

# Sexual dimorphism in *Australopithecus afarensis* was similar to that of modern humans

Philip L. Reno\*, Richard S. Meindl\*, Melanie A. McCollum\*†, and C. Owen Lovejoy\*\*

\*Matthew Ferrini Institute of Human Evolutionary Research, Department of Anthropology and Division of Biomedical Sciences, Kent State University, Kent, OH 44242; and †Division of Basic Medical Science, School of Medicine, Mercer College, Macon, GA 31207

Communicated by Tim D. White, University of California, Berkeley, CA, May 29, 2003 (received for review January 5, 2003)

The substantial fossil record for *Australopithecus afarensis* includes both an adult partial skeleton [Afar Locality (A.L.) 288-1, "Lucy"] and a large simultaneous death assemblage (A.L. 333). Here we optimize data derived from both to more accurately estimate skeletal size dimorphism. Postcranial ratios derived from A.L. 288-1 enable a significant increase in sample size compared with previous studies. Extensive simulations using modern humans, chimpanzees, and gorillas confirm that this technique is accurate and that skeletal size dimorphism in *A. afarensis* was most similar to that of contemporary *Homo sapiens*. These data eliminate some apparent discrepancies between the canine and skeletal size dimorphism in hominoids, imply that the species was not characterized by substantial sexual bimaturation, and greatly increase the probability that the reproductive strategy of *A. afarensis* was principally monogamy.

Correctly inferring the degree of sexual dimorphism in early hominids is crucial to understanding their paleobiology. Since the recovery and diagnosis of the early hominid species *Australopithecus afarensis* in the 1970s, estimates of its dimorphism have figured prominently in interpretations of its phylogeny and behavior (1–5). As a consequence of numerous non-systematic appraisals, it is now widely believed that *A. afarensis* was substantially more dimorphic than are modern humans (6). Some have gone beyond this orthodoxy to argue that sexually based variation exceeded that seen in any living hominoid (7). None of these analyses, however, has adequately compensated for the effects of temporal and geographic variation as opposed to normative population-level dimorphism. Because anatomical structure evolves through time, it is mandatory that sexual dimorphism within a species not be conflated with variation augmented by evolutionary change. Here we use the contemporaneous Afar Locality (A.L.) 333 hominid sample to show that dimorphism in *A. afarensis* is unlikely to have exceeded that of modern humans.

Reconstructing body size dimorphism in fossils is subject to the compounding errors of (i) small samples and (ii) the potential commingling of ecogeographical, and/or temporal variation with that associated with sex. Despite cogent discussions advocating exceptional care in the assessment of early hominid sexual dimorphism for these reasons (8–10), most commonly cited estimates continue to be derived from simple ratios of body mass predicted for a few isolated specimens whose sex was judged *a priori* (i.e., on the basis of size). This circular practice has methodically excluded intermediate specimens (Fig. 1) and greatly restricted sample size. Indeed, the most commonly cited estimate (see, for example, ref. 11) of dimorphism in *A. afarensis* (44.6 kg  $\pm$  18.5 for males; 29.3 kg  $\pm$  15.7 for females) relied on only three putative females, two of which are among the smallest specimens recorded for the species (6). Even so, because of small sample size, the 95% confidence limits still include monomorphism (3).

Systematic random sampling (e.g., "bootstrapping") of skeletal dimensions is both a more powerful and a more accurate basis for assessing sexual dimorphism in fossil samples (12–17). Such procedures compare prescribed indices [such as maximum/

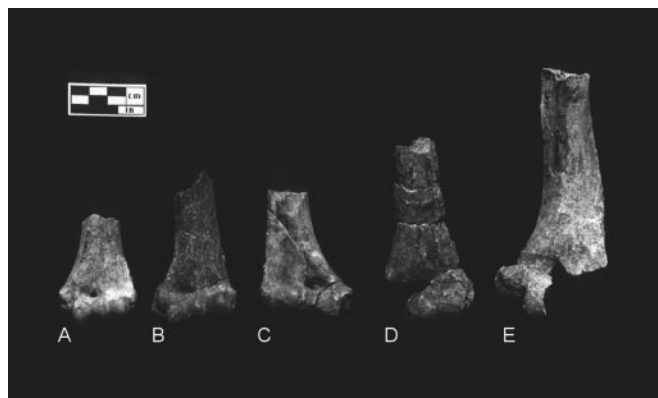


Fig. 1. Sample of some original specimens of the distal humerus from *A. afarensis*. (A) A.L. 288-1; (B) A.L. 322-1; (C) A.L. 137-48A; (D) A.L. 333-29; and (E) MAK VP 1/3. A simple nonsystematic comparison of A and E yields very high dimorphism; however, the presence of other specimens of intermediate size verifies that such estimates cannot be correct (see Table 1).

minimum ratios (MMRs) or coefficients of variation (CVs)] for fossil assemblages to those generated from samples of extant species. Although certainly superior to less systematic approaches, these newer methods still suffer from the problem that fossil assemblages rarely preserve sufficient examples of the same anatomical element. Furthermore, even with large samples, there also remains the likelihood of confounding ecogeographic and temporal variation in body size with that due to sex. By default, extant hominoid samples, which provide the standards to which fossil collections are compared, are all contemporary, whereas early hominid fossils have usually accumulated over a minimum of several hundred thousand years (e.g., see refs. 1 and 14 and below). Even nondirectional body-size fluctuations will, over time, inflate the size range of any fossil sample (e.g., those individuals depicted in Fig. 1), and both geographical and temporal factors are especially likely to affect estimates made using an MMR (12, 13, 16). Therefore, we are almost always faced with the issue of whether any estimate of fossil dimorphism reflects true biological dimorphism or instead indicates variation enhanced by the combined heterogeneities of geography, time, ecology, and even species composition itself.

## Materials and Methods

These issues are potentially resolvable for *A. afarensis*, because its fossil record includes a large geologically simultaneous death assemblage from a single stratum in a single locality (A.L. 333) (18). Therefore, no *a priori* assumptions regarding the potential impact of such factors are required, and this site represents a

Abbreviations: A.L., Afar Locality; BDI, Binomial Dimorphism Index; MMR, maximum/minimum ratio; TSD, template sexual dimorphism; CV, coefficient of variation; FHD, femoral head diameter; C.A., Combined Afar.

See commentary on page 9103.

†To whom correspondence should be addressed. E-mail: olovejoy@aol.com.

Table 1. *A. afarensis* sample used for simulations

Metric	Specimen(s)	Estimated FHD
Proximal humerus: maximum diameter of the head	A.L. 333-107*	39.4
Distal humerus: ML width measured tangent to the superior margin of the olecranon fossa	A.L. 137-48A	32.6
	A.L. 322-1	27.9
	A.L. 333-29	33.2
	A.L. 333w-31	34.3
	Mak VP 1/3	37.8
Distal humerus: maximum diameter of capitulum	A.L. 333w-22	39.5
Proximal radius: maximum diameter of the head	A.L. 333x-14 <sup>†</sup>	44.3
	A.L. 333x-15 <sup>†</sup>	44.5
Proximal ulna: ML width immediately distal to radial facet	A.L. 333x-5	37.1
	A.L. 333w-36	29.8
Proximal femur: maximum diameter of the head	A.L. 288-1ap	28.6
	A.L. 333-3	40.9
Proximal femur: maximum shaft diameter immediately below lesser trochanter	A.L. 211-1	41.6
	A.L. 333-95 <sup>†</sup>	43.0
	Mak VP 1/1	40.3
Proximal femur: neck height normal to long axis at midpoint	A.L. 333-117	38.7
Distal femur: ML width immediately above gastrocnemius tubercle	A.L. 333-4	35.2
	A.L. 333w-56	33.6
Proximal tibia: ML distance between centers of medial and lateral condyles	A.L. 129-1b	27.9
	A.L. 333x-26	38.5
	A.L. 333-42	36.7
Distal tibia: AP articular length at ML midpoint of articular surface	A.L. 333-6	37.2
	A.L. 333-7	42.9
	A.L. 333-96	38.4
Distal fibula: maximum transverse diameter of distal end	A.L. 333-9A	42.8
	A.L. 333-9B	38.9
	A.L. 333w-37	37.8
	A.L. 333-85	40.6

ML, mediolateral; AP, anteroposterior.

\*Because of slight eccentricity in this specimen, we used the average of the ML and AP diameters.

<sup>†</sup>These specimens lack epiphyseal fusion and therefore did not meet our requirement of being adults. However, because they constitute three of the largest fossils in the sample, their omission would further decrease estimates of hominid dimorphism, and they were therefore included.

unique opportunity to explore them in an early hominid species. The various postcranial fragments recovered at this occurrence, however, represent many different anatomical elements. Fortunately, an adult partial skeleton (A.L. 288-1, “Lucy”) is also available for this species. We therefore used ratios between a single skeletal dimension [femoral head diameter (FHD)] and other skeletal metrics preserved in A.L. 288-1 to predict FHDs for 22 of the specimens recovered at A.L. 333 (see accuracy assessment below) and seven additional specimens from other Hadar localities and Maka [Combined Afar (C.A.)] (Table 1). A.L. 288-1 also preserves a mandible, but we have not used it here for two reasons: (i) only three measurable adult specimens were available from A.L. 333, and (ii) postcrania are superior correlates of body size; indeed, the accuracy of judging body size dimorphism from mandibular data appears dubious (see below). FHD was selected because of its common use in size estimation. Our results would have been identical had we standardized to

Table 2. DSDs of actual DMs and the relevant values of BDI, CV, and MMR for the extant hominoid samples used in this study

Species	Males	Females	DSD	BDI	CV	MMR
<i>P. troglodytes</i>	22	25	1.052	1.114	6.53	1.287
<i>H. sapiens</i>	25	25	1.157*	1.160	8.76	1.415
<i>Gorilla gorilla</i>	25	25	1.257	1.250	12.61	1.559

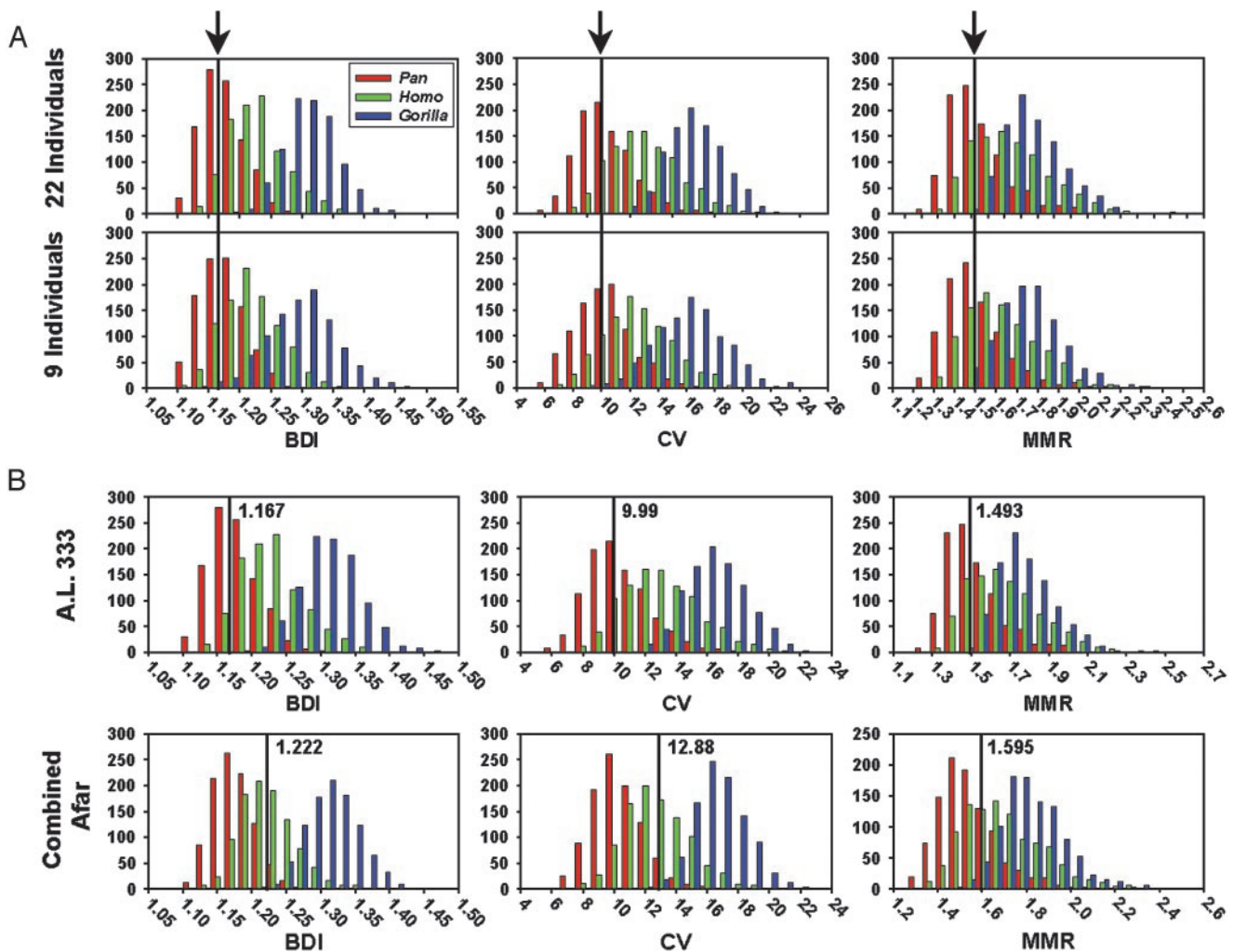
\*This is slightly higher than an average of nine different contemporary reports of femoral head dimorphism for various groups: Libben Site (C.O.L., unpublished observation), late Holocene Australians (36), contemporary central India (37), South African “whites” (38), South African “blacks” (38), contemporary Germans (39), South African “whites” (independent sample) (40), and two samples of European “whites” (41, 42). These ranged from a minimum of 1.11 (Libben) to a maximum of 1.17 [European “whites” (41)]. An unweighted mean of these nine reports was 1.139.

any other skeletal dimension, because all ratios and measures of dispersion [i.e., Binomial Dimorphism Index (BDI), CV, and MMR] would remain the same.

We calculated three measures of skeletal dimorphism for the A.L. 333 and C.A. samples: a MMR, CV, and BDI; formerly Technique Dimorphism (19). The last of these requires three assumptions: (i) both sexes are present in the sample; and (ii) any specimen has an equal prior probability of being male or female, but (iii) when two specimens are of different sex, the larger is male. To apply this simple algorithm, all specimens are first arrayed according to increasing size. There are then  $n - 1$  possible sex allocations (from one female/all-others-male to one male/all-others-female), and  $n - 1$  ratios for which a sexual dimorphism estimate can be calculated (mean of presumed males/mean of presumed females). BDI is the weighted mean of these  $n - 1$  estimates using each ratio's probability in the binomial expansion. The other indices (CV and MMR) were calculated as described (12, 13). We used the small sample correction for the CV (20). To judge the accuracy of these three methods (BDI, CV, and MMR), we applied them to identical anatomical arrays of skeletal metrics randomly selected from extant *Homo*, *Pan*, and *Gorilla* samples (Table 2) (i.e., the exact same metrics calculable for A.L. 333 and the expanded C.A. sample). We did so 1,000 times for each taxon. In each iteration, a template specimen (acting in the role of A.L. 288-1) was randomly selected to provide ratios for estimating FHDs. Because the sizes of the hominoid reference samples are finite ( $n \approx 50$ , Table 2), any single individual in the sample was selected multiple times to serve as the template. However, each randomly sampled anatomical array ( $n = 22$  or 29 representing 12 different metrics) was almost certainly unique for each of the 1,000 iterations.

In addition to the three sexual dimorphism indices (see above), we also calculated two measures of actual skeletal dimorphism (i.e., male mean/female mean based on known sex) for each simulation: the first using FHD estimated by the template method for each specimen [template sexual dimorphism (TSD)], and the second using the actual FHDs for each individual [we will refer to the latter as direct sexual dimorphism (DSD)]. A comparison of these two methods permits an assessment of the potential error that arises from using a template specimen, i.e., comparison of TSD and DSD allows direct assessment of the estimated (template) vs. real (actual FHD) dimorphism in each hominoid simulation. Because calculation of sexual dimorphism for any of the hominid samples (i.e., BDI, CV, MMR) requires the use of the template specimen (A.L. 288-1), they can be assessed only by comparison to TSD from the simulations.

For the A.L. 333 sample, we faced the taphonomic problem that <22 adults may be represented. Relying on adult mandibular dentitions, the adult minimum number of individuals at A.L.



**Fig. 2.** (A) Histograms generated by simulations of A.L. 333 sample for 22 metrics treated separately and for 22 metrics randomly obtained from only nine individuals (1,000 iterations each). The arrow and vertical line in each plot indicate dimorphism for the *A. afarensis* sample from A.L. 333. Note that restricting the source of these metrics to only nine individuals (the minimum number of individuals at A.L. 333 is nine) has no substantial effect on the dimorphism estimate. (B) Histograms generated for samples of 22 (A.L. 333) and 29 (C.A.) metrics. Note that the behavior of BDI and CV are almost identical, but that MMRs greatly overestimate dimorphism (see Table 3). Nonetheless, MMRs predict the same degree of dimorphism in *A. afarensis*, which is substantially greater for the C.A. sample than for A.L. 333, but still most similar to humans.

333 was nine (16). We therefore conducted additional simulations in which the number of hominoid individuals serving as a source of the 22 metrics in Table 1 was varied from 22 to 9. As shown in Fig. 2A, so restricting the number of adults did not significantly affect the outcome of the simulations.

## Results

As expected, our simulations (see Fig. 2 and Table 3) show body size dimorphism in *Homo* to be intermediate between non-dimorphic *Pan* and highly dimorphic *Gorilla*. For the most part, the template method tends to overestimate both means and dispersions of actual dimorphism values (compare TSD with DSD in Table 3). The CV does not produce a direct estimate of dimorphism, but its behavior closely mimicked that of BDI, which does. MMRs consistently failed to substantially distinguish *Pan* from *Gorilla* and greatly overestimated dimorphism in all three taxa (Fig. 3 and Table 3). Their very poor performance is likely the result of instabilities in the method itself but was amplified by use of a template (as noted earlier, use of ratios increased the dispersion of estimates). However, even when no template was used and only actual femoral head values were

used, the distributions of MMRs still grossly overestimated dimorphism and failed to substantially discriminate *Pan* from *Gorilla*. These methodological problems may not have been apparent until now, because MMRs have typically been applied to only very small samples. In contrast to MMR, both BDI and CV adequately quantified sample dimorphism, as evidenced by correlations with both TSD and direct sexual dimorphism (see the supporting information, which is published on the PNAS web site, [www.pnas.org](http://www.pnas.org)). Both performed almost identically in all simulations.

BDI and CV calculated for *A. afarensis*, whether from A.L. 333 or the entire C.A. sample, were most compatible with the *Homo* simulations. Regarding *Pan*, only the C.A. BDI and CV were significantly larger than the simulated distribution. However, both hominid samples differed significantly from *Gorilla* (in fact, the A.L. 333 BDI fell entirely outside the range of simulated values) (Table 4). Of crucial importance is the fact the C.A. sample yielded significantly higher dimorphism (e.g., BDI = 1.222) than did A.L. 333 (BDI = 1.167) (Fig. 2B), implying that the C.A. sample reflects not only sexual dimorphism but ecogeographic and temporal factors as well.

Table 3. Results of simulations

		<i>P. troglodytes</i>		<i>H. sapiens</i>		<i>G. gorilla</i>	
		TSD	DSD	TSD	DSD	TSD	DSD
A.L. 333 simulation: 1,000 iterations							
Actual DM*	Mean	1.038	1.047	1.157	1.155	1.299	1.261
	SD	0.045	0.029	0.053	0.022	0.050	0.025
BDI	Mean	1.166	1.113	1.216	1.149	1.296	1.230
	SD	0.035	0.017	0.046	0.020	0.043	0.027
CV†	Mean	10.00	6.64	12.58	8.55	15.90	12.55
	SD	0.020	0.008	0.025	0.010	0.020	0.010
MMR	Mean	1.488	1.251	1.637	1.335	1.730	1.455
	SD	0.154	0.026	0.195	0.052	0.144	0.069
C.A. simulation: 1,000 iterations							
Actual DM*	Mean	1.045	1.053	1.159	1.157	1.304	1.258
	SD	0.037	0.024	0.043	0.020	0.043	0.022
BDI	Mean	1.166	1.111	1.212	1.153	1.304	1.235
	SD	0.029	0.014	0.039	0.018	0.038	0.022
CV†	Mean	9.93	6.47	12.30	8.63	16.17	12.50
	SD	0.017	0.007	0.021	0.009	0.017	0.009
MMR	Mean	1.517	1.254	1.663	1.354	1.789	1.471
	SD	0.141	0.024	0.180	0.043	0.143	0.061
Minimum number of individuals of 9 at A.L. 333: 1,000 iterations							
Actual DM*	Mean	1.048	1.057	1.156	1.160	1.303	1.258
	SD	0.057	0.048	0.060	0.043	0.066	0.044
BDI	Mean	1.164	1.101	1.207	1.140	1.282	1.207
	SD	0.036	0.026	0.045	0.037	0.057	0.048
CV†	Mean	9.92	6.10	12.14	8.24	15.52	11.89
	SD	0.021	0.013	0.025	0.018	0.025	0.020
MMR	Mean	1.479	1.205	1.595	1.277	1.714	1.381
	SD	0.161	0.042	0.178	0.063	0.156	0.069

\*Actual DM is the male mean/female mean (known sex) for each randomly chosen sample.

†The CV results presented here are "raw," they do not provide a "direct" estimate of dimorphism. However, when graphically translated, their behavior is very similar to that of BDI (see Fig. 2). By convention, we report these values here multiplied by 100.

## Discussion

These results conform to a recent study that examined mandibular size in *A. afarensis* for changes over time (14). Its authors had previously concluded that *A. afarensis* might have been as dimorphic as *Gorilla* and *Pongo* (13). However, their postcranial samples were too small (femur = 5 and humerus = 3) to

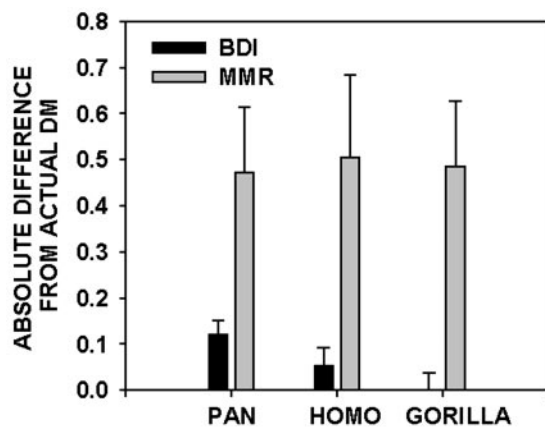


Fig. 3. Mean absolute differences (and standard deviations) between simulations of actual dimorphism (DM) and BDI and MMR using the template method (TSD) for the C.A. simulation (Table 3). BDI and MMR are the two methods in our study that produce direct estimates of dimorphism. BDI overestimates chimpanzee dimorphism, because the species is actually nondimorphic. For species with dimorphism as great as *Homo* and *Gorilla*, however, the actual DM is well within the 2-SD range of the dimorphism indices.

calculate CV, and they instead used MMRs. Since MMR is extremely sensitive to geographic and temporal variation, only by including data from all sampled individuals in the calculation of the index (e.g., CV or BDI) can we more reliably estimate the variation that is accountable by sexual dimorphism. Their larger sample for the mandibular corpus [ $n = 17$  (geometric mean of mandible height and thickness at  $M_1$ )] had yielded a CV of 11.7 for *A. afarensis* [compared with 12.3 for (very dimorphic) gorillas and 7.78 for (nondimorphic) chimpanzees]. However, subsequent amplification of that sample (to  $n = 20$ ) and removal of the four most recent specimens (still maintaining a temporal range of  $\approx 320,000$  years) reduced the *A. afarensis* CV to 8.49 (14), well below those for comparable measures in isolated contemporary modern human populations such as Zulu (10.2) and Spitalfields (10.1) (21). Moreover, as noted earlier, basing an estimate of body size dimorphism on the mandible may be unwarranted. The same metric in a second, independent, sample (21) yielded almost identical CVs for humans (10.4) and gorillas (10.5). If only corpus height was used (which presumably more directly reflects canine dimorphism), mandibles performed better (13.9 for gorilla vs. 11.6 for humans), but in chimpanzees, the female mean was larger than that of the males.<sup>§</sup> In any case, if the four most recent *A. afarensis* specimens are once again excluded from the calculations (see above), the CV of mandib-

<sup>§</sup>In fact, the known range of female body mass of one subspecies of chimpanzee (*Pan troglodytes troglodytes*) exceeds that of all known males from another (*Pan troglodytes schweinfurthii*) (22, 23). If samples from each were combined (as could occur, for example, in the assembly of fossil fragments from different sites or time periods), dimorphism would be overestimated.

**Table 4. Exact counts of the number of simulation values that fell less (<) or greater (>) than the *A. afarensis* value**

	Fossil assemblage dimorphism	<i>P. troglodytes</i>		<i>H. sapiens</i>		<i>G. gorilla</i>	
		<	>	<	>	<	>
A.L. 333		<	>	<	>	<	>
BDI	1.167	559	441	140	860	0	1000
CV	9.99	562	438	143	857	1	999
MMR	1.493	616	384	252	748	13	987
C.A., full sample		<	>	<	>	<	>
BDI	1.222	965	35	641	359	9	991
CV	12.88	952	48	640	360	21	979
MMR	1.595	771	229	396	604	58	942
Minimum number of individuals of 9 at A.L. 333		<	>	<	>	<	>
BDI	1.167	544	456	208	792	20	980
CV	9.99	528	472	194	806	15	985
MMR	1.493	629	371	321	679	51	949

Although these simulations do not constitute traditional tests of hypotheses, they can be converted to *P* values by dividing each count by 1,000. They then represent a test of the directional null hypothesis that the *A. afarensis* dimorphism value could have been produced by a population as sexually dimorphic as *Pan*, *Homo*, or *Gorilla*. For nondirectional *P* values see the supporting information.

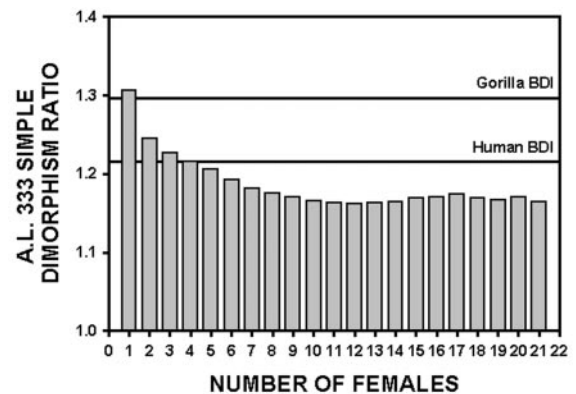
ular corpus height (10.2) (14) still falls below that of modern humans.

We addressed one additional potential taphonomic problem. The smallest estimated FHD for A.L. 333 was 29.8 (Table 1). Although this value is just over 1 mm greater than “Lucy” (28.6), it could hypothetically imply underrepresentation of “Lucy”-sized females at the site (although an abundance of small juvenile specimens makes systematic preservation/recovery bias at A.L. 333 very unlikely). Nevertheless, we sequentially incremented our A.L. 333 sample with “Lucy”-sized specimens (i.e., FHDs of 28.6) until its BDI equaled that of gorillas. This required the addition of eight “Lucy”-sized metrics to the previous total of 22 (i.e., a new  $n = 30$  total elements). However, the addition of these hypothetical elements also increases the minimum number of individuals at A.L. 333 to a total of between 10 (the original nine plus one represented by eight new elements) and 17 (the original nine plus eight new individuals, each represented by a single element) and increases the metric sample by more than one-third. This is obviously an artificial and nonrepresentative inflation of the actual A.L. 333 sample. Moreover, there is no *a priori* reason to presume that diminutive specimens like A.L. 288-1 represent the average size of *A. afarensis* females. Indeed, if they did, most intermediate specimens would then be male, and male *A. afarensis* body size would then be far more variable than in any other living hominoid. Similarly, any contention that A.L. 333 represents a single polygynous male accompanied by multiple mates and juveniles would require uniquely extreme size variation in females. Moreover, if sex ratios were like those of most primate groups (varying anywhere from an approximately equal sex ratio to only a single male), the dimorphism of A.L. 333 must have been within or below the modern human range (Fig. 4).

The evidence that *A. afarensis* is characterized by only slight to moderate degrees of skeletal dimorphism resolves the paradox articulated by Plavcan and van Shaik (4), who noted that the largely monomorphic canines of *A. afarensis* make its supposed great body mass dimorphism (relying again on ref. 6) difficult to interpret (see also ref. 24). They also observe that this is not necessarily an enigma, because body mass dimorphism often does not reflect male–male competition but can arise from other factors such as substrate preferences, predator avoidance, and phylogenetic inertia. Nevertheless, the issue is largely resolved by the results of the present study and especially by the distribution of the skeletal dimensions presented in Fig. 2 for both A.L. 333

and the entire *A. afarensis* sample (see also Fig. 1). These distributions are wholly inconsistent with marked bimaturism, as in gorillas and orangutans [i.e., the telic heteromorphosis of Jarman (25)], to which *A. afarensis* has been consistently compared in the past. They are instead comparable with the homeomorphic dimorphism that characterizes humans and chimpanzees.

Derived hominids possess a number of unique/unusual characters, including concealed ovulation (from both sexes) (26), elaborate epigamies in both sexes, relatively small testes (compared with body mass), relatively short sperm (26), permanently enlarged mammae, and a dramatically expanded cerebral capacity unparalleled in other mammals (27). It has been proposed that all but the last of these characters spring from a social complex including male provisioning driven by female choice that enabled *Australopithecus* to counteract restrictions of re-



**Fig. 4.** Simple ratio of male/female FHDs (using A.L. 288-1 as a template) for A.L. 333 (for Combined Hadar, see the supporting information) as a function of the number of females preserved [i.e., the full range of all ratios used to calculate BDI (TSD in Table 3)]. A gorilla-level dimorphism was present at this site only if it contained a single female specimen. In all other cases (female  $n = 2$ –21), dimorphism was near or well below the average modern human BDI (estimated by TSD; Table 3). This calculation presumes that males are always larger than females, which is almost certainly incorrect at this level of probable dimorphism, and thereby is also an overestimate of actual dimorphism. Indeed, if more than one-half the sample is female, its BDI (calculated by TSD and thereby overestimated) is still very close to human values of actual (known sex) dimorphism (see Table 3).

productive rate imposed by excessive K-selection (28). Although tool using scenarios have been argued to account for canine reduction, such “disuse” models fail to adequately explain directional selection for crown reduction in males and the myriad other unique anatomical characters of derived hominids. One obvious possibility is that small-canined males would be less effective competitors in a polygynous mating strategy and would thereby prove to be more reliable provisioners (and thereby differentially chosen by females). However, female choice does not provide an adequate explanation for the patterns of skeletal dimorphism observed across hominoids. Most notably because chimpanzees exhibit virtually no significant skeletal size dimorphism (body mass dimorphism is moderate), despite their demonstrably polygynous reproductive strategy. This near monomorphism is in stark contrast to the marked skeletal dimorphism of gorillas and orangutans and suggests that skeletal dimorphism in itself is a poor predictor of reproductive strategy in hominoids.

In polygynous species in which males must rely on substantial body mass and weaponry (especially large canines) to compete for access to mates, it is typical for male maturation to be delayed and growth thereby to be prolonged to accentuate these characteristics (telic heteromorphism) (25, 29, 30). Because hominoid male canine size is largely a product of prolonged growth (31), a greater time to maturity in gorillas and orangutans (29, 30, 32) is consistent with the greater individuation of male success in these species, as is reflected in their more marked canine, skeletal, and body mass dimorphism.

Male kin-related communities of *P. troglodytes* rely heavily on territorial maintenance by “patrols.” Selection may have therefore favored more rapid male skeletal maturation to accelerate their participation in cooperative territorial defense (this would also account for the species’ reduced canine dimorphism compared with that in gorillas and orangutans) (33). *Pan paniscus* is slightly bimaturational by virtue of a later cessation of growth in males. Leigh and Shea (30) attribute this greater bimaturationality to reduced feeding competition among females in *P. paniscus*, but an equally likely explanation is that bonobos instead represent the primitive condition, and female *P. troglodytes* have slightly delayed sexual maturation (thereby eliminating bimaturationality in the species) because of their more intense female–female competition.

In any case, the minimal expression of bimaturationality in both species increases the likelihood that australopithecine groups were not polygynous if they exhibited a female transfer system. As Hamada and Udono (33) have argued, “the social system and ecology of human ancestors, who evolved a characteristic growth pattern, must have been different from that of chimpanzees” (ref. 33, p. 283). First, their marked demographic success and capacity to invade new potentially dangerous habitats strongly suggest that they, like chimpanzees, dwelled in multimale groups (27, 28). If such groups were also (like chimpanzees) involved in significant territorial defense, largely by kin-groups, a similarly weak degree of chimpanzee-like skeletal dimorphism would be expected, as would greater canine dimorphism.

Instead, the moderate skeletal dimorphism of *A. afarensis* (greater than *Pan* and less than *Gorilla*) suggests a somewhat longer developmental period in males compared with females and is therefore inconsistent with a chimpanzee-like territorial strategy. At the same time, it is also markedly inconsistent with strategies like those of gorillas and orangutans, in which skeletal dimorphism is much more pronounced. Therefore, the co-occurrence of moderate skeletal dimorphism, such as that found in modern humans and *A. afarensis*, and a reduced male canine is fully consistent with a pair-bonded reproductive strategy in early hominids; that is, if their reproductive strategy was chimpanzee-like, hominids should show only minimal skeletal dimorphism, or if it was orangutan- or gorilla-like, they should show greater skeletal dimorphism. Canine dimorphism should be present in either case. Early hominid skeletal dimorphism is consistent with another special hominid character, the failure of male canine eruption to be delayed and thereby coincident with somatic maturation (as it is in all other hominoid species) (34, 35). Thus, observed levels of body size dimorphism in *A. afarensis* do not imply that monogamy is any less probable than polygyny as the fundamental social system of these early hominids.

We thank Gen Suwa, Richard J. Smith, Robert Eckhardt, and Tim White for detailed and critical reviews of this manuscript. Louise Humphrey, Chris Dean, and Chris Stringer kindly provided unpublished data, and Brian Richmond and Sang-Hee Lee brought key references to our attention. Kevin Kern contributed to data collection and computer programming. This research was supported by National Science Foundation Grants SBR-9729060 and BCS-9919211 (to C.O.L.).

- White, T. D., Moore, R. V. & Suwa, G. (1984) *J. Vert. Paleo.* **4**, 575–583.
- Zihlman, A. (1976) in *Les Plus Anciens Hominides*, eds Tobias, P. V. & Coppens, Y. (Centre National de la Recherche Scientifique, Paris), p. 32768.
- McHenry, H. M. (1994) *J. Hum. Evol.* **27**, 77–87.
- Plavcan, J. M. & van Schaik, C. P. (1997) *J. Hum. Evol.* **32**, 345–374.
- Plavcan, J. M. (2000) *J. Hum. Evol.* **39**, 327–344.
- McHenry, H. M. (1992) *Am. J. Phys. Anthropol.* **87**, 407–431.
- Zihlman, A. L. (1985) in *Hominid Evolution: Past, Present and Future*, ed. Tobias, P. V. (Liss, New York), pp. 213–220.
- Jungers, W. L. (1985) in *Size and Scaling in Primate Biology*, ed. Jungers, W. L. (Plenum, New York), pp. 345–381.
- Smith, R. J. (1996) *Curr. Anthropol.* **37**, 451–481.
- Eckhardt, R. B. (2000) *Human Paleobiology* (Cambridge Univ. Press, Cambridge, U.K.).
- Ward, C. V. (2003) *Yrbk. Phys. Anthropol.* **45**, 185–215.
- Richmond, B. G. & Jungers, W. L. (1995) *J. Hum. Evol.* **29**, 229–245.
- Lockwood, C. A., Richmond, B. G., Jungers, W. L. & Kimbel, W. H. (1996) *J. Hum. Evol.* **31**, 537–548.
- Lockwood, C. A., Kimbel, W. H. & Johanson, D. C. (2000) *J. Hum. Evol.* **39**, 23–55.
- Arsuaga, J. L., Carretero, J. M., Lorenzo, C., Gracia, A., Martinez, I., Bermudez de Castro, J. M. & Carbonell, E. (1997) *Science* **277**, 1086–1088.
- Lockwood, C. A. (1999) *Am. J. Phys. Anthropol.* **108**, 97–127.
- Lee, S.-H. (2001) *Anthropol. Rev.* **64**, 21–39.
- White, T. D. & Johanson, D. C. (1989) in *Hominidae*, ed. Giacobini, G. (Jaka, Milan), pp. 97–101.
- Lovejoy, C. O., Kern, K. F., Simpson, S. W. & Meindl, R. S. (1989) in *Hominidae*, ed. Giacobini, G. (Jaka, Milan), pp. 103–108.
- Sokal, R. R. & Rohlf, F. J. (1995) *Biometry* (Freeman, New York).
- Humphrey, L. T., Dean, M. C. & Stringer, C. B. (1999) *J. Anat.* **195**, 491–513.
- Videan, D. N. (2000) Master’s thesis (Miami University, Oxford, OH).
- Smith, R. J. & Jungers, W. J. (1997) *J. Hum. Evol.* **32**, 523–559.
- Plavcan, J. M. & Kelley, J. (1996) *Am. J. Phys. Anthropol.* **99**, 379–388.
- Jarman, P. (1983) *Biol. Rev.* **58**, 485–520.
- Dixon, A. F. (1998) *Primate Sexuality: Comparative Studies of the Prosimians, Monkeys, Apes and Human Beings* (Oxford Univ. Press, Oxford).
- Lovejoy, C. O. (1993) in *The Origin and Evolution of Humans and Humanness*, ed. Rasmussen, D. T. (Jones and Bartlett, Boston), pp. 1–28.
- Lovejoy, C. O. (1981) *Science* **211**, 341–350.
- Shea, B. T. (1985) *Am. J. Primatol.* **8**, 183–188.
- Leigh, S. R. & Shea, B. T. (1995) *Am. J. Primatol.* **36**, 37–60.
- Schwartz, G. T. & Dean, C. (2001) *Am. J. Phys. Anthropol.* **115**, 269–283.
- Vancatova, M., Vancata, V., Jarabkova, Z., Zlamalova, H., Skrivankova, J. & Janecek, J. (1999) *Var. Evol.* **7**, 31–45.
- Hamada, Y. & Udono, T. (2002) *Am. J. Phys. Anthropol.* **118**, 268–284.
- Simpson, S. W., Lovejoy, C. O. & Meindl, R. S. (1990) *J. Hum. Evol.* **19**, 285–297.
- Simpson, S. W., Lovejoy, C. O. & Meindl, R. S. (1991) *Am. J. Phys. Anthropol.* **86**, 113–120.
- Brown, P. (2000) *J. Hum. Evol.* **38**, 743–749.
- Purkait, R. & Chandra, H. (2002) *Forensic Sci. Commun.* **4**, 1–7.
- Asala, S. A. (2001) *Forensic Sci. Int.* **117**, 15–22.
- Mall, G., Graw, M., Gehring, K. & Hubig, M. (2000) *Forensic Sci. Int.* **113**, 315–321.
- Steyn, M. & Iscan, M. Y. (1997) *Forensic Sci. Int.* **90**, 111–119.
- Maltby, J. R. D. (1918) *J. Anat.* **52**, 363–382.
- Dwight, T. (1904) *Am. J. Anat.* **4**, 19–31.