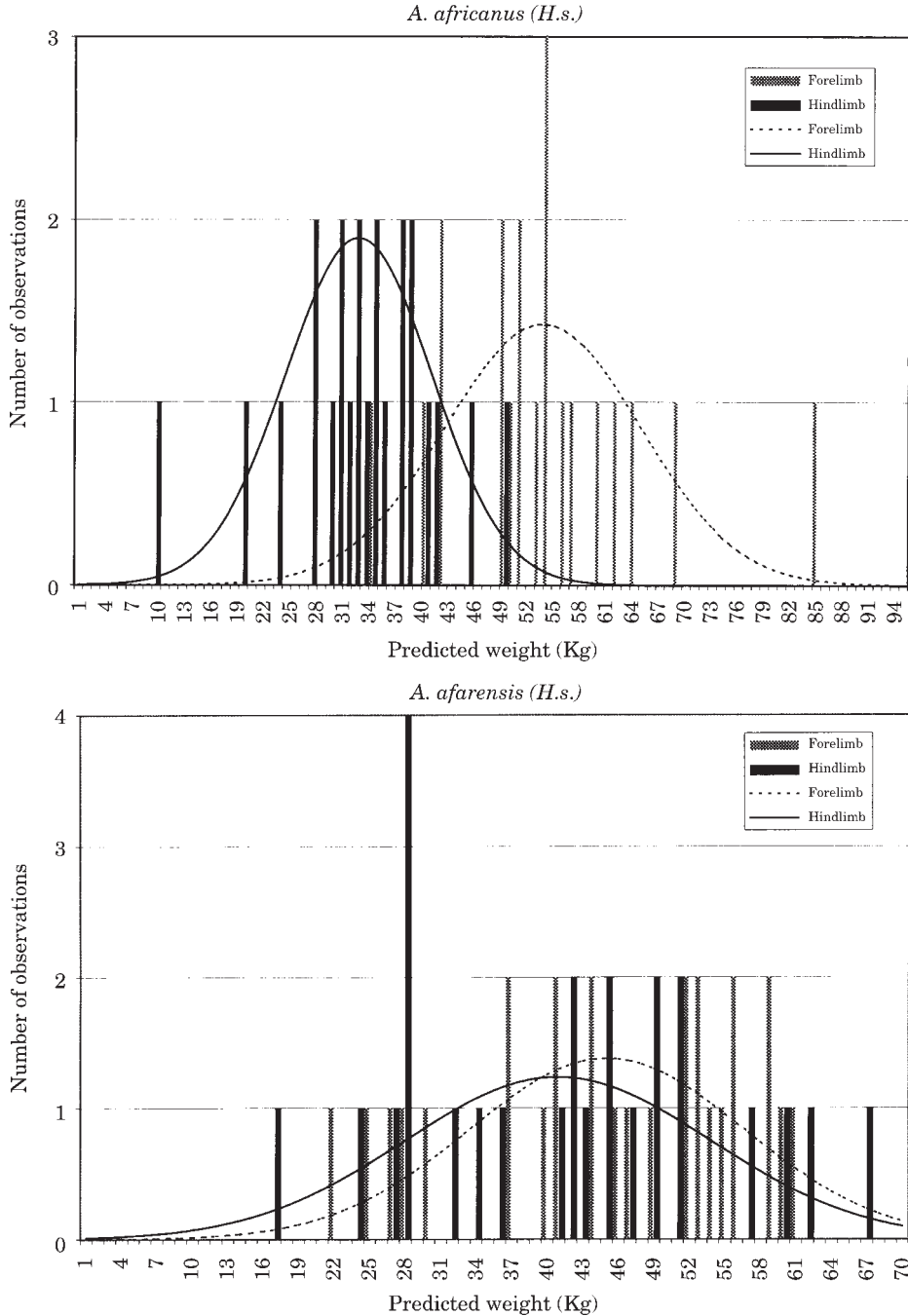
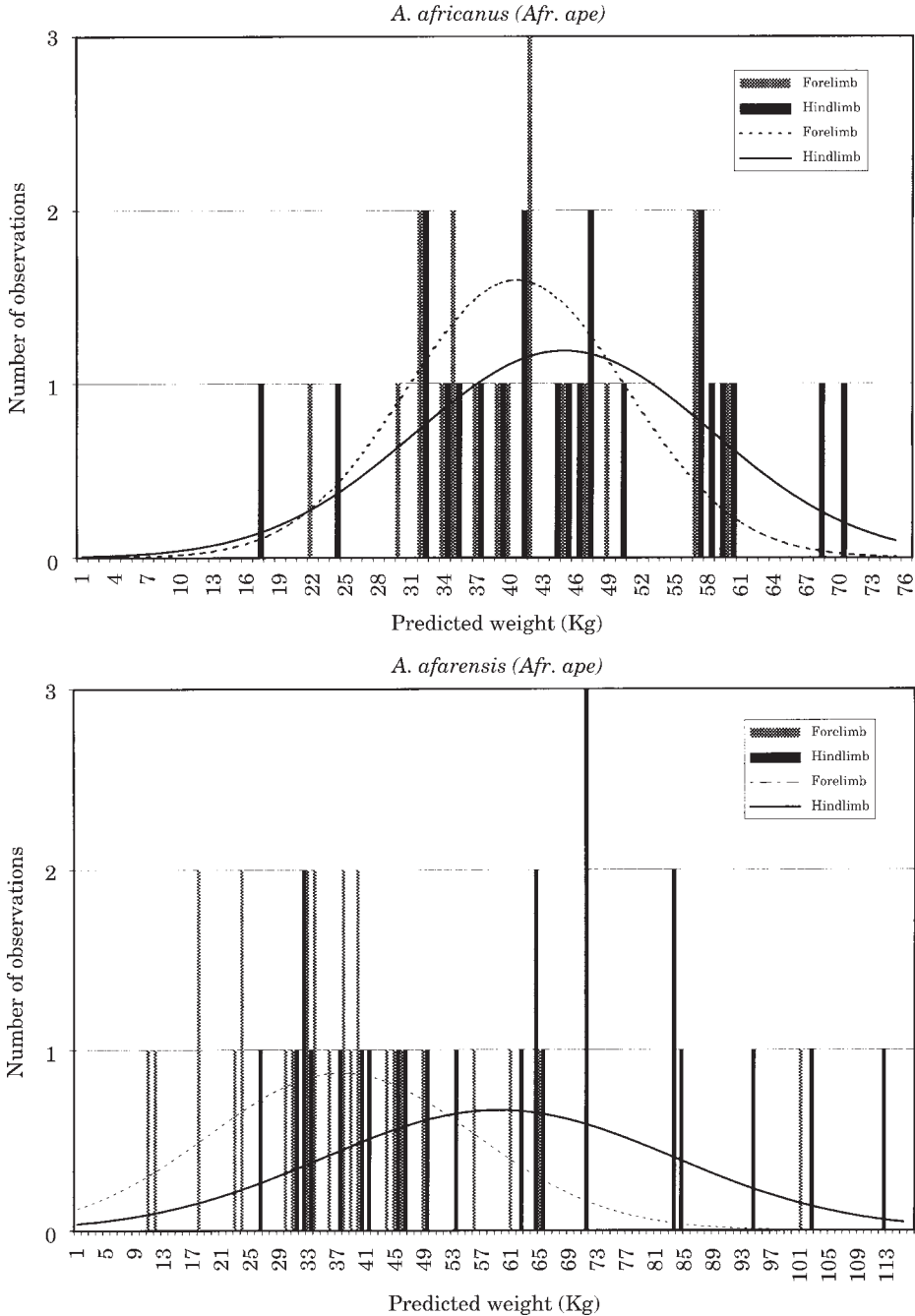Figure 5. (a) Frequency distribution of predicted body weights in *A. africanus* using RMA formulae derived from the human sample. Light bars are forelimb elements; dark bars are hindlimbs. Note that the forelimb elements predict mostly large weights and the hindlimb elements predict mostly small weights. (b) Frequency distribution of predicted body weights in *A. afarensis* using RMA formulae derived from the human sample. Note that unlike *A. africanus*, the distribution of large and small weights derived from fore- and hindlimb elements is approximately equal.

Figure 6. (a) Frequency distribution of predicted body weights in *A. africanus* using RMA formulae derived from the African ape sample. Light bars are forelimb elements; dark bars are hindlimbs. Unlike the distribution derived from the human-based formulae, the number of small and large weights derived from fore- and hindlimbs are approximately equal in number. (b) Frequency distribution of predicted body weights in *A. afarensis* using RMA formulae derived from the African ape sample. Those weights derived from the forelimb are skewed towards the small end of the scale and those from the hindlimb yield larger than expected values.

A. africanus has many features usually associated with arboreality (Ciochon & Corruccini, 1976; Vrba, 1979; Berger, 1994), but so does the shoulder of *A. afarensis* (Stern & Susman, 1983; Susman *et al.*, 1984; Larson, 1995). The two species appear to be similar in wrist morphology (McHenry, 1983). The hand morphology of *A. africanus*, however, appears to be less arboreally adapted than that of *A. afarensis* (Ricklan, 1987, 1990; Marzke *et al.*, 1992). Hausler & Schmid (1995) reconstruct the pelvis girdle of *A. africanus* to be slightly more primitive than that of *A. afarensis*, but the whole issue of pelvic reconstruction and its implications is highly controversial (Wood & Quinney, 1996; Hausler & Schmid, 1997). Berger & Tobias (1996) describe a new *A. africanus* tibia, Stw 514, as ''. . . being even more ape-like than those of *A. afarensis*'' (p. 347). Clarke & Tobias (1995) provide evidence that the foot of a Member 2 Sterkfontein hominid that possibly belongs to *A. africanus* had a more abducted hallux than that of *A. afarensis*.

The apparent primitiveness of the *A. africanus* proportions contrasts with the craniodental evidence. Compared to *A. afarensis*, the skulls and teeth of *A. africanus* are less primitive in that they share numerous specializations with early species of *Homo* (Skelton & McHenry, 1992; Strait *et al.*, 1997; White *et al.*, 1981; Kimbel, 1986). Relative to *A. afarensis*, for example, *A. africanus*'s canines are reduced, brains are expanded, muzzles are shortened, temporomandibular joints are deepened, lower third premolars are much more bicuspid, and mandibular symphyses are more vertical. These craniodental features imply that *A. africanus* is more closely related to early *Homo* than is *A. afarensis*. In fact, there is a remarkable sequence in craniodental morphology from primitive to derived that follows time. *Ardipithecus ramidus* (White *et al.*, 1994, 1995) is the oldest and most primitive, *A. anamensis* is less primitive and is slightly later in time

(Leakey *et al.*, 1995), *A. afarensis* is next followed by *A. africanus*, *H. habilis/rudolfensis*, *H. erectus/ergaster*, and *H. sapiens*. Specializations appear in many of these species, of course, so that the known sample does not necessarily represent the exact ancestor-descendant relationships, but in each sample there is a remarkable accumulation of shared derived traits. It is a surprise, therefore, to find the postcranial proportions appearing through the same series in such an unexpected way. The published record of *A. ramidus* does not allow direct comparisons, but the next oldest species, *A. anamensis*, has a large hindlimb without an exceptionally large forelimb (Leakey *et al.*, 1995). The tibia attributed to *A. anamensis* corresponds to a modern human weighing between 47 and 55 kg. The radius attributed to *A. anamensis*, KNM-ER 20419, has a head diameter matching a 61·2 kg human (Heinrich *et al.*, 1993) and the distal humerus, KNM-KP 271, corresponds to a 58·1 kg human (McHenry, 1992). These specimens are not associated, however, but it is significant that unlike *A. africanus*, this species has a large hindlimb element. As shown here, the joint sizes of the forelimbs relative to the hindlimbs in *A. afarensis* are within the range of modern *H. sapiens*. But the later and less craniodentally primitive species, *A. africanus*, *A. (Paranthropus) robustus* (McHenry, 1974, 1978), *A (P.) boisei* (McHenry, 1978; Grausz *et al.*, 1988; Walker *et al.*, 1989) and *H. habilis sensus stricto* (Johanson *et al.*, 1987; Hartwig-Scherer & Martin, 1991; Leakey *et al.*, 1989), have more primitive fore- to hindlimb proportions. However one arranges the phylogeny, there must have been homoplasy. Homoplasy is common in the phylogeny of animals and plants (Sanderson, 1991; Sanderson & Donoghue, 1989; Sanderson & Hufford, 1996). It is also apparent in the craniodental evolution of Hominidae (McHenry, 1994*b*). The pattern revealed by the new postcranial material from Sterkfontein reveals yet another example.

Summary

The fact that *A. africanus* was bipedal was established 50 years ago with the discovery of pelvic remains and its human-like gait has been particularly emphasized by many (e.g., Broom & Robinson, 1947; Robinson, 1972; Lovejoy *et al.*, 1973) but not by all (e.g., Zuckerman *et al.*, 1973). Discoveries in the 1970s at Hadar and Laetoli showed that *A. afarensis* was also a committed biped (Johanson *et al.*, 1982; Latimer, 1988, 1991; Latimer & Lovejoy, 1989, 1990*a,b*; Latimer *et al.*, 1987; Lovejoy, 1988; Leakey *et al.*, 1976; Tuttle *et al.*, 1991; McHenry, 1994*a*; and references therein), although not necessarily identical to modern humans (e.g. Stern and Susman, 1983; Susman *et al.*, 1984; Susman and Stern, 1991; McHenry, 1994*a*; and references therein). Before the new discoveries at Sterkfontein Member 4, the comparison of the postcrania of the two species was limited to only a few elements and these showed that the two species were quite similar (McHenry, 1986). The new fossils change that picture.

The new Sterkfontein Member 4 post-cranial material shows that by modern human standards, the forelimbs of *A. africanus* are larger than expected when compared to hindlimb joint-size. This contrasts sharply with the more human-like fore- to hindlimb proportions seen in *A. afarensis*. In this respect, the earlier and craniodentally more primitive species, *A. afarensis*, is more human-like in its postcrania than is *A. africanus*. Since the two known associated partial skeletons of *H. habilis* appear to have the more primitive fore- to hindlimb proportions of *A. africanus*, the evolution of the human body form is more complicated than previously understood. Perhaps *A. africanus* and *H. habilis* evolved craniodental characters in parallel with the lineage leading to later *Homo*. On the other hand, perhaps the fore- to hindlimb proportions of *A. afarensis* (and possibly *A. anamensis*) evolved independently of the lineage leading to *Homo* and does not imply a close phylogenetic link with *Homo*. Whatever the phylogeny, homoplasy is present.

References

Aiello, L. C. (1992). Allometry and the analysis of size and shape in human evolution. *J. hum. Evol.* **22,** 127–147.

Aiello, L. C. & Wood, B. A. (1994). Cranial variables as predictors of hominine body mass. *Am. J. phys. Anthrop.* **95,** 409–426.

Berger, L. R. (1994). Functional Morphology of the Hominoid Shoulder: Past and Present. Ph.D. Dissertation, University of the Witwatersrand.

Berger, L. R. & Tobias, P. V. (1996). A chimpanzee-like tibia from Sterkfontein, South Africa and its implications for interpretations of bipedalism in *Australopithecus africanus. J. hum. Evol.* **30,** 343–348.

Broom, R. & Robinson, J. T. (1947). Further remains of the Sterkfontein ape-man, *Plesianthropus. Nature* **160,** 430–431.

Ciochon, R. L. & Corruccini, R. S. (1976). Shoulder joint of Sterkfontein *Australopithecus. S. Afr. J. Sci.* **72,** 80–82.

Clarke, R. J. (1988). A new *Australopithecus* cranium from Sterkfontein and its bearing on the ancestry of *Paranthropus.* In (F. E. Grine, Ed.) *Evolutionary History of the ''Robust'' Australopithecines*, pp. 285–292. New York: Aldine de Gruyter.

Clarke, R. J. & Tobias, P. V. (1995). Sterkfontein Member 2 foot bones of the oldest South African hominid. *Science* **269,** 521–524.

Dagosto, M. & Terranova, C. J. (1992). Estimating the body size of Eocene primates: a comparison of results from dental and postcranial evidence. *Int. J. Primatol.* **13,** 307–344.

Gould, S. J. (1995). A task for paleobiology at the threshold of majority. *Paleobiology* **21,** 1–14.

Grausz, H. M., Leakey, R. E. F., Walker, A. C. & Ward, C. V. (1988). Associated cranial and post-cranial bones of *Australopithecus boisei*. In (F. E. Grine, Ed.) *Evolutionary History of the ''Robust'' Australopithecines*, pp. 127–132. New York: Aldine de Gruyter.

Hartwig-Scherer, S. (1993). Body weight prediction in early fossil hominids: towards a taxon-''Independent'' approach. *Am. J. phys. Anthrop.* **92,** 7–36.

Hartwig-Scherer, S. & Martin, R. D. (1991). Was ''Lucy'' more human than her ''child''? Observations on early hominid postcranial skeletons. *J. hum. Evol.* **21,** 439–449.

Hausler, M. & Schmid, P. (1995). Comparison of the pelves of Sts 14 and AL 288-1: implications for birth and sexual dimorphism in australopithecines. *J. hum. Evol.* **29,** 363–383.

Hausler, M. & Schmid, P. (1997). Assessing the pelvis of AL 288-1: a reply to Wood and Quinney. *J. hum. Evol.* **32,** 99–102.

Heinrich, R. E., Rose, M. D., Leakey, R. E. & Walker, A. C. (1993). Hominid radius from the Middle Pliocene of Lake Turkana, Kenya. *Am. J. phys. Anthrop.* **92,** 139–148.

Johanson, D. C., Taieb, M. & Coppens, Y. (1982). Pliocene hominids from the Hadar Formation, Ethiopia (1973[EN-]1977): Stratigraphic, chronologic, and paleoenvironmental contexts, with notes on hominid morphology and systematics. *Am. J. phys. Anthrop.* **57,** 373–402.

Johanson, D. C., Massao, F. T., Eck, G. G., White, T. D., Walter, R. C., Kimbel, W. H., Asfaw, B., Manega, P., Ndessokia, P. & Suwa, G. (1987). New partial skeleton of *Homo habilis* from Olduvai Gorge, Tanzania. *Nature* **327,** 205–209.

Jungers, W. L. (1982). Lucy's limbs: skeletal allometry and locomotion in *Australopithecus afarensis*. *Nature* **297,** 676–678.

Jungers, W. L. (1985). Body size and scaling of limb proportions in primates. In (W. L. Jungers, Ed.) *Size and Scaling in Primate Biology*, pp. 345–382. New York: Plenum Press.

Jungers, W. L. & Stern, J. T. (1983). Body proportions, skeletal allometry and locomotion in the Hadar hominids: a reply to Wolpoff. *J. hum. Evol.* **12,** 673–684.

Kimbel, W. H. (1986). Calvarial morphology of *Australopithecus afarensis*: a comparative phylogenetic study. Ph.D. Dissertation, Kent State University.

Kimbel, W. H., Johanson, D. C. & Rak, Y. (1994). The first skull and other new discoveries of *Australopithecus afarensis* at Hadar, Ethiopia. *Nature* **368,** 449–451.

Kimbel, W. H. & Rak, Y. (1993). The importance of species taxa in paleoanthropology and an argument for the phylogenetic concept of the species category. In (W. H. Kimbel and L. B. Martin, Eds) *Species, Species Concept, and Primate Evolution*, pp. 461–483. New York: Plenum Press.

Kimbel, W. H., White, T. D. & Johanson, D. C. (1984). Cranial morphology of *Australopithecus afarensis*: a comparative study based on a composite reconstruction of the adult skull. *Am. J. phys. Anthrop.* **64,** 337–388.

Larson, S. G. (1995). New characters for the functional interpretation of primate scapulae and proximal humeri. *Am. J. phys. Anthrop.* **98,** 13–35.

Latimer, B, M. (1988). Functional analysis of the Pliocene hominid ankle and pedal bones recovered from the Hadar Formation, Ethiopia: 1974–1977 collections. Ph.D. Dissertation, Kent State University.

Latimer, B. M. (1991). Locomotor adaptations in *Australopithecus afarensis*: the issue of arboreality. In (Y. Coppens and B. Senut, Eds.) *Origine(s) de la bipedie chez les hominides*, pp. 169–176. Paris: Cahiers de Paleoanthropologie, CNRS.

Latimer, B. M. & Lovejoy, C. O. (1989). The calcaneus of *Australopithecus afarensis* and its implications for the evoluton of bipedality. *Am. J. phys. Anthrop.* **78,** 369–386.

Latimer, B. M. & Lovejoy, C. O. (1990a). Hallucial tarsometatarsal joint in *Australopithecus afarensis*. *Am. J. phys. Anthrop.* **82,** 125–134.

Latimer, B. M. & Lovejoy, C. O. (1990b). Metatarsophalangeal joints of *Australopithecus afarensis*. *Am. J. phys. Anthrop.* **83,** 13–23.

Latimer, B. M., Ohman, J. C. & Lovejoy, C. O. (1987). Talocrural joint in African hominoids: implication for *Australopithecus afarensis*. *Am. J. phys. Anthrop.* **74,** 155–175.

Leakey, M. D., Hay, R. L., Curtis, G. H., Drake, R. E., Jackes, M. K. & White, T. D. (1976). Fossil hominids from the Laetolil Beds. *Nature* **262,** 460–466.

Leakey, M. G., Feibel, C. S., McDougall, I. & Walker, A. (1995). New four-million-year-old hominid species from Kanapoi and Allia Bay, Kenya. *Nature* **376,** 565–571.

Leakey, R. E. F., Walker, A., Ward, C. V. & Grausz, H. M. (1989). A partial skeleton of a gracile hominid from the Upper Burgi Member of the Koobi Fora Formation, East Lake Turkana, Kenya. In (G. Giacobini, Ed.) *Hominidae: Proceedings of the 2nd International Congress of Human Paleontology Turin, September 28–October 3, 1987*, pp. 167–174, Milan: Jaka.

Lovejoy, C. O. (1988). Evolution of human walking. *Sci. Am.* **259,** 118–126.

Lovejoy, C. O., Heiple, K. G. & Burstein, A. H. (1973). The gait of *Australopithecus*. *Am. J. phys. Anthrop.* **38,** 757–780.

Marzke, M. W., Wullstein, K. L. & Viegas, S. F. (1992). Evolution of the power (''squeeze'') grip and its morphological correlates in hominids. *Am. J. phys. Anthrop.* **89,** 283–298.

McHenry, H. M. (1974). How large were the Australopithecines? *Am. J. phys. Anthrop.* **40,** 329–340.

McHenry, H. M. (1978). Fore- and hindlimb proportions in Plio-Pleistocene hominids. *Am. J. phys. Anthrop.* **49,** 15–22.

McHenry, H. M. (1983). The capitate of *Australopithecus afarensis* and *Australopithecus africanus. Am. J. phys. Anthrop.* **62,** 187–198.

McHenry, H. M. (1986). The first bipeds: a comparison of the *Australopithecus afarensis* and *Australopithecus africanus* postcranium and implications for the evolution of bipedalism. *J. hum. Evol.* **15,** 177–191.

McHenry, H. M. (1992). Body size and proportions in early hominids. *Am. J. phys. Anthrop.* **87,** 407–431.

McHenry, H. M. (1994*a*). Early hominid postcrania: Phylogeny and function. In (R. S. Corruccini and R. L. Ciochon, Eds.) *Integrative Pathways to the Past: Paleoanthropological Papers in Honor of F. Clark Howell,* pp. 251–268. Ingelwood Cliffs, New Jersey: Prentice-Hall.

McHenry, H. M. (1994*b*). Tempo and mode in human evolution. *Proc. Natl Acad. Sci., U.S.A.* **91,** 6780–6786.

McHenry, H. M. & Corruccini, R. S. (1978). The femur in early human evolution. *Am. J. phys. Anthrop.* **49,** 473–488.

McHenry, H. M. & Skelton, R. L. (1985). Is *Australopithecus africanus* ancestral to *Homo*? In (P. V. Tobias, Ed.) *Hominid Evolution: Past, Present, and Future,* pp. 221–226. New York: Alan R. Liss.

McKee, J. K. (1993). Faunal dating of the Taung hominid fossil deposit. *J. hum. Evol.* **25,** 363–376.

McKee, J. K., Thackerary, J. F. & Berger, L. R. (1995). Faunal assemblage seriation of Southern African Pliocene and Pleistocene fossil deposits. *Am. J. phys. Anthrop.* **96,** 235–250.

Ricklan, D. E. (1987). Functional anatomy of the hand of *Australopithecus africanus. J. hum. Evol.* **16,** 643–664.

Ricklan, D. E. (1990). The precision grip in *Australopithecus africanus*: Anatomical and behavioral correlates. In (G. H. Sperber, Ed.) *From Apes to Angels: Essays in Honor of Phillip V. Tobias,* pp. 171–183. New York: Wiley-Liss.

Robinson, J. T. (1972). *Early Hominid Posture and Locomotion.* Chicago: University of Chicago Press.

Sanderson, M. J. (1991). In search of homoplastic tendencies: statistical inference of topological patterns in homoplasy. *Evolution* **45,** 351–358.

Sanderson, M. J. & Donoghue, M. J. (1989). Patterns of variation in levels of homoplasy. *Evolution* **43,** 1781–1795.

Sanderson, M. J. & Hufford, L. (1996). *Homoplasy: The Recurrence of Similarity in Evolution.* San Diego: Academic Press.

Skelton, R. R. & McHenry, H. M. (1992). Evolutionary relationships among early hominids. *J. hum. Evol.* **23,** 309–349.

Smith, R. J. (1980). Rethinking allometry. *J. Theor. Biol.* **87,** 97–111.

Smith, R. J. (1984). Determination of relative size. The ''criterion of subtraction'' problem in allometry. *J. Theor. Biol.* **108,** 131–142.

Smith, R. J. (1993*a*). Logarithmic transformation bias in allometry. *Am. J. phys. Anthrop.* **90,** 215–228.

Smith, R. J. (1993*b*). Bias in equations used to estimate fossil primate body mass. *J. hum. Evol.* **25,** 31–41.

Smith, R. J. (1994). Regression models for prediction equations. *J. hum. Evol.* **26,** 239–244.

Smith, R. J. (1996). Biology and body size in human evolution: Statistical inference misapplied. *Curr. Anthrop.* **37,** 451–460.

Stern, J. T. & Susman, R. L. (1983). The locomotor anatomy of *Australopithecus afarensis. Am. J. phys. Anthrop.* **60,** 279–318.

Strait, D. S., Grine, F. E. & Moniz, M. A. (1997). A reappraisal of early hominid phylogeny. *J. hum. Evol.* **32,** 17–82.

Susman, R. L. & Stern, J. T. (1991). Locomotor behavior of early hominids: epistemology and fossil evidence. In (Y. Coppens and B. Senut, Eds) *Origine(s) de la bipedie chez les hominides,* pp. 121–132. Paris: Cahiers de Paleoanthropologie, CNRS.

Susman, R. L., Stern, J. T. & Jungers, W. L. (1984). Arboreality and bipedality in the Hadar hominids. *Folia Primat.* **43,** 113–156.

Tuttle, R. H., Webb, D. M. & Tuttle, N. I. (1991). Laetoli footprint trails and the evolution of hominid bipedalism. In (Y. Coppens and B. Senut, Eds), *Origine(s) de la bipedie chez les hominides,* pp. 187–198. Paris: Cahiers de Paleoanthropologie, CNRS.

Vrba, E. S. (1979). A new study of the scapula of *Australopithecus africanus* from Sterkfontein. *Am. J. phys. Anthrop.* **51,** 117–129.

Walker, A., Ward, C. V., Leakey, R. E. F. & Grausz, H. M. (1989). Evolution in the *Australopithecus boisei* lineage. In (G. Giacobini, Ed.) *Hominidae: Proceedings of the 2nd International Congress of Human Paleontology Turin, September 28–October 3, 1987,* pp. 133–140. Milan: Jaka.

Walter, R. C. (1993). Age of Lucy and the first family: Single-crystal 40Ar/39Ar dating of the Denen Dora and lower Kada Hadar members of the Hadar Formation, Ethiopia. *Geology* **22,** 6–10.

White, T. D. (1985). The hominids of Hadar and Laetoli: an element-by-element comparison of the dental samples. In (E. Delson, Ed.) *Ancestors: The Hard Evidence,* pp. 138–152. New York: Alan R. Liss.

White, T. D., Johanson, D. C. & Kimbel, W. H. (1981). *Australopithecus africanus*: its phylogenetic position reconsidered. *S. Afr. J. Sci.* **77,** 445–470.

White, T. D., Suwa, G. & Asfaw, B. (1994). *Australopithecus ramidus*, a new species of early hominid from Aramis, Ethiopia. *Nature* **371,** 306–312.

White, T. D., Suwa, G. & Asfaw, B. (1995). Corrigendum: *Australopithecus ramidus*, a new species of early hominid from Aramis, Ethiopia. *Nature* **375,** 88.

Wood, B. A. & Quinney, P. S. (1996). Assessing the pelvis of AL 288-1. *J. hum. Evol.* **31,** 563–568.

Zuckerman, S. S., Ashton, E. H., Flinn, R. M. & Oxnard, C. E. (1973). Some locomotor features of the pelvic girdle in primates. *Symp. Zoo. Soc. Lond.* **33,** 71–165.