

Body Size and Proportions in Early Hominids

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ABSTRACT The discovery of several associated body parts of early hominids whose taxonomic identity is known inspires this study of body size and proportions in early hominids. The approach consists of finding the relationship between various measures of skeletal size and body mass in modern ape and human specimens of known body weight. This effort leads to 78 equations which predict body weight from 95 fossil specimens ranging in geological age between 4 and 1.4 mya. Predicted weights range from 10 kg to over 160 kg, but the partial associated skeletons provide the essential clues as to which predictions are most reliable. Measures of hindlimb joint size are the best and probably those equations based on the human samples are better than those based on all Hominoidea.

Using hindlimb joint size of specimens of relatively certain taxonomy and assuming these measures were more like those of modern humans than of apes, the male and female averages are as follows: *Australopithecus afarensis*, 45 and 29 kg; *A. africanus*, 41 and 30 kg; *A. robustus*, 40 and 32 kg; *A. boisei*, 49 and 34 kg; *H. habilis*, 52 and 32 kg. These values appear to be consistent with the range of size variation seen in the entire postcranial samples that can be assigned to species. If hominoid (i.e., ape and human combined) proportions are assumed, the males would be 10 to 23 kg larger and the females 4 to 10 kg larger.

The discovery of several associated body parts of early hominids whose taxonomic identity is known provides the opportunity to reassess body weight and proportions. The importance of such an effort is becoming clearer by the publication of numerous books and papers on the central role played by body size in the biology of animals (e.g., Calder, 1984; Damuth and MacFadden, 1990; Jungers, 1985; Schmidt-Nielson, 1984). Especially illuminating is Foley's (1987) *Another Unique Species* which relates body size in early hominids to numerous variables such as metabolic costs, mobility, thermoregulation, brain size, longevity, predator-prey relationship, home-range size, diet, foraging behavior, and much else.

In two recent and independent attempts to estimate early hominid body weight, Jungers (1988c) and McHenry (1988), come

to similar conclusions. Jungers (1988c) used 9 linear measurements of sacral and hindlimb joint surfaces with a comparative sample of all large-bodied hominoid species and two lesser apes to predict mean species weights of 51 kg for *Australopithecus afarensis*, 46 kg for *A. africanus*, and 49 kg for the "robust" australopithecines. If the modern *Homo sapiens* sample is excluded from the calculations (and Jungers gives reasons why it should be), the averages are about 9 kg larger. McHenry (1988) found that African apes and a sample of modern North American *H. sapiens* have the same relationship between femoral shaft size and body weight. Using the resulting formula, McHenry (1988) reported weights of 51 kg

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for *A. afarensis*, 46 kg for *A. africanus*, 48 kg for *A. robustus*, 46 kg for *A. boisei*, 41 kg for *H. habilis*, and 59 kg for early *H. erectus*.

Both studies had certain limitations, however. First, they used a modern human sample that consisted of relatively large-bodied individuals, but many fossil hominids are very small-bodied. The smallest human female in McHenry's (1988) study, for example, weighed 42.2 kg, but some of the fossil hominids were apparently less than 30 kg. Extrapolating down is problematic, especially when the correlation coefficient within the sample is not close to 1.0. McHenry (1988) tried to do so with his human sample in which the correlation between femoral shaft size and body weight was 0.67, but found the results unsatisfactory. Both authors expressed more faith in the inter-species regression with high correlations. Another limitation was that neither study was able to make use of new knowledge about associated partial skeletons of fossil hominids of known species that have since become available. There are now 13 such specimens between 3.2 and 1.3 mya representing *A. africanus*, *A. boisei*, *A. robustus*, and *H. habilis* and *H. erectus*.

This study seeks to reassess body weight in early hominids by using an expanded comparative data set which includes human individuals closer in size to the smallest early hominids and an expanded fossil data set which includes associated partial skeletons and numerous new fossils that have become available recently. The approach goes through the following steps: 1) A series of equations is derived which relates known body weight with 13 measures of skeletal size in a comparative sample of hominoids and within a sample of modern humans. 2) Fossil hominoid body weights are estimated from these equations. 3) Body proportions are assessed from these estimated body weights in associated partial skeletons. 4) The average male and female body weights of hominid species are estimated based on those variables found to be most reliable. 5) Body size variation within each of the Plio-Pleistocene hominid species is assessed using all available postcrania.

MATERIALS AND METHODS

Table 1 lists the comparative sample. All specimens derive from adult associated skeletons and, with the exception of the *Homo sapiens* sample, they are wild-collected. The human sample is from skeletons derived from cadavers of North Americans of mixed ancestry (i.e., European and/or African). A. Schultz collected 20 of these specimens (now housed at the Anthropologisches Institut, Zurich) and 38 are part of the Terry Collection (Smithsonian Institution). There are 6 skeletons of the diminutive Khoisan people and 2 African Pygmies which are from the British Museum of Natural History. Body weights for these specimens are estimated by calculating stature using humeral, femoral, and tibial lengths following Olivier's (1976) correlation axis and by deriving weight from stature using the power curve given in Jungers and Stern (1983). The stature of one Pygmy subject is given in Flower (1889). The estimated body weights from these human skeletons appear to be reasonable approximations when checked against actual stature/weight data from small-statured people. For example, Dietz et al. (1989: 517) report 8 stature and weight averages for Efe Pygmies (2 sexes, 4 age classes) which can be compared with weights predicted by the procedure described above. The average difference between actual and predicted weight is 1.1 kg. Despite the uncertainty of such calculated weights, the author agrees with Jungers (1982, 1988a), Jungers and Stern (1983), Wolpoff (1973, 1983a, 1983b), and many others that humans of small size are essential to the effort to derive weights from fossil specimens such as the diminutive Lucy (A.L. 288-1). In some samples elements were unavailable as noted in Table 1.

The variables are as follows:

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

3. RADTV: The mediolateral diameter of the radial head.

4. C7: The product of the anteroposterior and transverse diameters of the superior aspect of the seventh cervical vertebral body.

5. T12: The anteroposterior diameter of the superior surface of the 12th thoracic vertebral body multiplied by the transverse diameter of the same surface.

6. L5: The anteroposterior diameter of the superior surface of the fifth lumbar vertebral body multiplied by the transverse diameter of the same surface.

7. SAC: The product of the anteroposterior and transverse diameters of the superior aspect of the sacral body.

8. FEMHEAD: The maximum superoinferior diameter of the femoral head.

9. FEMSHFT: The product of the anteroposterior and transverse diameters of the femoral shaft taken just inferior to the lesser trochanter.

10. DISTFEM: The product of the biepicondylar and shaft anteroposterior diameters of the distal femur (measurements 12 and 13 of McHenry and Corruccini, 1978).

11. PROXTIB: The product of the anteroposterior and transverse diameters of the proximal 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.

12. DISTTIB: The product of the anteroposterior 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 lat-

eral surface of the medial malleolus at the point of greatest curvature (medially).

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

Table 3 lists the fossils of this study. The author took all fossil measurements on original specimens. Some measurements required the reconstruction of damaged parts. The femoral head size of Sts 14 is estimated to be 30.0 mm following McHenry (1975c). I use 45.4 mm for the femoral head size estimated from the KNM-ER 3229 os coxae which is the average predicted by the human formulae relating acetabular and femoral head size given in McHenry (1975c). Reconstruction of the Stw 443 acetabulum yields dimensions compatible with a femoral head size of about 36 mm.

The relationship between these variables and body weight is derived by least squares regression, major axis, and reduced major axis methods using log-transformed (base 10) data. There is considerable literature on which regression approach is most appropriate (e.g., Jungers, 1985; Sokal and Rohlf, 1981). Since the purpose of this study is the prediction of one variate from another, least squares may be superior. However, there is variability in both variates in any bivariate formula, so model II approaches should be used such as major axis or reduced major axis (Sokal and Rohlf, 1981). Fortunately for this study the correlations are high enough so that it makes very little difference which three methods are used. The lowest correlation is 0.917 (WT vs. sacrum in Hominoidea), but the difference between the predicted weights is not great (1.6 kg for the smallest fossil and 0.9 kg for the largest). In this study an average of the predictions from the three methods will be used.

There are 2 sets of analyses. The first uses the male and female means of all species plus the Khoisan and Pygmy means. The second uses the human means only (male and female North Americans, Khoisan, and Pygmy).

The degree of sexual dimorphism is estimated in two ways. The first is the ratio of male to female. The second is the coefficient

TABLE 1. Means, standard deviations, and sample sizes for sampled taxa

	WT	Humhead	Elbow	Radtv	C7	T12	L5	Sac	Femhead	Femshft	Distfem	Protib	Disttib	Talus
<i>H. sapiens</i> M	64.9	44.3	1,047.9	23.5	393.10	1,368.2	1,823.7	1,627.9	47.5	860.5	336.3	3,731.4	1,013.6	28.2
	9.41	1.80	107.2	1.61	50.20	128.3	206.7	246.6	2.0	84.60	34.0	301.2	100.8	1.9
	32	32	32	32	32	32	32	32	32	32	32	32	32	32
<i>H. sapiens</i> F	54.2	38.9	787.9	20.1	316.6	1,027.9	1,469.4	1,290.0	41.5	736.5	279.4	2,965.9	779.5	25.5
	9.47	1.70	72.7	1.20	39.4	130.8	159.6	143.2	1.7	88.5	27.0	290.4	100.4	1.6
	23	23	23	23	23	23	23	23	23	23	23	23	23	23
<i>H. sapiens</i> (Khoisan)	46.0	33.7	570.2	18.2	281.40	769.2 ¹	1,334.3 ¹	1,192.8	36.0 ¹	499.6 ¹	205.3	2,475.8	594.0	21.1
	5.20	1.22	42.6	0.98	41.9	63.3	58.0	83.8	0.28	27.7	16.6	222.0	55.9	2.0
	6	6	6	6	6	2	2	2	2	2	6	6	6	5
<i>H. sapiens</i> (Pygmy)	30.4	30.8	472.7	16.40	257.3	—	—	985.1	33.0	398.6	161.7	1,826.9	451.4	19.5
	2.76	0.64	8.5	0.35	4.80	—	—	75.1	1.4	34.8	6.51	51.0	55.0	1.1
	2	2	2	2	2	—	—	2	2	2	2	2	2	2
<i>P. troglodytes</i> M	54.2	41.6	979.9	25.4	201.5	790.6	952.8	906.9	34.8	653.3	174.8	2,223.9	510.7	16.7
	9.47	3.59	154.1	1.80	44.6	96.6	179.0	67.0	2.5	80.2	26.5	286.7	75.7	0.85
	6	5	5	6	6	6	6	6	6	6	5	6	6	5
<i>P. troglodytes</i> F.	39.7	37.8	814.0	22.60	164.7	642.9 ²	826.4 ²	739.2	30.4 ²	509.3 ²	154.8	1,848.4	419.2	16.3
	10.3	1.70	120.2	1.54	19.2	93.8	88.6	70.8	2.0	75.5	23.5	182.3	54.9	0.96
	9	9	9	9	9	8	8	9	9	9	9	9	9	9
<i>P. paniscus</i> M.	47.8	37.1	848.2	22.9	170.7	639.2 ³	768.3 ³	637.5	32.5 ³	542.9 ³	156.6	2,042.6	472.0	18.5
	8.44	0.80	94.8	0.50	40.2	114.7	86.2	61.9	3.1	63.2	22.5	294.2	33.6	0.65
	5	4	4	4	5	4	3	5	4	4	5	5	5	5
<i>P. paniscus</i> F.	33.1	36.8	713.4	20.9	149.4	543.2 ⁴	732.8 ⁴	710.0	30.8 ⁴	516.5 ⁴	146.7	1,782.3	403.3	17.0
	3.98	2.60	104.4	2.10	33.1	119.0	109.6	125.8	1.38	35.9	13.1	154.9	49.3	0.74
	7	4	4	4	4	6	5	5	7	7	5	5	5	5

<i>G. gorilla</i> M.	157.9	64.4	2,341.3	33.6	485.6	1,758.6 ⁵	2,240.6 ⁵	1,347.0	50.1 ⁵	1,496.5 ⁵	398.1	4,780.5	971.3	25.2
	23.43	4.50	428.8	2.30	116.6	438.9	617.4	264.8	2.2	188.7	35.9	378.3	112.3	2.20
	8	5	5	5	5	8	8	5	8	8	5	5	5	5
<i>G. gorilla</i> F.	75.4	48.5 ⁶	1,256.8 ⁶	25.93 ⁶	317.2 ⁶	1,017.3	1,277.4	1,006.9 ⁶	40.0	958.8	225.9 ⁶	2,761.9 ⁶	696.6 ⁶	20.5 ⁶
	15.54	2.10	102.7	0.35	41.9	211.7	329.9	78.7	2.0	134.5	14.9	281.0	35.9	0.49
	4	3	3	3	3	4	4	3	4	4	3	3	3	2
<i>P. pygmaeus</i> M.	78.8	468.8	1,411.5	25.4	394.4	922.0 ⁷	1,230.4 ⁷	1,013.0	38.0 ⁷	513.9 ⁷	179.8	2,384.8	649.8	22.3
	9.02	21.6	196.1	1.8	67.7	277.6	150.3	132.7	1.6	61.5	24.0	279.9	89.2	1.5
	8	8	8	8	8	8	8	8	8	8	8	7	6	7
<i>P. pygmaeus</i> F.	38.8	380.7	925.0	20.8	297.3	738.7 ⁸	905.5 ⁸	863.5	31.0 ⁸	349.9 ⁸	124.0	1,626.4	413.8	17.4
	9.52	22.2	122.2	1.3	45.8	142.6	182.0	247.2	1.4	61.4	16.2	190.9	61.9	1.3
	10	9	9	9	9	10	10	9	10	10	10	10	10	9
<i>H. syndac-</i> <i>tylus</i> M.	11.3	25.0	338.9	15.5	—	—	—	—	21.2 ⁹	159.4 ⁹	42.0	642.0	141.7	—
	1.04	1.0	26.6	0.30	—	—	—	—	1.3	11.5	4.8	29.1	17.7	—
	3	3	3	3	—	—	—	—	3	3	3	3	3	—
<i>H. syndac-</i> <i>tylus</i> F.	11.3	23.2	318.1	14.7	—	—	—	—	19.8 ¹⁰	137.5 ¹⁰	38.1	574.7	126.9	—
	1.76	0.76	9.2	0.79	—	—	—	—	0.64	8.5	0.71	50.0	4.3	—
	3	3	3	3	—	—	—	—	3	3	3	3	3	—
<i>H. lar</i> M.	5.5	18.1	241.5	12.6	44.4	179.8	255.8	216.6	16.2	112.2	29.6	473.7	101.3	7.7
	0.92	1.2	29.6	0.76	5.5	27.5	31.9	48.5	1.0	21.8	4.1	74.2	13.0	0.50
	5	5	5	5	5	5	5	5	5	5	5	5	5	4
<i>H. lar</i> F.	5.2	18.2	222.5	12.4	48.2	184.1	238.9	198.2	16.1	104.9	27.7	459.9	93.3	7.0
	0.40	0.61	13.5	0.23	0.22	1.9	11.5	21.2	0.79	8.4	1.6	38.1	3.0	0.60
	3	3	3	3	2	2	2	3	3	3	3	3	3	2

¹This variable could not be determined for all the specimens in this sample. Average WT for the reduced sample for this variable alone was 44.5. The following footnotes present similar WT determinations from partial samples.

²WT = 38.2.

³WT = 40.5.

⁴WT = 35.4.

⁵WT = 157.9.

⁶WT = 68.0.

⁷WT = 77.6.

⁸WT = 36.7.

⁹WT = 12.1.

¹⁰WT = 10.5.

of variation corrected for bias according to formula 4.10 in Sokal and Rohlf (1981).

RESULTS AND DISCUSSION

Table 1 presents the means, standard deviations, and numbers of specimens in the samples. Table 2 gives the correlations between body weight and each of the variables plus the least squares, major axis, and reduced major axis formulae. Among hominoid means the correlation ranges between 0.92 and 0.99. If *Homo sapiens* samples are excluded, the correlations are higher due to the fact that human proportions are unique among the Hominoidea. The correlations using the human means alone range from 0.92 to 0.99.

Table 4 provides the fossil measurements and body weight estimates. The predicted weights range from 10 to 114 kg, but analysis of the associated skeletons shows that many of these predictions are not reasonable. The weights reported in Table 4 should be regarded as a first step toward establishing the average body size and range of variation of early hominid species. Two important further steps are the analysis of the associated skeletons and the consideration of the taxonomy of the postcranial fossils.

Associated skeletons and body proportions

The associated skeletons give essential clues as to which estimates in Table 4 are the most reliable for establishing the average and range of variation of body weights of early hominid species. Of the associated skeletons, none is more useful than A.L. 288-1.

In this study A.L. 288-1 is surprisingly human-like in fore- and hindlimb joint size. The body weight of 27.3 kg is often cited as appropriate for this individual (Johanson and Edey, 1981; Jungers, 1982). Using the human formulae, the humeral head predicts 26.6, the elbow, 30.2, the radius, 27.6, the femoral head, 27.6, the proximal tibia, 27.7, the distal tibia, 24.2, and the talus, 26.8. Using the hominoid formulae, the values scatter between 12.3 (for the radius) and 36.9 (for the talus). The one striking exception is the sacrum where the human formulae predict 16.5 and the hominoid formulae

predict a more reasonable 27.9. As will be discussed below and by Sanders (1990), all of the associated skeletons have sacral bodies that are relatively very small.

The proximal femoral shaft module appears to overestimate the body weight in A.L. 288-1. By the human formulae, the weight is predicted to be 37.0 kg compared to the 27.3 kg that is usually associated with this skeleton. Femoral shaft size appears to overestimate body weight in all of the non-*Homo* fossil femora. The average overestimation is by 1.34 times for the 10 non-*Homo* femoral shafts that can be checked independently by other hindlimb variables such as femoral head size, distal femoral size, tibial measurements, or talar size. The discrepancy between shaft size and other predictors of body weight appears to be the same for small and large specimens. For example the large proximal femur, A.L. 333-3, has a shaft which yields an estimated weight of 70.6 kg, but its head predicts 50.1 kg which is 71% as large. The greatest discrepancy between shaft and another variable occurs with SK 82 where the femoral head predicts a weight that is only 65% of the weight predicted by its shaft. The smallest difference is Sts 14 which is 86%, but the shaft is badly damaged and the head is reconstructed. The large *Homo* femora (KNM-ER 1472 and 1481A) have approximately the same predicted weight from femoral shaft size and other measurements (within 3%). Unfortunately, the small *Homo* (i.e., O.H. 62) have no independent check, but other evidence supports the view that shaft size overestimates the weight. O.H. 62 appears to be smaller than A.L. 288-1, perhaps standing only 1 m tall (Jungers, 1988a), yet its femoral shaft predicts 33 kg. All 10 of the non-*Homo* femoral shafts that can be checked with other variables appear to overestimate body weight.

Using the human formulae for all estimates except the sacrum and adjusting the femoral shaft estimate by 0.74, the average weight of A.L. 288-1 is 27.3 kg. This is exactly the weight preferred by Jungers (1982) who cites Johanson and Edey (1981). Using hominoid hindlimb joints for comparison, Jungers (1988c) reports an estimate of 30.4 kg. The average for the 5 hindlimb joint pre-

TABLE 2. Correlations and formulae (least squares, major axis, and reduced major axis) relating body weight and measures of skeletal size

	Humhead	Elbow	Radtv	C7	T12	L5	Sac	Femhead	Femshft	Distfem	Proxtib	Disttib	Talus
Hominoidea													
LS r	0.985	0.966	0.948	0.943	0.968	0.951	0.917	0.970	0.973	0.961	0.973	0.965	0.929
Slope	2.7018	1.4115	3.2772	1.2072	1.3782	1.3574	1.3691	2.6465	1.1823	1.0829	1.2770	1.1806	2.1194
Int	-2.6388	-2.4855	-2.7422	-1.2158	-2.3132	-2.4210	-2.3845	-2.4093	-1.5745	-1.8467	-2.5918	-1.5390	-1.0558
SEE	0.075	0.112	0.137	0.141	0.104	0.131	0.168	0.093	0.102	0.120	0.100	0.113	0.155
MA													
Slope	2.7752	1.4806	3.6146	1.2997	1.4407	1.4532	1.5446	2.7930	1.2217	1.1326	1.3224	1.2319	2.3987
Int	-2.7517	-2.6817	-3.1810	-1.4302	-2.4901	-2.7039	-2.8932	-2.6269	-1.6775	-2.0011	-2.7380	-1.6721	-1.4037
RMA													
Slope	2.7431	1.4617	3.4553	1.2807	1.4244	1.4277	1.4927	2.7284	1.2152	1.1271	1.3127	1.2232	2.2804
Int	-2.7022	-2.6280	-2.9739	-1.3861	-2.4440	-2.6288	-2.7429	-2.5310	-1.6605	-1.9840	-2.7066	-1.6493	-1.2564
Intra homo													
LS r	0.944	0.9430	0.955	0.919	0.999	0.983	0.968	0.976	0.978	0.968	0.991	0.974	0.937
Slope	1.8308	0.8635	1.9910	1.6152	0.6552	1.1593	1.4991	1.7125	0.7927	0.9600	1.0583	0.9005	1.7712
Int	-1.1930	-0.7788	-0.8912	-2.3489	-0.2443	-1.9630	-2.9735	-1.0480	-0.5233	-1.5678	-1.9537	-0.8790	-0.7521
SEE	0.057	0.057	0.051	0.068	0.004	0.022	0.043	0.033	0.032	0.043	0.023	0.039	0.060
MA													
Slope	2.0082	0.9104	2.1485	1.8371	0.6555	1.1831	1.5706	1.7754	0.8069	0.9919	1.0689	0.9227	1.9623
Int	-1.4703	-0.9119	-1.0938	-2.9013	-0.2451	-2.0389	-3.1953	-1.1481	-0.5628	-1.6754	-1.9903	-0.9418	-1.0135
RMA													
Slope	1.9404	0.9152	2.0859	1.7573	0.6556	1.1797	1.5492	1.7538	0.8107	0.9921	1.0683	0.9246	1.8903
Int	-1.3642	-0.9257	-1.0132	-2.7027	-0.2456	-2.0281	-3.1290	-1.1137	-0.5733	-1.6762	-1.9880	-0.9473	-0.9148

TABLE 3. *Fossils used in this study*

Kanapoi		KNM-ER 1500	Partial skeleton
KNM-KP-271	L. distal humerus	KNM-ER 1503	R. proximal femur
Mabaget		KNM-ER 1504	R. distal humerus
KNM-BC 1745	L. proximal humerus (subadult)	KNM-ER 1505	L. proximal femur
Hadar	(Sidi Hakoma Member)	KNM-ER 1810	L. proximal tibia
A.L. 128-1	L. proximal femur	KNM-ER 1812d	R. radial head
A.L. 129-1a	R. distal femur	KNM-ER 2596	L. distal tibia
b	R. proximal tibia	KNM-ER 3228	R. coxa
c	R. proximal femur	KNM-ER 3728	R. femur
A.L. 137-48a	R. distal humerus	KNM-ER 3735	Partial skeleton
A.L. 211-1	R. proximal femur	KNM-ER 3736	R. proximal radius
A.L. 322-1	L. distal humerus	KNM-ER 5880	R. proximal femur
Hadar	(Denan Dora Member)	East Rudolf	(KBS member, 1.9-1.8)
A.L. 288-1	Partial skeleton	KNM-ER 736	L. femur shaft
A.L. 333w-56	R. distal femur	KNM-ER 738	L. proximal femur
A.L. 333-3	R. proximal femur	KNM-ER 813a	R. talus frag.
A.L. 333-4	R. distal femur	KNM-ER 815	L. proximal femur
A.L. 333-6	L. distal tibia	KNM-ER 1464	R. talus
A.L. 333-7	L. distal tibia	KNM-ER 1476a	L. talus frag.
A.L. 333-42	L. proximal tibia	b	L. proximal tibia
A.L. 333-95	R. proximal femur (subadult)	KNM-ER 1591	R. humerus
A.L. 333-106	Cervical vertebra	KNM-ER 1592	R. distal femur
A.L. 333-107	R. proximal humerus	KNM-ER 1808	Partial skeleton
A.L. 333x-14	Radial head (subadult)	KNM-ER 1809	R. femur shaft
A.L. 333w-26	R. proximal tibia	KNM-ER 3951	L. distal femur
Sterkfontein	(Member 4)	KNM-ER 5428	R. talus
Tm 1,513	L. distal femur	KNM-ER 6020	L. distal humerus
Sts 7	R. humerus	East Rudolf	(Okote member, 1.6-1.5)
Sts 14	Partial skeleton	KNM-ER 737	L. femur shaft
Sts 34	R. distal femur	KNM-ER 739	R. humerus
Sts 73	Last thoracic vertebra	KNM-ER 741	L. proximal tibia
Stw 8	Lumbar vertebrae	KNM-ER 803	Partial skeleton
Stw 25	R. femur head	KNM-ER 993	L. distal femur
Stw 41	Thoracic vertebrae	KNM-ER 1463	R. femur
Stw 99	R. femur	KNM-ER 1465	L. proximal femur
Stw 328	R. proximal humerus	KNM-ER 1807	R. femur shaft
Stw 358	L. distal tibia	KNM-ER 3888	R. proximal radius
Stw 389	L. distal tibia	Olduvai	(Bed I—Lower Bed II)
Stw 392	R. femur head	OH 8	Foot
Stw 403	R. femur head	OH 20	L. proximal femur frag.
Stw 431	Partial skeleton	OH 35	L. tibia
Sterkfontein	(Member 5)	OH 53	R. femoral shaft
Stw 88	R. talus	OH 62	Partial skeleton
Stw 311	L. femur head	Swartkrans	(Member 1)
Omo	(Member D)	SK 50	R. coxal frag.
Omo 119-2718	L. proximal humerus	SK 82	R. proximal femur
Omo	(Member E thru H)	SK 97	R. coxal frag.
Omo 75s-1317	R. proximal radius	SK 3155a	R. coxal frag.
Omo L 754-8	Femoral shaft fragment	SK 3981a,b	Thoracic and lumbar vertebra
East Rudolf	(Upper Burgi, member, 2.0-1.9 my)	Swartkrans	(Member 2)
KNM-ER 1471	R. proximal tibia	SK 18b	L. proximal radius
KNM-ER 1472	R. femur	SK 3699	R. proximal radius
KNM-ER 1473	R. proximal humerus	Kromdraai	
KNM-ER 1475	R. proximal femur	TM 1517	R. distal humerus
KNM-ER 1481a	L. femur		R. partial talus
b	L. proximal tibia		
c	L. distal tibia		

dictions based on hominoid formulae in this study (including the sacrum) is 30.3 kg. The absolute difference between predictions based on hominid and hominoid regressions is relatively trivial in these small size ranges. The problem (to be discussed below) comes at larger body sizes where humans and apes diverge sharply from each other in

the relationship between body weight and skeletal size. Using unadjusted femoral shaft diameters of humans and African apes, McHenry (1988) reports a body weight for A.L. 288-1 of 29.9 kg, but that study suffered from the lack of small bodied humans (the smallest human in the sample was 42.2 kg) and from the assumption that just be-

cause modern humans and African apes have an exceptionally high correlation between femoral shaft size and body weight, the early hominids would have shared this relationship. Judging from the relationship between femoral shaft size and all other hindlimb variables in the present study, it appears that femoral shafts of early hominids were unusually robust. Ruff (1988) aptly points out that one would expect that an animal whose weight passes solely through two limbs instead of four would have greater robusticity in those two limbs relative to body weight. It appears that modern *H. sapiens* is an unusual exception in having such gracile femoral shafts relative

to body weight. Ruff (1988) explores the reasons for this exception.

It appears from these considerations that A.L. 288-1 was much more robust than modern humans. This becomes very clear when her stature is reconstructed. Jungers (1988a) reviews the most recent attempts to calculate stature (including Geissman, 1986) and finds that this individual stood about 3' 6" (107 cm). This is in the range of what the original describers estimated (Johanson and White, 1979) and what the reconstructed skeleton appeared to be (Schmid, 1983). According to the Jungers and Stern (1983) power curve relating pygmy stature to body weight, one can calcu-

TABLE 4. Predicted body weights

Fossil measurement	All Hominoidea			Homo sapiens			
	LS	MA	RMA	LS	MA	RMA	
1. Humhead							
KNM-BC 1745 ¹	27.8	18.3	18.0	18.2	28.2	26.9	27.4
A.L. 288-1r	27.3	17.4	17.1	17.3	27.3	25.9	26.5
A.L. 333-107	35.1 ²	34.4	34.4	34.4	43.3	43.0	43.1
Omo 119-2718	37.8 ²	42.0	42.3	42.2	50.0	49.8	49.7
Sts 7	39.7	48.0	48.4	48.2	54.2	55.0	54.7
Stw 328	34.2 ²	32.1	32.0	32.0	41.3	40.8	41.0
KNM-ER 1473	42.9 ²	59.1	60.1	59.7	62.5	64.3	63.6
2. Elbow							
KNM-KP 271	869.1	46.0	46.8	46.6	57.4	58.1	58.1
A.L. 137-48a	525.6	22.6	22.2	22.3	37.2	36.7	36.7
A.L. 288-1m	420.5	16.5	16.0	16.1	30.7	30.0	29.9
A.L. 322-1	526.2 ²	22.7	22.2	22.4	37.2	36.8	36.7
Stw 433	769.5	38.8	39.0	39.0	51.7	52.0	52.0
TM 1517	677.7	32.4	32.4	32.4	46.3	46.3	46.3
KNM-ER 3735A	528.9 ²	22.8	22.4	22.5	37.4	36.9	36.9
KNM-ER 739	1116.2	65.5	67.7	67.1	71.3	72.9	73.0
KNM-ER 1504	707.1	34.4	34.5	34.4	48.1	48.1	48.1
KNM-ER 6020	1063.9	61.2	63.1	62.6	68.4	69.8	69.9
3. Radiv							
A.L. 288-1p	15.0	12.9	11.8	12.3	28.2	27.1	27.5
A.L. 333x-14	22.2	46.8	48.5	47.7	61.6	62.9	62.4
Stw 139	22.7 ²	50.3	52.5	51.5	64.4	66.0	65.4
Stw 431	22.2	46.8	48.5	47.7	61.6	62.9	62.4
Omo 75s-1317	19.1	28.6	28.1	28.3	45.6	45.6	45.6
KNM-ER 1500E	20.0	33.2	33.2	33.2	50.0	50.3	50.2
KNM-ER 3735E	20.0 ²	33.2	33.2	33.2	50.0	50.3	50.2
KNM-ER 1812D ¹	16.6	18.0	17.0	17.5	34.5	33.7	34.0
KNM-ER 3736	20.7	37.2	37.6	37.4	53.6	54.1	53.9
KNM-ER 3888	20.9	38.4	39.0	38.7	54.6	55.3	55.0
SK 18b	19.8	32.1	32.1	32.1	49.0	49.2	49.1
SKX 3699	19.1	28.6	28.1	28.3	45.6	45.6	45.6
4. C7							
A.L. 333-106	191.9 ²	34.7	34.4	34.5	21.8	19.6	20.4
KNM-ER 164C	326.2 ²	65.8	68.6	68.1	51.4	52.0	51.8
5. T12							
A.L. 288-1ac	479.6 ²	24.1	23.6	23.7	32.5	32.5	32.5
Sts 14 g, f	438.9 ²	21.3	20.7	20.9	30.7	30.7	30.7
Sts 41	747.3	44.4	44.6	44.6	43.5	43.5	43.5
Sts 73	744.2	44.1	44.4	44.3	43.4	43.4	43.4
Stw 457a	807.7	49.4	49.9	49.8	45.8	45.8	45.8
SK 3981a	529.2	27.6	27.2	27.3	34.7	34.7	34.7

(Continued)

TABLE 4. Predicted body weights (continued)

Fossil measurement	All Hominoidea			Homo sapiens		
	LS	MA	RMA	LS	MA	RMA
6. L5						
Sts 14a	520.8	18.5	17.5	17.8	15.4	15.0
Stw 8	803.4	33.3	32.9	33.0	25.4	25.0
Stw 463	808.5 ²	33.6	33.2	33.3	25.6	25.2
SK 3981b	936.0	40.9	41.1	41.0	30.3	30.0
7. Sac						
A.L. 288-1an	636.4	28.5	27.4	27.7	17.0	16.2
Sts 14	461.7	18.3	16.7	17.1	10.5	9.8
Stw 479	721.6	33.8	33.2	33.4	20.5	19.7
KNM-ER 3735J	777.0 ²	37.4	37.3	37.3	22.9	22.1
8. Femhead						
A.L. 288-1ap	28.6	27.9	27.6	27.7	27.9	27.4
A.L. 333-3	40.2	68.6	71.4	70.1	50.0	50.1
Sts 14	30.0 ²	31.6	31.5	31.6	30.3	29.8
Stw 25	32.4	38.8	39.1	38.9	34.6	34.2
Stw 99	38.0 ²	59.1	61.0	60.2	45.4	45.4
Stw 311	35.7	50.1	51.3	50.7	40.8	40.6
Stw 392	31.5	36.0	36.1	36.1	33.0	32.5
Stw 443	36.0 ²	51.2	52.5	51.9	41.4	41.2
KNM-ER 1472	40.0 ²	67.7	70.4	69.2	49.6	49.7
KNM-ER 1481	43.4	84.0	88.4	86.4	57.0	57.4
KNM-ER 3228	45.4 ²	94.6	100.3	97.7	61.6	62.2
KNM-ER 738	33.8	43.3	44.0	43.7	37.2	36.8
KNM-ER 1503	35.1	47.9	48.9	48.4	39.7	39.4
SK 82	34.0	44.0	44.7	44.4	37.6	37.2
SK 97	36.8	54.3	55.8	55.1	43.0	42.8
SK 3155	30.0 ²	31.6	31.5	31.6	30.3	29.8
9. Femshaft						
A.L. 128-1	466.0	38.0	38.2	38.2	39.1	38.9
A.L. 211-1	795.3	71.6	73.5	73.2	59.7	59.9
A.L. 288-1ap	436.1	35.2	35.3	35.2	37.1	36.9
A.L. 333-3	976.5	91.2	94.4	93.9	70.2	70.7
A.L. 333-95 ¹	849.1	77.3	79.6	79.2	62.9	63.2
A.L. 333w-40	950.4	88.4	91.3	90.8	68.8	69.2
Sts 14	404.8 ²	32.2	32.2	32.2	35.0	34.8
Stw 99	864.4	79.0	81.3	80.9	63.8	64.1
Orno L 754-8	931.7 ²	86.3	89.1	88.7	67.7	68.1
KNM-ER 1472	684.5	59.9	61.2	61.0	53.0	53.1
KNM-ER 1475	693.6	60.9	62.2	61.9	53.6	53.7
KNM-ER 1481a	657.3	57.1	58.2	58.0	51.3	51.4
KNM-ER 1500d	514.0	42.7	43.1	43.0	42.2	42.1
KNM-ER 3728	559.4	47.2	47.8	47.7	45.2	45.1
KNM-ER 736	1,136.2	109.1	113.6	112.8	79.2	79.9
KNM-ER 738	583.7	49.7	50.3	50.2	46.7	46.7
KNM-ER 815	504.6	41.8	42.1	42.1	41.6	41.5
KNM-ER 1503	684.6	60.0	61.2	61.0	53.0	53.1
KNM-ER 1592	1,052.8 ²	99.7	103.5	102.9	74.6	75.2
KNM-ER 1809 ¹	548.6	46.1	46.7	46.6	44.5	44.4
KNM-ER 737	988.0	92.5	95.8	95.2	70.9	71.4
KNM-ER 803	921.2	85.2	87.9	87.5	67.1	67.5
KNM-ER 993	821.5	74.4	76.4	76.1	61.3	61.5
KNM-ER 1463 ¹	597.9	51.1	51.8	51.7	47.6	47.6
KNM-ER 1465 ¹	757.2	67.5	69.2	68.9	57.4	57.6
KNM-ER 1807	956.3 ²	89.0	92.0	91.5	69.1	69.5
OH 20	674.2 ²	58.9	60.0	59.8	52.4	52.5
OH 53	624.0 ²	53.7	54.6	54.5	49.3	49.3
OH 62	379.3	29.8	29.7	29.7	33.2	33.0
SK 82	760.0	67.8	69.5	69.2	57.6	57.8
SK 97	792.2	71.3	73.1	72.8	59.5	59.7
KNM-ER 5880A	731.6 ²	64.9	66.3	66.1	55.9	56.0
10. Distfem						
A.L. 129-1a	1,406.4	36.5	36.7	36.7	28.5	28.0
A.L. 333-4	2,082.2	55.8	57.2	57.0	41.5	41.3
A.L. 333w-56	2,025.7	54.2	55.5	55.3	40.4	40.2
TM 1513	1,635.7	43.0	43.5	43.5	32.9	32.5
Sts 34	1,932.9	51.5	52.6	52.5	38.6	38.4
KNM-ER 1472	2,238.4	60.4	62.1	61.9	44.5	44.4
KNM-ER 1481A	2,439.4	66.3	68.4	68.2	48.3	48.4
KNM-ER 3951	2,462.0 ²	66.9	69.2	68.9	48.7	48.8
KNM-ER 993	1,972.5 ²	52.7	53.8	53.7	39.4	39.2

(Continued)

TABLE 4. Continued

Fossil measurement		All Hominoidea			Homo sapiens		
		LS	MA	RMA	LS	MA	RMA
11. Proxtib							
A.L. 129-1b	1,595.6	31.5	31.4	31.5	27.3	27.1	27.1
A.L. 288-1aq	1,625.2	32.2	32.2	32.2	27.8	27.7	27.7
A.L. 333x-26	2,730.3	62.6	64.0	63.7	48.2	48.2	48.2
A.L. 333-42	2,560.0	57.6	58.8	58.5	45.0	45.0	45.0
KNM-ER 1471	2,244.0	48.7	49.4	49.2	39.1	39.0	39.1
KNM-ER 1481B	2,463.8	54.9	55.9	55.7	43.2	43.2	43.2
KNM-ER 1500A	1,904.4 ²	39.5	39.7	39.7	32.9	32.8	32.8
KNM-ER 1476B	2,071.4	44.0	44.4	44.3	36.0	35.8	35.9
KNM-ER 1810	2,713.2 ²	62.1	63.5	63.2	47.9	47.8	47.9
KNM-ER 741	2,700.8 ²	61.7	63.1	62.8	47.6	47.6	47.6
12. Disttib							
A.L. 288-1ar	329.4	27.1	26.9	26.9	24.4	24.1	24.0
A.L. 333-6	470.9 ²	41.4	41.8	41.7	33.7	33.5	33.4
A.L. 333-7	612.5	56.4	57.7	57.5	42.7	42.6	42.6
A.L. 333-96	441.0 ²	38.3	38.5	38.5	31.8	31.5	31.5
Stw 358	318.5	26.1	25.8	25.9	23.7	23.3	23.3
Stw 389	539.7	48.6	49.4	49.3	38.1	37.9	37.9
KNM-ER 1481C	606.9	55.8	57.1	56.9	42.4	42.3	42.3
KNM-ER 2596	408.7	35.0	35.1	35.1	29.7	29.4	29.3
OH 35	445.2	38.7	39.0	38.9	32.1	31.8	31.7
KNM-ER 1500 C	496.7	44.1	44.6	44.5	35.4	35.1	35.1
13. Talus							
A.L. 288-las	17.3	37.0	36.8	36.9	27.6	26.1	26.6
Stw 88	19.2	46.1	47.3	46.8	33.2	32.0	32.4
Stw 102	18.6	43.1	43.8	43.5	31.4	30.0	30.5
Stw 347	17.6	38.4	38.4	38.4	28.4	27.0	27.5
OH 8	18.7	43.6	44.4	44.0	31.7	30.4	30.9
KNM-ER 813A	24.6	78.0	85.7	82.3	51.5	52.0	51.8
KNM-ER 1464	23.8	72.7	79.1	76.3	48.5	48.7	48.7
KNM-ER 1476A	19.0	45.1	46.1	45.7	32.6	31.3	31.8
KNM-ER 5428	32.3	138.9	164.6	153.2	83.4	88.7	86.7
TM 1517	19.6	48.2	49.7	49.0	34.4	33.3	33.7

¹Subadult.²Estimated.

late a body weight for A.L. 288-1 of 19.7 kg. Perhaps that is what she weighed, but judging from her limb robusticity and joint size, this figure is much too low. If it is much too low, then she was much heavier and more robust than a modern *H. sapiens* of similar stature. Aiello (1990) shows that many Plio-Pleistocene hominids (A.L. 288-1, Sts 14, OH 62, A.L. 333-3, KNM-ER 1463, 993, and 1503) have estimated stature/weight relationships exceeding the range of variation observed in a modern human sample.

These findings on the body proportions of A.L. 288-1 can be checked simply by comparing the specimen with equivalent sized skeletons from the comparative samples. Table 5 compares A.L. 288-1 with a 27 kg *P. paniscus* specimen and an Akka Pygmy specimen with an estimated body weight of 28.4 kg. The three specimens are strikingly similar in most widths although the bonobo is

slightly larger in the hindlimb. But there are 3 conspicuous differences: The humerus is longer in the bonobo relative to the fossil or the human, the sacrum is much larger in the human than it is in the bonobo or fossil, and the femur is much longer in the human than it is in the other two. There are other differences that are not included in the table, of course, such as the numerous pelvic dimensions in which A.L. 288-1 is much more like the human than the ape.

There are other associated postcranial parts from Hadar, but none is as telling as A.L. 288-1. Johanson and Coppens (1976) report that the proximal femur, A.L. 128-1, and knee, 129-1a and b, are from the same individual. Using the human formulae, the femoral shaft predicts a weight (39 kg) that is 1.4 times higher than the weights predicted from the distal femur (28.2) and proximal tibia (27.7). The hominoid formulae

TABLE 5. Comparison of A.L. 288-1 with *Pan paniscus* and *Akka Pygmy*

	<i>Pan paniscus</i> 29060 (Tervuren), Wt = 27.0 kg	A.L. 288-1	<i>Homo sapiens</i> Pygmy, Wt = 28.2
Humerus head diameter	33.8	27.3	31.2
Humerus distal articular wd	33.5	29.0	30.3
Humerus capitulum ht	17.1	14.5	15.8
Humerus biepicondylar wd	54.1	41.0	46.1
Humerus length	289	235	244
Radius head diameter	17.6	15.0	16.1
Ulna troclear tv wd	15.0	12.7	14.9
Ulna troclear ap wd	18.4	12.7	12.8
Ulna distal head diameter	15.6	12.3	10.8
Capitate ht	21.7	16.3	17.0
Capitate ap diameter	17.1	12.5	14.1
Sacrum body ap wd	18.7	18.5	24.2
Sacrum body tv wd	26.2	34.4	42.9
Acetabulum ht	35.1	37.0	38.9
Ilium minimum wd	32.6	39.3	44.6
Femur head diameter	28.3	28.6	32.2
Femur shaft tv wd	22.0	24.5	22.2
Femur shaft ap wd	21.6	17.8	20.7
Femur length	288	280	333
Tibia proximal tv wd	48.8	49.7	53.5
Tibia proximal ap wd	32.9	32.7	33.9
Tibia talar facet tv wd	19.9	18.0	20.4
Tibia talar facet ap wd	18.3	18.3	21.5
Talus tibial facet wd	17.5	17.3	18.7

yield less consistent results in that the distal femur corresponds to a weight of 36.6 kg, but the proximal tibia yields 31.5 kg.

The A.L. 333 site probably contains associated skeletal parts of the same individuals, but since there are at least 9 adults (according to Johanson et al., 1982), it is difficult to determine which piece goes with which individual. There are at least 3 adult and 1 subadult large-bodied individuals represented in the postcranial collection. This minimum number of large adults is apparent because there are 3 adult large left distal fibulae (A.L. 333-9B and 85, 333w-37). At least one large subadult is represented by a large proximal femur with an unfused head epiphysis (A.L. 333w-33), two radial heads (A.L. 333x-14 and 15), and a proximal femur with an unfused head (A.L. 333-95), but it is possible that these belong to more than one individual. There are at least 2 small-bodied adults as indicated by the presence of 2 left tibiae (A.L. 333-6 and 96). The hindlimb joints of the large-sized hominids predict an average weight of 44.6 kg (40.3 to 50.1) with the human formula and 60.1 kg (56.7 to 70) with the hominoid formulae. Curiously, the subadult radial head (A.L. 333-14) corresponds to weights of 62.3 kg using the hu-

man formulae and 47.7 kg with the hominoid formulae. This may indicate that the human-like forelimb proportions characteristic of A.L. 288-1 are not the same as in some other early hominids. The A.L. 333-14 radial head is simply too large to fit with any of the hindlimb material at A.L. 333 if human proportions are assumed. If we assume that it comes from the same subadult individual represented by the A.L. 333-95 proximal femur, then the forelimbs were clearly much larger relative to hindlimbs than is true of modern humans.

The skeleton of the diminutive *A. africanus*, Sts 14, is similar to A.L. 288-1 in having a relatively larger hindlimb than sacrum, but the difference is even greater. Using an estimated femoral head diameter of 30 mm, the body weight is predicted to be 30 kg with the human formulae and 31.6 with the hominoid formulae. However, the sacrum is so small that it corresponds to a 10 kg human or a 17.4 kg hominoid. The fifth lumbar vertebra is also proportionately small so that it corresponds to a 15.1 kg human or a 17.9 kg hominoid. The 12th thoracic vertebral body predicts 30.7 kg with human formulae and 21 with hominoid. As with all the non-*Homo* fossil femora, the shaft estimates are high

(34.8 and 32.2 for human and hominoid formulae, respectively).

Similar proportions are true of the larger *A. africanus* partial skeleton, Stw 431. The reconstructed femoral head corresponds with a 41.3 kg human or a 51.9 kg hominoid. The sacral and fifth lumbar vertebral bodies are much smaller, so that the human formulae predict 20 and 25.3 kg while the hominoid formulae estimate 33.5 and 33.0 kg. Unlike A.L. 288-1 but like the composite large skeletons from A.L. 333, the forelimbs are much larger than expected. Using the human formulae, the elbow gives a weight of 51.9 kg and the radius, 62.3 kg. The corresponding weights with the hominoid formulae are 38.90 and 47.7 kg. As with Sts 14, the 12th thoracic estimates are closer to those derived from the femur (45.8 by the human formulae and 49.7 by the hominoid).

The body weight of the partial skeleton of *A. boisei*, KNM-ER 1500 (Grausz et al., 1988), can be predicted from three of the variables in this study. The radial head corresponds to a 50.2 kg human and 33.2 kg hominoid. The proximal tibia predicts 32.8 and 39.6 kg with the two sets of formulae. The distal tibia predicts 35.2 and 44.4 kg. Unlike A.L. 288-1, but like the composite A.L. 333 and Stw 431, the forelimb of ER 1500 appears to be too large if human proportions are assumed. There is reasonable correspondence between fore- and hindlimb estimates if body weight is predicted using the human formulae for the hindlimb and hominoid formulae for the forelimb.

Similarly, there is more reasonable correspondence between weight predicted from the forelimb and hindlimbs when a mixture of hominid and hominoid formulae are applied to two other partial skeletons thought to be associated, TM 1517 and KNM-ER 1503/1504. The former is part of the type specimen of *Paranthropus robustus* from Kromdraai and the latter is from Koobi Fora. The human formulae predict a weight of 33.8 kg from the TM 1517 talus and the hominoid formulae predict 32.4 kg from the TM 1517 humerus. Likewise, the hominoid formulae predict 49 kg from the talus and the human formulae give 46.3 kg from the elbow. The same pattern is true of KNM-ER 1503/1504. The human formulae predict the

femoral head to come from an individual weighing 39.5 kg, which corresponds better with the hominoid formulae's prediction of 34.4 kg from the elbow than with the 48.1 predicted by the human formulae. The hominoid formulae predict 48.4 kg from the femoral head which is very close to the 48.1 predicted by the human formulae from the elbow.

Taxonomy of postcrania

The associated partial skeletons give the first clue as to which of the body weight estimates in Table 4 are reasonable, but the taxonomic problem remains. The craniodental fossils show that at least two species of hominid coexisted at sites between about 2.3 and 1.3 mya. Most of the postcranial specimens listed in Table 4 within this time period are not associated with taxonomically identifiable craniodental material.

Some isolated postcrania can be classified with reasonable certainty. For the Hadar and Sterkfontein 4 material the consensus view is taken that they are not mixed samples and that the former is *Australopithecus afarensis* and the latter is *A. africanus*. Since almost all of the taxonomically identifiable material at Swartkrans and Kromdraai is robust *Australopithecus* according to Howell (1978) and Susman (1988a,b), the postcrania will be considered as the robust form of the South African australopithecine (whether two species as Howell, 1978, describes, or one).

A major difficulty is classifying the postcranial material from sites between 2.3 and 1.3 million years ago. This is because there is more than one hominid species represented and most of this material is not associated with craniodental elements of known species. The problem was recognized in 1948 when the "Telanthropus" material was found at Swartkrans and thought to be contemporaneous with *Paranthropus* (Broom and Robinson, 1949). Before that date the hominid postcrania were identified by geological context so specimens from Sterkfontein were *Plesianthropus*, and those from Kromdraai and Swartkrans, *Paranthropus* (Broom and Schepers, 1946). By geological context Broom and Robinson (1949) placed the SK 18 proximal radius with *Telanthro-*

pus but later Robinson (1961) changed his mind and referred all "Telanthropus" specimens to *Homo erectus*.

A major change in thinking about postcranial taxonomy came in 1959 when Napier (1959) described two metacarpals from Swartkrans and made the first *morphological* assessment of taxonomy. He noted human-like features of the SK 85 specimen and attributed that specimen to *Homo*. He noted some ape-like traits of the SK 84 thumb metacarpal and attributed that specimen to *Paranthropus*. He did note, however, that SK 84 had some human-like attributes and argued that *Paranthropus* must have had a hand adapted to tool manufacture and use, a claim championed by Susman (1988a,b) on the basis of the much enlarged Swartkrans sample of postcrania. In another paper Napier (1964) extended his analysis of all the Plio-Pleistocene hominid postcrania pointing out other pongid-like traits of *Paranthropus* in the hip, thigh, and ankle. Robinson (1972) drew attention to numerous ways in which the postcrania of *Paranthropus* appeared to differ from those of more recent *Homo* and all of the Sterkfontein material known to that date.

The attempt to establish the taxonomy of postcrania found in East Africa proved to be very difficult from the first discoveries in 1960 to the present. The original describers (Davis, 1964) of the tibia and fibula found in situ at the "Zinj" excavation site (FLK 1) made no taxonomic assessment. Day and Napier (1964) cautiously avoided giving a taxonomic assessment of the Olduvai foot (O.H. 8). But in the introduction of the new species, *H. habilis*, Leakey et al. (1964) attributed the Olduvai hand as part of the holotype of that species and foot as part of the paratype. Furthermore they stated that "probably" the clavicle and "possibly" the tibia and fibula belonged to *H. habilis*. Subsequently these specimens have been the center of a lively exchange over their taxonomy and functional anatomy (e.g., Archibald et al., 1972; Day, 1974; Day and Wood, 1968; Lewis, 1980; Lisowski et al., 1974, 1976; Oxnard, 1972; Wood, 1973a,b, 1974a,b). For example, the tibia and fibula (O.H. 35) have been classified as *H. habilis* (Leakey et al., 1964), *A. robustus* (Wood, 1974b), and *A. af-*

ricanus (Howell, 1978). Susman and Stern (1982) showed that there was strong evidence indicating that the tibia, fibula, foot, and hand of Olduvai belonged to one juvenile individual and that the individual is the *H. habilis* type specimen (O.H. 7). Such a wonderful simplification has problems such as the stratigraphic and areal separation of the specimens and the fact that the epiphysis of the distal tibia is fused in this composite juvenile specimen. (Susman and Stern answer these criticisms in footnote 35). Morphological assessment of postcranial taxonomy continued as more Olduvai specimens were unearthed, so the big toe (O.H. 10) became *cf. H. habilis* (Day and Napier, 1966) and the proximal femur fragment (O.H. 20) was *A. boisei* (Day, 1969).

The same difficulties arose with the discoveries of postcrania from East Rudolf. At first it seemed reasonable to classify isolated postcranials that resembled humans as *Homo* and those that retained ape-like traits or Swartkrans-like traits as *Australopithecus* (e.g., Day, 1976). This seemed especially appealing for the femur because some (KNM-ER 1472 and 1481a) were strikingly more like *H. sapiens* than others (e.g., KNM-ER 1503; McHenry and Corruccini, 1976, 1978). But there were always critics of the morphologically based taxonomy (e.g., Lovejoy, 1978; Wolpoff, 1976) and new discoveries showed that almost all of the traits earlier used to distinguish *Homo* femora from those of *Australopithecus* were found in both.

A major breakthrough came in the 1980s with the discovery of specimens that had taxonomically diagnostic craniodental parts associated with postcrania of the same individual. The nearly complete *Homo erectus* skeleton, KNM-WT 15000, showed what that species looked like below the head (Brown et al., 1985). There are now partial skeletons of 9 individuals known in East Africa between 2.2 and 1.5 million years ago. These include 3 of *H. erectus* (KNM-ER 803 and 1808, KNM-WT 15000), 3 of *A. boisei* (Omo 323, possibly KNM-ER 801/1464/1824/1825 and certainly 1500), and 3 of *H. habilis* (KNM-ER 1812 and 3735, O.H. 62). If Susman and Stern (1982) are correct about the Olduvai holotype, then one can add one more

TABLE 6. *Body weight predicted from hindlimb joint size*

	Intra-human formulae			Inter-hominoid formulae		
	Male	Female	Species	Male	Female	Species
<i>A. afarensis</i> ¹	44.6	29.3	37.0	60.1	35.6	47.9
<i>A. africanus</i> ²	40.8	30.2	35.5	52.8	36.8	44.8
<i>A. robustus</i> ³	40.2	31.9	36.1	49.8	40.3	45.1
<i>A. boisei</i> ⁴	48.6	34.0	41.3	76.0	42.0	59.0
<i>H. habilis</i> ⁵	51.6	31.5	41.6	75.0	41.5	58.3

¹Based on A.L. 333-3, 4, 7, 333w-56, and 333x-26 for male and 129-1a, b, 288-1, and 333-6 for female.

²Based on Sts 34, Stw 99, 311, 389, and 443 for male and Sts 14, Stw 25, 102, 347, 358, 392, and TM 1513 for female.

³Based on SK 82 and 97 for male and SK 3155 and TM 1517 for female.

⁴Based on KNM-ER 1464 for male and 1500 for female.

⁵Based on KNM-ER 1472, 1481, and 3228 for male and O.H. 8 and 35 for female.

H. habilis skeleton (O.H. 7/8/35). In South Africa the taxonomy of postcranial material in mixed sites is less problematic because the bulk of this material is from Sterkfontein Member 4 (*A. africanus*) and Swartkrans Member 1 which contains 95% *A. robustus*. But uncertainty remains, especially considering the occurrence of such widely different morphological patterns in the two thumb metacarpals (Sk 84 and SKX 5020; Susman, 1988a,b; Ricklan, 1990; Trinkaus and Long, 1990).

Weight estimates of species

The lessons learned from the partial skeletons and from previous attempts to classify isolated postcrania suggest to this author that a two step approach is appropriate. First, Table 6 gives body weight estimates of species based on hindlimb joint size of specimens of relatively certain taxonomic affinity. Second, these estimates are checked against all available evidence of postcranial size variation in all species. The second step is not only a check on the accuracy of the estimates in Table 6, but also a means of assessing the range of variation of body size within each species.

Australopithecus afarensis

Table 6 reports an average male body weight for *A. afarensis* as 45 kg (assuming human proportions) based on the large-sized hindlimb joints from Hadar (femoral head, A.L. 333-3, distal femora, A.L. 333-4 and 333w-56, proximal tibiae, A.L. 333-42 and 333x-26, and distal tibia, A.L. 333-7). The female weighs 29 kg based on the hindlimb joints of A.L. 288-1, 129-1a and b, and 333-6.

Using the hominoid regressions, the estimates are 60 and 36 kg for male and female. The average for the species is 37 kg using the human formula which is almost exactly what McHenry (1982) reported. Using the hominoid equations the species average is 48 kg which is closer to what the femoral shaft predicted in McHenry (1988) and what Jungers (1988c) found using sacral and hindlimb joint size among all Hominoidea.

It is difficult to assess whether human or hominoid formulae give the best results. Common sense might favor the human equations simply because all known hominids are bipedal. A substantial amount of the body weight in great apes is supported by the forelimb while walking and the hindlimb is consequently much smaller relative to body weight than it is in humans. Jungers (1988b) showed, however, that when sacral and hindlimb joint sizes are considered together in a multivariate analysis, A.L. 288-1 is intermediate between apes and modern humans. This finding led him to prefer weight predictions based on hominoid species excluding *H. sapiens*. On the other hand, Ruff (1988) showed that the femoral head volume of A.L. 288-1 is close to what is predicted for a human of such small body size. In the present study, support is found for Ruff's (1988) observations about femoral head size. In fact, the human based formulae give more consistent predictions for all joints except those of the lower back. Perhaps the difference between Junger's finding and this is due to the fact that he included the sacrum and his human sample did not include small-bodied individuals. There is no question that A.L. 288-1 has very

different limb proportions from modern humans, of course, but the primary difference appears to be mostly in limb lengths and lower-back size.

The weight estimate given in Table 6 for male *A. afarensis*, 45 kg, can be checked using evidence other than hindlimb joint size. Table 4 includes two large (presumably male) forelimbs, a humeral head (A.L. 333-107) which corresponds to a human of 43 kg, and a radial head (A.L. 333x-14) which projects a weight of 62 kg on the human regressions. The latter is high, but too much emphasis should not be placed on it because, within the *H. sapiens* sample, the relationship between radial head size and body weight is quite variable. The individual in the modern sample whose radius most closely matches A.L. 333x-14 in size happens to be a 50 kg male, but most radii near that size come from heavier people. Four large (presumably male) femoral shafts predict weights of between 52 kg (A.L. 333-3) and 44 kg (A.L. 211-1) if multiplied by the correction factor of 0.74 as discussed above. As a further check, all of the Hadar postcrania can be compared to human skeletons of known weight. The largest fossils are about the same size as a 54 kg *H. sapiens* and smaller than a 62 kg individual except for shaft robusticity, femoral neck length, and radial head size.

The same checks can be applied to the estimate of 29 kg for the female *A. afarensis*. The presence of the partial skeleton, A.L. 288-1, and the hindlimb, A.L. 128/129-1, inspires confidence in the prediction. These partial skeletons also provide the opportunity to compare the relative size of much more fragmentary material. Another check is provided by the African Pygmy skeleton of Table 5 which is similar in size to A.L. 288-1. From these comparisons it is clear that A.L. 288-1 is the smallest individual in the Hadar hominid postcranial collection. The two humeri from the same geological member as A.L. 288-1 (Sidi Hakoma) which appear in Table 4, A.L. 137-48A and 322-1, both correspond to humans of 37 kg. There are no specimens from A.L. 333 as small as A.L. 288-1, although there are clearly two size morphs at that site (McHenry, 1986). The only small specimen from that site for which a weight

estimate is made is the A.L. 333-6 distal tibia (34 kgs).

The ratio of male to female body weights derived from the intrahuman formulae given in Table 6 is 1.52. That compares with 1.22 for the *H. sapiens* sample used in this study, 1.37 for *P. troglodytes*, 1.44 for *P. paniscus*, 2.09 for *G. gorilla*, and 2.03 for *P. pygmaeus*. Using the inter-hominoid formulae, the ratio is 1.69. Both values for sexual dimorphism in body size in *A. afarensis*, therefore, are well above *H. sapiens* and *Pan*, but well below those of *Gorilla* and *Pongo*.

If the specimens that go into producing the male and female averages given in Table 6 are treated as a single sample without dividing them into sex categories, then the average for *A. afarensis* is 40 or 52 kg using human or hominoid formulae, respectively. These values are somewhat higher than the midpoint between the male and female given above, because the mean is skewed by the fact that there are more large, presumably male, specimens. But these values may be closer to the mark if it is true that there was body size overlap between the sexes and therefore that many specimens cannot be confidently sorted into male and female categories according to size. As Leutenegger and Shell (1987) point out and Kimble and White (1988) concur, a better measure of sexual dimorphism for species in which there is overlap in size is the coefficient of variation of the entire sample. These authors show the superiority of this method for teeth, but there remains a problem when dealing with an apparently highly dimorphic sample with unequal sample sizes of the two sexes. In the case of the values reported in Table 6, there are 6 male specimens and 3 female. With human formulae, the smallest male is 40 kg (A.L. 333w-56) and the largest female is 34 kg (A.L. 333-6), so the sexing by size seems appropriate. But it still could be the case that the intermediates were simply not recovered, so that the gap between the large and small morphs is a product of sampling error. If this is true, then the coefficient of variation is a useful test, but for the Hadar sample of postcrania this author believes that it underestimates the difference between males and females

because there are more male postcranial fossils recovered. The coefficient of variation (adjusted for small sample size according to equation 10.4 in Sokal and Rohlf, 1981) of the 12 estimates of body weight in *A. afarensis* is 22.0 using the human formulae and 26.4 using the hominoid equations. These are above the value in the human sample (17.3) and below or close to those in *P. troglodytes* (28.8) and *P. paniscus* (25.0).

These estimates for sexual dimorphism in body size in *A. afarensis* are similar to those preferred by Lovejoy et al. (1989) and McHenry (1991) but below those reported by McHenry (1986, 1988). In McHenry (1986) the size differences between the most complete distal femora, ulnae, and capitates were compared to the ratio between male and female averages in hominoid species. Unfortunately the most complete distal femora, A.L. 333-4 and 129-1a, are also the largest and smallest specimens in the collection so that the resulting ratio overestimates the true difference between males and females. The same problem affects the results found in comparing the only two capitates, A.L. 333-40 and 288-1w, because the former presumably belongs to one of the large-bodied males from the A.L. 333 site and the latter is the capitate of the diminutive "Lucy." The ulnar comparison used two specimens from the A.L. 333 site and found a ratio of large to small shaft diameters slightly greater than the ratio of known male to female *Gorilla* and *Pongo*. In this measure, *H. sapiens* was also found to be highly dimorphic (actually more dimorphic than *Gorilla*). Shaft diameters may well have been more dimorphic than hindlimb joints and presumably body size in early hominids. For example, the adjusted coefficient of variation of femoral shaft size (FEMSHFT) is 33 among the 6 Hadar femora compared to 13 in humans, 19 in chimpanzees, 24 in gorillas, and 25 in orangutans. This accounts for the high level of body size dimorphism reported in McHenry (1988), since that study was based on femoral shaft size. Jungers (1988c) compared the maximum and minimum body weights in the Hadar and comparative samples and found that *A. afarensis* was similar to *P. troglodytes*.

Australopithecus africanus.

The average male body weight reported in Table 6 for *A. africanus* is based on the femoral head size of Stw 99 and 311, the estimated femoral head size of Stw 443, the distal femur, Sts 34, and the distal tibia, Stw 389. The human formulae predict a weight of 41 kg and the hominoid equations predict 53 kg. These values are somewhat lower than those predicted for forelimb and upper trunk elements and much greater than those predicted from the lower back. The Sts 7 proximal humerus corresponds to a human weighing 55 kg and a hominoid weighing 48 kg. The Stw 139 radius, like the A.L. 333x-14 radius, is very large (it predicts a body weight of 65 kg), but there is a good reason to reject such a high estimate. That reason is the partial skeleton, Stw 431, in which the radius corresponds to a 62 kg human, but the rest of its body is much smaller (its elbow predicts 52 kg, its 12th thoracic/vertebra, 46 kg, its fifth lumbar vertebra, 25 kg, and its sacrum, 20 kg, compared to the value derived from its estimated femoral head size which corresponds to a 41 kg human). If Stw 431 is truly an associated skeleton of one individual, then one has to use extreme caution in deriving body weight estimates from isolated elements. This specimen is one of the chief reasons why Table 6 is confined to hindlimb joints. T12 gives a weight estimate which is closer to what is expected, however, which is useful to know because there are two other 12th thoracic vertebrae: Sts 73 and Stw 41 predict weights of 43 and 44 kg using human formulae.

The average weight of a female *A. africanus* is 30 or 37 kg by human or hominoid formulae. Seven specimens make up this estimate including 3 femoral heads (Sts 14, Stw 25, and 392), one distal femur (TM 1513), one distal tibia (Stw 358), and two tali (Stw 102 and 347). As with *A. afarensis* there exists a partial skeleton of a small-bodied, presumably female individual (Sts 14) to provide a valuable check on the estimate. As noted above, the Sts 14 skeleton has the same peculiar pattern seen in the other associated skeletons: T 12 and estimated femoral head size correspond to a human of 30–31 kg, but L5 and the sacrum are

extraordinarily small, corresponding to weights of 15 and 10 kg using the human formulae. One other specimen provides a check: Stw 8 includes a fifth lumbar which corresponds to a human of 25 kg.

The estimated weight of *A. africanus* with sexes combined is 36 and 45 kg using human and hominoid formulae. The former is the same as that reported in McHenry (1976, 1982) and the latter is about the same as that derived from femoral shaft size given in McHenry (1988). Jungers (1988c) estimated 46 kg using all hominoid species and 53 kg using hominoids minus hominids. These high values are considerably above what other investigators have reported. Robinson (1972) estimated the female to weigh 18 to 27 kg and the male only slightly more. Wolpoff (1973) predicted 37 kg as a species average. Pilbeam and Gould (1974) used 32 kg. Reed and Falk (1977) estimated 24 to 25 kg for the female. Steudel (1980) found that cranial dimensions corresponded to body weights of 32 to 35 kg. Suzman (1980) re-studied the whole issue and cautiously suggested after many adjustments that the range probably lay between 25 and 45 kg. The average of the Sterkfontein weights reported in Krantz (1977) is 37 kg (excluding the non-hominid Sts 68 radius).

The values reported in Table 6 show a slightly lower level of body size sexual dimorphism in *A. africanus* than that reported for *A. afarensis*. The ratio of male to female weight is 1.35 using the human formulae and 1.43 using the hominoid equations. These values are most comparable to those of the *P. troglodytes* sample where the ratio is 1.37. It is well below the ratio seen in *Gorilla* (2.09) or *Pongo* (2.03). The adjusted coefficient of variation of the 12 weight estimates is 18.8 which is closer to *H. sapiens* (17.3) than to *P. troglodytes*. However, looking at the entire postcranial sample, the range of size variation of *A. africanus* is very similar to that seen in *A. afarensis*. Just as in *A. afarensis*, the smallest postcranial specimens of *A. africanus* such as the Sts 14 partial skeleton, the Stw 418 first metacarpal, the Stw 390 ulna, or the Stw 477 third metatarsal are about the same size as those of the female Pygmy used in this study with an estimated weight of 28 kg. The largest

specimens, such as the Stw 382 second metacarpal, the Stw 435 third metatarsal, and the Stw 99 femur, are slightly larger than those of a 55 kg *H. sapiens* skeleton. The Stw 99 femur is only slightly smaller than the largest Hadar femur (A.L. 333-3) in widths of the head, neck, and shaft, and is slightly larger than that specimen in neck length. These are the small and large extremes, of course. There are many intermediate-sized specimens. For example, the proximal ulna is represented by 7 specimens which span from small (Stw 326 and 390) to intermediate (Stw 349, 380, and 398) to large (Stw 113 and 432).

A much greater degree of body size sexual dimorphism was reported by Wolpoff (1973) and McHenry (1976) on the basis of the few postcrania fossils then available. The large size of the Sts 7 humerus and the Sts 73 vertebra seemed to indicate that males were considerably larger than the tiny Sts 14 female. Robinson (1972) was not particularly impressed by the difference, however, stating that "... males and females differed a little in robustness" (1972: 232). The Sts 7 humerus is very large compared to what might be expected in humeral size for Sts 14, but the Stw 43 partial skeleton shows that forelimbs were proportionately larger than expected from hindlimb size.

Australopithecus robustus

The hominid postcranial sample from Kromdraai and Swartkrans was relatively meager until the late 1980s when over three dozen new specimens came to light from Swartkrans. Unfortunately, the new material is mostly isolated pieces of hands and feet without any hindlimb joints complete enough for use here. The estimates in Table 6 are based on old material. The male is predicted to weigh 40 kg based on the femoral head size of SK 82 and 97 using human formulae and 50 kg using hominoid equations. This seems quite small, especially considering Robinson's (1972) prediction that the species might average up to 90 kg. But there is some additional evidence that supports the idea that the South African robust australopithecines were rather small-bodied. The largest hindlimb specimens out

of the 25 published postcranial pieces from Member 1 of Swartkrans are smaller than the 54 kg human skeleton except in a few dimensions which seem to be uniquely large in all australopithecines such as femoral neck length and shaft robusticity. The ischial length of the badly damaged pelvic fragment, SK 50, is estimated to be 70.3 ± 3 mm (McHenry, 1975a), which is considerably larger than the 62 mm of the 54 kg human standard, however. In estimated acetabular size, SK 50 is much smaller than this human: McHenry (1975b) estimated 37.8 mm which corresponds exactly to what would be expected for the SK 82 femur and much less than the 45 mm of the 54 kg human. The larger forelimbs are about the same size as the 54 kg human. The largest of these is the SKX 5020 first metacarpal (Sushman, 1988a,b) which is very similar to the 54 kg human in length and width dimensions. A recently discovered distal humerus fragment, SKX 3774, is similar in size to the type specimen from Kromdraai, TM 1517. Both are the same size as in the 54 kg human. The vast majority of the postcranial sample is much smaller than these specimens.

Two of the small specimens are used to predict the female mean in Table 6: The subadult pelvic fragment, SK 3155b, and the Kromdraai talus, TM 1517, predict 32 kg using the human formulae and 40 kg assuming general hominoid proportions. Obviously such an estimate needs independent checking. The fact that SK 3155b is subadult may not be too much of a problem since the three bones were almost completely fused, so that the acetabulum would not have grown substantially. The width of the tibial facet of the talus is hardly the best way to estimate body weight, especially when the specimen is said to be from the same individual as the TM 1517 humerus. That humerus corresponds to a human of 46 kg and a hominoid of 32 kg (Table 4). But as shown with all associated australopithecine skeletons except A.L. 288-1, forelimb estimates of body weight are problematic.

A check on the estimated female body weight of *A. robustus* is provided by comparing the size of the smaller specimens against the female Pygmy whose weight is esti-

mated to be 28 kg. A first metatarsal, SKX 5017, is very much like that of the Pygmy in length and robusticity, except the fossil's midshaft is more robust in the plantodorsal direction. The SKX 5019 and 5022 middle hand phalanges are within the Pygmy range of sizes. The SK 45690 proximal phalanx of the hallux is exactly the same length as the Pygmy's. The SKX 5018 proximal hand phalanx is shorter than those of A.L. 288-1x.

Table 4 gives several estimates of body weight based on the forelimb and spine that can serve as an additional check on the values reported in Table 6 which are based only on hindlimb joint size. The SK 3951a and b vertebrae together yield a weight of 32 kg, but given the problems reported above relating to lower-back size, little faith can be given to the reliability of such predictions. The same can be said for predictions derived from the distal humerus (TM 1517) and proximal radius (SKX 3699) which both correspond to a 46 kg human. The proximal radius from Member 2 of Swartkrans, SK 18b, is attributed to *Homo* (Robinson, 1953; Brain, 1978). It corresponds to a 49 kg human.

The predicted average weight for *A. robustus* is 36 kg using the human formulae and 45 kg according to the hominoid predictions. This is well below most previous estimates. McHenry (1975d) published a value of 36 kg based on the SK 3981 vertebrae, but later (McHenry, 1976) raised the value by incorporating the SK 82 and 97 femora. In the latter study, McHenry (1976) used femoral head diameter, total neck length, and shaft widths which predicted 50 kg for SK 82 and 53 kg for SK 97 based on a human comparative sample. The evidence from associated skeletons reported above supports the view that femoral neck length and shaft diameters are disproportionately large in *Australopithecus*. Neck length is also exceptionally large in early *Homo*. The author now favors using femoral head size for body weight estimates as Burns (1971), Wolpoff (1976), and Walker (1973) urged long ago. McHenry (1988) gave a species estimate of 48 kg based on femoral shaft size in African apes and modern humans. Jungers (1988c) reported an estimate of 49 kg based on sacral and hindlimb joint size of Hominoidea and 62 kg

in formulae derived from apes only. His estimate is an average of 4 specimens. These are femoral heads, SK 82 and 97, the acetabulum, SK 3155b, and the patella of uncertain taxonomy, SKX 1084. If one takes the midpoint between the estimates derived from the large specimens which are presumably male and the small one (SK 3155b), the species estimate becomes 45 kg using the all-hominoid regression which is exactly what the hominoid formulae in the study predict.

The ratio of male to female body weights of *A. robustus* reported in Table 6 is 1.26 or 1.24 depending on which formulae are used. This is close to the ratio found in the *H. sapiens* sample (1.22). The adjusted coefficient of variation is also in the human range (15.9 for human formulae and 23.4 for hominoid formulae). This low level of size variation in the South African robust species is seen also in molar breadths (Kimbel and White, 1988).

Australopithecus boisei

Most of the sites which have produced craniodental material attributable to *A. boisei* have also produced specimens of early *Homo*. This is true of all sites from which hominid postcrania have been found (i.e., Turkana, Olduvai, and Omo). Most of these postcranial remains are unassociated with taxonomically identifiable craniodental material. The body weight estimates given in Table 6 are derived from two exceptions. The male is 49 kg based on the human formulae and 76 kg based on the hominoid equations using the KNM-ER 1464 talus. That specimen is closely associated with *A. boisei* material at Area 6A, Ileret. At least three mature adults (KNM-ER 801, 802, and 3737) and two immature individuals (KNM-ER 1171 and 1816) are represented by dental remains attributable to *A. boisei* (Howell, 1978; Leakey and Leakey, 1978). Several other postcranial fragments are present including a metatarsal (KNM-ER 1823), a distal humerus (KNM-ER 1824), and an atlas (KNM-ER 1825), but these are quite fragmentary. Numerous other postcranial specimens have been assigned to *A. boisei* on the basis of morphology, but as pointed out

above, there are problems with this procedure. Howell (1978) assigns several of the specimens given in Table 4 to that species including the massive humerus, KNM-ER 739, the femora, KNM-ER 738, 815, 993, 1463, 1465, 1503, 1505, 1592, 3728, and O.H. 20, and the tibia, KNM-ER 741. If the human formulae for the hindlimb are used and the femoral shaft estimates are adjusted by multiplying by 0.74, then the average large-bodied *A. boisei* on Howell's classification is 45 kg (based on KNM-ER 741, 993, 1465, 1503, 1592, and O.H. 20). The largest of these specimens is the distal half of a femur, KNM-ER 1592, which was found in Area 12 in the KBS Member. Its distal end is poorly preserved, but the shaft has a clearly defined linea aspera. This author prefers to leave this specimen unclassified since he can find no diagnostic characteristics. Judging from the small *A. boisei* skeleton, KNM-ER 1500, there is one peculiarity that might be diagnostic of the species' femur. That trait is a sharp ridge that runs from the lesser trochanter supermedially along the posteroinferior surface of the neck. This trait is not present in the Hadar, Sterkfontein, nor Swartkrans femora. Nor is it present in femora assigned to *Homo*. It is present in KNM-ER 815, 1463, 1465, 1500, 3728, 5880, and O.H. 20 and 53. These femora are all in collection areas that contain *A. boisei* craniodental material. Using human formulae with the shaft correction the average prediction from the large specimens (KNM-ER 1464, 1465, 5880, and O.H. 20) is 43 kg.

The estimate for the female *A. boisei* is 34 kg using the human formulae and 42 kg with the hominoid equations. This is based on the proximal and distal tibia of the associated skeleton, KNM-ER 1500 (Grausz et al., 1988). That skeleton's femoral shaft yields an estimate of 31 kg using the human formulae if corrected by 0.74. Howell (1978) places 4 small femora in *A. boisei* on morphological grounds (KNM-ER 738, 815, 1463, and 3728). Using the human formulae and the 0.74 correction, they correspond to an average weight of 34 kg. The average estimate of the KNM-ER 1500 specimen and the small femora with a pronounced postero-

inferior neck ridge (KNM-ER 815, 1463, 3728, and O.H. 53) is also 34 kg.

Unfortunately these estimates cannot be easily checked using forelimb material because the relationship between forelimb size and body weight in *A. boisei* is far from clear. The KNM-ER 1500 associated partial skeleton has larger forelimbs than expected from her hindlimb size. Her radius, KNM-ER 1500E, corresponds to a human weighing 50 kg, but her tibia predicts 34 kg. The large humerus, KNM-ER 739, has often been regarded as a robust australopithecine (e.g., Leakey, 1971; McHenry, 1973; Day, 1976; Howell, 1978). Its size corresponds to a human of 72 kg.

Table 6 reports an average weight for *A. boisei* as 41 kg assuming human proportions and 59 kg using hominoid formulae. McHenry (1988) estimated 46 kg and Jungers (1988c) predicted 49 or 58 kg depending on the inclusion or exclusion of humans in his hominoid species sample. The body weight of this species will never be known precisely, but these analyses agree on the apparent fact that *A. boisei* was robust in its masticatory apparatus, but not in its body size. The possibility remains, however, that this species had relatively large and powerfully built forelimbs. If the KNM-ER 739 humerus is combined with the Omo L 40-19 ulna, the resulting forelimb is impressively long and robust. This is especially noticeable when compared to the relatively small forelimb of the *H. erectus* skeleton, KNM-WT 15000. This does not appear to be the case for *A. robustus*: there are no forelimb remains that approach the massive size seen in some of the East African hominids, although the Kromdraai type specimen, TM 1517, shows that forelimbs were somewhat larger than expected from hindlimb size.

The ratio of male to female estimated body weight in *A. boisei* from Table 6 is 1.43 assuming human proportions and 1.81 with hominoid proportions. These values are as high or higher than those of chimpanzees (1.37 for *P. troglodytes*, 1.44 for *P. paniscus*), but lower than in *Gorilla* (2.09) of *Pongo* (2.03). This degree of body size dimorphism seems low in the light of the strong dimor-

phism present in the crania classified as *A. boisei*.

Homo habilis

The taxonomy of early *Homo* is problematic. Howell (1978) defined the species to include a wide variety of specimens including the large KNM-ER 1470 and small 1813 crania, but Leakey et al. (1978), Stringer (1986), Lieberman et al. (1988), and many others recognize more than one species among these specimens. Common among most of these classifications is the view that the smaller specimens such as KNM-ER 1813 are taxonomically distinct from the larger ones such as KNM-ER 1470. If this is true, then perhaps the predictions given in Table 6 for *H. habilis* should be regarded as estimates of the two species' mean body weight: The larger "species" is what Table 6 refers to as the male *H. habilis* and the smaller "species" is the female.

Table 6 reports a body weight estimate of the male *H. habilis* as 52 and 75 kg using the human and hominoid formulae, respectively. The fossils are identified as *Homo* by their morphology because they resemble *H. erectus* very closely and do not have the peculiarities of the australopithecines. The KNM-ER 1481 hindlimb provides 4 estimates (femoral head, distal femur, proximal and distal tibia). The KNM-ER 1472 femur and the estimated head size that would fit the KNM-ER 3228 pelvic bone provide the other estimates. Since the morphology of these bones is decidedly human-like, the human formulae probably give the most appropriate predictions. Howell (1978) assigns a few other large postcranial specimens to *H. habilis*. The KNM-ER 1473 humeral head corresponds to a human of 64 kg. The KNM-ER 1475 femoral shaft fits a human of 54 kg.

The estimated body weight of the female *H. habilis* is 32 and 42 kg using the human and hominoid formulae. This is based on the O.H. 8 talus and O.H. 35 distal tibia which Susman and Stern (1982) believe came from the same individual as the *H. habilis* type specimen, O.H. 7. This can be checked by reference to the femoral shaft size of O.H. 62

which corresponds to a 33 kg human and a 30 kg hominoid. These predictions from shaft size are not adjusted by multiplying by 0.74, because the two male *H. habilis* femora (KNM-ER 1472 and 1481) have a human-like relationship between joint and shaft size. However, O.H. 62 may have different proportions. Relative to forelimb size, its hindlimbs are disproportionately small (Johanson et al., 1986). Jungers (1988a) estimated a stature of less than 100 cm for O.H. 62. That corresponds to a body weight of less than 17 kg using the power-curve in Jungers and Stern (1983). If the 0.74 correction is made to the human shaft estimate, the weight prediction becomes 24 kg.

Another check is the KNM-ER 3735 partial skeleton (Leakey et al., 1989), but it is so abraded and fragmentary that much caution is necessary. Table 4 lists predictions from its humerus (37 and 23 kg using human and hominoid formulae), radius (50 and 33 kg), and sacrum (22 and 37 kg). Its humerus and distal femoral shaft are about the same size as what is probably an associated partial skeleton of KNM-ER 1503, 1504, 1505, and 1822. If so, perhaps the best estimate of its weight is 40 kg based on the human formulae for femoral head size of KNM-ER 1503. Two other specimens listed in Table 4 may belong to female *H. habilis*. Howell (1978) puts the proximal tibia, KNM-ER 1471, into this taxon. It corresponds to a 39 kg human and a 49 kg hominoid. The proximal radius, KNM-ER 1812D, is associated with a mandible and M3 which is probably *Homo* and may even be the same individual as KNM-ER 1502 which is grouped with the skull, KNM-ER 1813, into what Leakey et al. (1978) regard as a gracile hominid species similar to *A. africanus*. The radius corresponds to a 34 kg human or an 18 kg hominoid.

Combining the estimates in Table 6 yields a species estimate for *H. habilis* of 42 and 58 kg with human and hominoid formulae. McHenry (1982) reported 48 kg, but this was based only on what the author now regards as the male femora (KNM-ER 1472 and 1481). Based on the close relationship between body weight and femoral shaft size in modern humans and African apes, McHenry (1988) predicted a species average of 41 kg.

The ratio of male to female body weight estimates for *H. habilis* is 1.64 or 1.81 depending on human or hominoid formulae. Those are among the largest of any early hominid species. They are intermediate between the highly dimorphic *Pongo* (2.03) and *Gorilla* (2.09) and the mildly dimorphic *P. troglodytes* (1.37). As defined by Howell (1978), *H. habilis* clearly was a highly dimorphic species, especially in its crania.

SUMMARY AND CONCLUSIONS

1. This study explores the relationship between body weight and skeletal size in extant species of Hominoidea in order to predict the body weight of extinct species of hominid. The diameters of fore- and hindlimb joints, femoral shafts, vertebral bodies, and sacral body have high correlations with body weight among species of Hominoidea and within *H. sapiens*.

2. The fore- and hindlimb joints of the partial skeleton of *A. afarensis*, A.L. 288-1, consistently predict a body weight close to 27 kg using formulae based on the *H. sapiens* sample. The formulae based on all hominoid species predict inconsistent weights: Those predicted from the forelimb are apparently too low (12 to 17 kg) while those from the talus are too high (37 kg).

3. The shaft diameters of the A.L. 288-1 femora appear to overestimate the body weight as do those of all other australopithecine femora whose weight can be predicted by measures of hindlimb joint size. Using the formulae derived from the human sample the average overestimation is 1.35 times which is exactly the amount of overestimation found for A.L. 288-1 and very close to the amount found for the nine other australopithecine femora that are complete enough to provide an independent check.

4. The sacral body is exceptionally small in A.L. 288-1 relative to fore- and hindlimb joint size if human proportions are assumed. Sacral size is also relatively very small in the associated skeletons of *A. africanus*.

5. Forelimb joint size in all associated partial skeletons except *H. erectus* and A.L. 288-1 is larger than expected from hindlimb joint size relative to modern humans. Relatively larger forelimbs appear to be charac-

teristic of *A. africanus*, *A. robustus*, *A. boisei*, *H. habilis*, and probably the male *A. afarensis*.

6. Despite the discovery of associated partial skeletons of *A. boisei*, *H. habilis*, *H. erectus*, and perhaps *A. robustus*, the identification of isolated postcrania from sites with contemporaneous species of hominid cannot be certain. This is due partly to the incomplete and fragmentary nature of the collection, but is also due to the apparent fact that these species were rather similar in some aspects of their postcranial anatomy.

7. Using hindlumb joint size of specimens of relatively certain taxonomy and assuming these measures were more like modern humans than apes, the species body weights are as follows: *A. afarensis*, 37 kg, *A. africanus*, 36 kg, *A. robustus*, 36 kg, *A. boisei*, 41 kg, and *H. habilis*, 42 kg. These values appear to be consistent with the range of size variation seen in the entire postcranial samples that can be assigned to species.

8. Sexual dimorphism in body size as judged by hindlimb joint size or by the entire postcranial sample appears to be greater in most, but not all, early hominid species than it is in modern *H. sapiens*. The range of postcranial size variation in *A. afarensis* and *A. africanus* is similar to that of *Pan* and less than those of *Gorilla* and *Pongo*. The greatly expanded postcranial sample of *A. robustus* has a surprisingly low level of size variation and presumably sexual dimorphism which resembles that of modern *H. sapiens*. The body weight of *A. boisei* may have been much more sexually dimorphic (greater than chimps but less than gorillas), but there remains uncertainty about which isolated specimens belong to the male of that species. *H. habilis* as defined by Howell (1978) with the addition of the small Olduvai material is among the most sexually dimorphic of all the species of early hominid. Its dimorphism is intermediate between *Pan* and *Gorilla*.

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