

Mandibular size and shape variation in the hominins at Dmanisi, Republic of Georgia

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Abstract

The hominin fossils of Dmanisi, Republic of Georgia, present an ideal means of assessing levels of skeletal size and shape variation in a fossil hypodigm belonging to the genus *Homo* because they have been recovered from a spatially and temporally restricted context. We compare variation in mandible size and shape at Dmanisi to that of extant hominoids and extinct hominins. We use height and breadth measurements of the mandibular corpus at the first molar and the symphysis to assess size, and analyze shape based on size-adjusted (using a geometric mean) versions of these four variables. We compare size and shape variation at Dmanisi relative to all possible pairs of individuals within each comparative taxon using an exact resampling procedure of the ratio of D2600 to D211 and the average Euclidean distance (AED) between D2600 and D211, respectively. Comparisons to extant hominoids were conducted at both the specific and subspecific taxonomic levels and to extinct hominins by adopting both a more, and less speciose, hominin taxonomy. Results indicate that the pattern of variation for the Dmanisi hominins does not resemble that of any living species: they exhibit significantly more size variation when compared to modern humans, and they have significantly more corpus shape variation and size variation in corpus heights and overall mandible size than any extant ape species. When compared to fossil hominins they are also more dimorphic in size (although this result is influenced by the taxonomic hypothesis applied to the hominin fossil record). These results highlight the need to re-examine expectations of levels of sexual dimorphism in members of the genus *Homo* and to account for marked size and shape variation between D2600 and D211 under the prevailing view of a single hominin species at Dmanisi.

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Introduction

The Plio-Pleistocene sediments at the site of Dmanisi in the Georgian Caucasus contain a rich faunal assemblage, remains of fossil hominins, and lithic artifacts all from a restricted time interval and spatial distribution (Gabunia and Vekua, 1995; Vekua et al., 2002). Initially, the Dmanisi finds were of particular interest because they identified members of the genus *Homo* in western Asia in the earliest Pleistocene and because they indirectly supported claims of the presence of *H. erectus*

in southeast Asia in the early Pleistocene (Swisher et al., 1994; Larick et al., 2001). As the fossil assemblage has grown, Dmanisi has been recognized as providing a key evolutionary window into the events surrounding the dispersal of *Homo* from Africa with particular regard to the biological nature of these hominins (Gabunia and Vekua, 1995; Brauer and Schultz, 1996; Rosas and Bermudez de Castro, 1998; Gabunia et al., 2000a; Gabunia et al., 2000b; Gabunia et al., 2001; Gabunia et al., 2002; Vekua et al., 2002; Lordkipanidze et al., 2005; Rightmire et al., 2006). Because of the restricted time interval represented at the site, Dmanisi reveals a snapshot into the evolutionary history of a hominin taxon rarely available in the fossil record. Combined with the already large (by paleoanthropological standards) and ever growing number of

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skeletal remains recovered from the site, Dmanisi provides an important case study for understanding population-level skeletal variation in fossil hominins (Wood, 1988, 1991b, 1993; Lam et al., 1996; Lockwood et al., 1996, 2000; Lockwood, 1999; Silverman et al., 2001; Rightmire et al., 2006).

To date, most studies of the Dmanisi craniodental remains have noted levels of size and shape variation suggestive of a single species with moderate to high sexual dimorphism (Gabunia et al., 2000b; Gabunia et al., 2002; Vekua et al., 2002; Macaluso et al., 2004; Lee, 2005; Lordkipanidze et al., 2005; Rightmire et al., 2006). Marked size dimorphism is present, however, in the mandibular remains of Dmanisi, due primarily to the recovery of a large mandible (D2600) that differs substantially in size from three other mandibles. This difference has led to ongoing debate as to whether D2600 can be accommodated within the same species as the other Dmanisi craniodental fossils (Gabunia et al., 2002; Rightmire et al., 2006). Previous quantitative comparisons of mandibular size at Dmanisi have been limited to length and breadth dimensions of the dental arcade (Gabunia et al., 2002) and have not included the relative size of the mandibular corpus, the dimensions of which differ substantially between large and small specimens (Rightmire et al., 2006). Neither has this disparity been evaluated within the context of living apes and other fossil hominin species.

We compare mandibular size and shape variation at Dmanisi to that present in a large sample of extant hominoids and Plio-Pleistocene fossil hominins. We address whether mandibular size variation at Dmanisi is different from that of living and extinct taxa believed to possess similar levels of body size sexual dimorphism (BSSD). We examine shape variation in the mandibular corpora of Dmanisi and compare this variation to that of extant hominoids. The results have implications for expectations of BSSD in Pleistocene *Homo* and/or the number of hominin species recognized at Dmanisi.

Specifically, we consider the probability of sampling two individuals from extant species of hominoids or extinct species of hominins whose degree of size and shape variation exceeds that observed between the large (D2600) and small (D211) Dmanisi mandibles. Based on assessments of BSSD in hominins and hominoids (McHenry, 1996) and on the assumption of a single species being present at Dmanisi (Vekua et al., 2002), our null hypothesis is that the size and shape differences between the Dmanisi mandibles is not significantly greater than that found within comparative taxa. While we acknowledge the possibility that levels of dimorphism in extinct taxa may exceed those of modern taxa (sensu Kelley and Plavcan, 1998), we suggest that rejection of the null hypothesis for some, or all, of the comparative taxa would support alternative hypotheses of either greater skeletal sexual dimorphism at Dmanisi than is currently assumed for an early Pleistocene *Homo* species, or the presence of more than one species at Dmanisi.

Materials and methods

Published data on two of the four mandibles (the large D2600 mandible and the small D211 mandible) recovered

from the site of Dmanisi were included in this analysis (Gabunia and Vekua, 1995; Rightmire et al., 2006). A third mandible, D2735, was not included as it is from a sub-adult individual as evidenced by the partially-erupted third maxillary molars of the associated D2700 cranium (Rightmire et al., 2006). A fourth mandible, D3900, was excluded as it is edentulous and exhibits significant pathological resorption of the mandibular corpus (Lordkipanidze et al., 2005). Measurement data taken from the literature were limited to the height and breadth dimensions of the mandibular corpus at the lower first molar and at the mandibular symphysis (see Appendix 1 for measurement definitions and also Wood, 1991a). These variables were selected because collectively they provide a reasonable measure of overall mandibular corpus size in addition to being available for the majority of mandibular fossil specimens, thus maximizing sample sizes in the comparison to extinct hominin material.

The extant hominoid comparative sample includes the following taxa: *Gorilla gorilla gorilla*, *G. g. graueri*, *G. g. berengei*, *Pongo pygmaeus pygmaeus*, *P. p. abelii*, *Pan troglodytes troglodytes*, *P. t. schweinfurthi*, *Pan paniscus*, and *Homo sapiens* (Table 1). The *G. g. graueri* sample includes a small number of individuals alternatively classified as *G. g. rex-pygmaeorum*, which for simplicity are included in the former based on molecular evidence (Jensen-Seaman and Kidd, 2001) and the ongoing debates about gorilla taxonomy (Grubb et al., 2003). Measurement data for extant taxa were collected by NJC. In all cases only wild-caught, non-pathological adult (defined on the basis of possessing fully erupted third molars) specimens were included in the analysis. Comparative analyses of extant samples were conducted with both subspecific and specific groupings and on samples having equal representation of males and females. For the purpose of this study, we have included within the species taxon *G. gorilla*, the subspecies *G. g. gorilla*, *G. g. graueri*, and *G. g. berengei*, and within the species taxon *P. pongo*, the subspecies *P. p. pygmaeus* and *P. p. abelii*. These taxonomic classifications are not made in order to further any particular taxonomic classification scheme of gorillas or orangutans, but rather to create comparable levels of expected variation in more and less inclusive groups for comparison to the Dmanisi material.

Kelley and Plavcan (1998) demonstrated that dental metric variation in the Miocene hominoid *Lufengpithecus lufengensis* exceeded that of any living ape species and that living apes do not adequately represent the range of BSSD among fossil hominoids. They caution against the use of extant analogues and single measures of metric variation (e.g., coefficient of variation) to test species composition in fossil samples. We believe that because our analysis focuses on a fossil hypodigm dated to the early Pleistocene and attributed to the genus *Homo*, that the extant hominoids we have included for comparison provide an adequate and legitimate upper limit of BSSD and associated skeletal metric variation.

The comparative sample of Plio-Pleistocene hominin mandibles attributed to *Australopithecus*, *Paranthropus*, and *Homo* taxa are listed in Appendix 1. These data were taken from the literature (see Appendix 1 for references) and only include

Table 1
Comparison of mandibular size and shape variation at Dmanisi to extant hominoid species and subspecies for different corpus size variables¹

Taxon	n _F	n _M	GM ²			SYMPHYSIS HEIGHT			SYMPHYSIS BREADTH			CORPUS AT M ₁ HEIGHT			CORPUS AT M ₁ BREADTH			SHAPE ANALYSIS ³		
			Max	M/ \bar{F}	p	Max	M/ \bar{F}	p	Max	M/ \bar{F}	p	Max	M/ \bar{F}	p	Max	M/ \bar{F}	p	Max	M/ \bar{F}	p
Dmanisi (D211 and D2600)			1.39			1.59			1.25			1.66			1.14			0.169		
Species Comparisons																				
<i>P. pygmaeus</i>	28	28	1.62	1.20	0.051	1.68	1.22	**	2.00	1.20	ns	1.76	1.20	**	1.67	1.20	ns	0.199	0.009	**
<i>G. gorilla</i>	55	55	1.64	1.21	*	1.81	1.28	*	1.72	1.24	ns	1.78	1.22	**	1.68	1.10	ns	0.214	0.054	*
<i>P. troglodytes</i>	44	44	1.42	1.07	**	1.52	1.07	***	1.73	1.08	ns	1.58	1.07	***	1.63	1.07	ns	0.219	0.002	*
<i>P. paniscus</i>	16	16	1.33	0.96	**	1.38	0.96	**	1.56	0.97	ns	1.46	0.96	**	1.53	0.94	ns	0.167	0.011	**
<i>H. sapiens</i>	26	26	1.47	1.08	**	1.80	1.07	**	1.77	1.09	ns	1.79	1.10	**	1.46	1.03	ns	0.330	0.021	ns
Subspecies Comparisons ⁴																				
<i>P. p. pygmaeus</i>	22	22	1.62	1.21	0.055	1.66	1.23	**	1.96	1.19	ns	1.74	1.22	**	1.67	1.21	ns	0.199	0.016	**
<i>P. p. abelii</i>	6	6	1.41	1.17	*	1.45	1.16	*	1.49	1.21	ns	1.56	1.12	*	1.46	1.17	ns	0.140	0.034	*
<i>G. g. gorilla</i>	13	13	1.53	1.22	0.052	1.77	1.29	*	1.72	1.30	ns	1.55	1.22	**	1.47	1.10	ns	0.196	0.060	**
<i>G. g. berengei</i>	10	10	1.34	1.17	**	1.58	1.30	**	1.55	1.22	ns	1.55	1.16	**	1.28	1.04	ns	0.187	0.085	*
<i>G. g. graueri</i>	32	32	1.57	1.21	*	1.61	1.27	**	1.58	1.23	ns	1.75	1.25	**	1.57	1.12	ns	0.157	0.044	***
<i>P. t. troglodytes</i>	26	26	1.42	1.08	**	1.52	1.08	***	1.73	1.09	ns	1.58	1.09	***	1.57	1.07	ns	0.203	0.006	**
<i>P. t. schweinfurthi</i>	18	18	1.31	1.06	**	1.43	1.06	**	1.54	1.05	ns	1.29	1.04	**	1.63	1.08	ns	0.205	0.012	*
<i>P. paniscus</i>	16	16	1.33	0.96	**	1.38	0.96	**	1.56	0.97	ns	1.46	0.96	**	1.53	0.94	ns	0.167	0.011	**
<i>H. s. sapiens</i>	26	26	1.47	1.08	**	1.80	1.07	**	1.77	1.09	ns	1.79	1.10	**	1.46	1.03	ns	0.330	0.021	ns

¹ Bold values indicate that the maximum ratio of the Dmanisi mandibles is found in less than 5% of all possible pairwise comparisons of the extant samples. * = p < 0.05; ** = p < 0.01; *** = p < 0.001; ns = p > 0.10.

² Values for GM and individual size variables are maximum ratios for pairs of specimens and ratios of sex-specific means for extant taxa.

³ Values are for maximum average Euclidean distance between pairs of specimens and distance between sex-specific means for extant taxa.

⁴ Please note that values for *P. paniscus* and *H. sapiens* are the same for species and subspecies comparisons.

adult specimens (note: age designation also taken from the literature) with no major pathological conditions. Given that comparative fossil data were taken from the literature and not measured by the authors, the precise location of some measurements differs slightly between specimens (e.g., for some fossil specimens published corpus breadth measurements were only available for the P₄/M₁ intertooth boundary rather than at the M₁). The published location of each measurement is listed in Appendix 1. These cases of measurement discrepancy do not prevent reasonable comparison, as measurement locations usually differed only between fossil species samples rather than within them (with the exception of specimens attributed to *H. erectus sensu lato*), and because the measure of mandible size used in this analysis (see below) is believed to be robust against these discrepancies. As analyses of shape variation were limited to extant taxa (with the exception of a visual, non-statistical, inspection of shape variability in *H. erectus sensu lato*), these discrepancies also do not negate these results. Due to the fragmentary nature of many fossils, data at all measurement locations are not available for each specimen. Consequently, sample sizes for particular taxa differ between analyses depending upon the linear measurements used (see below).

Analysis of size variation

Based on the four measured variables (i.e., symphysis height, symphysis breadth, corpus height at M₁, and corpus breadth at M₁), five analyses of size variation were conducted using each of the four variables individually, as well as a measure of overall mandible size. A measure of overall mandible

size was calculated as the geometric mean (GM = n th root of the product of n variables) of the included variables and was chosen because it combines any number of linear measurements into an overall measure of size (Mosimann, 1970; Jungers et al., 1995).

For each analysis an *exact* resampling procedure selects all possible combinations of two mandibles from each comparative taxon using a program written by ADG in the software package R (www.r-project.org) (Ihaka and Gentleman, 1996). For each pair of specimens a ratio of their size (larger divided by smaller) is calculated to represent mandibular size variation. Calculating this ratio for every possible pair of specimens generates a distribution of all possible values of that ratio for a particular comparative sample. The ratio for the pair of Dmanisi specimens is then compared against the distribution for the comparative sample to determine the probability that specimens of equal or greater size difference could be found in the comparative sample (e.g., Richmond and Jungers, 1995; Grine et al., 1996; Lague and Jungers, 1996; Lockwood et al., 1996, 2000; Arsuaga et al., 1997; Lorenzo et al., 1998; Lockwood, 1999; Aiello et al., 2000; Silverman et al., 2001).

This probability is calculated as $(D + 1)/(T + 1)$, where D is the number of times a ratio in the comparative taxon equals or exceeds that of the Dmanisi sample, and T is the total number of pairwise comparisons in the comparative taxon. Given that we are testing the null hypothesis that dimorphism at Dmanisi is not greater than that of other taxa, we use a one-tailed test of significance. The calculated probability is considered statistically significant if the Dmanisi ratio is not found in the sample distribution or if the ratio falls within the uppermost 5% of the comparative sample distribution. Using this

methodology, the size dimorphism present between the large and small Dmanisi mandibles is placed in a comparative context and conclusions about intraspecific and interspecific variation are drawn.

Comparison of size variation at Dmanisi to that of extinct fossil hominin taxa involved an assessment of whether, for each analysis, the highest dimorphism ratios found in the hominin samples exceeded those of Dmanisi. Tests of statistical significance based on ratio distributions were only conducted when 15 or more specimens were available for a particular hominin taxon, providing at least 100 possible pairs of specimens. As the size variation present in a hominin taxon is heavily influenced by the fossils included in it, and due to ongoing debate about the taxonomic affiliation of some fossils, we present two taxonomic hypotheses for the fossil hominins (Appendix 1). The first, more taxonomically conservative hypothesis recognizes the taxa *H. habilis sensu lato* and *H. erectus sensu lato* (hereafter referred to as *H. habilis s. l.* and *H. erectus s. l.*, respectively). We refer to this taxonomic hypothesis as the short taxonomy and believe it to be a conservative estimate of acceptable variation in fossil hominin taxa.

The second, more taxonomically liberal hypothesis divides the fossils attributed to *H. habilis s. l.* into two taxa, *H. rudolfensis* and *H. habilis sensu stricto* (hereafter referred to as *H. habilis s. s.*), to represent these earliest fossils of the genus *Homo* from Africa (Wood, 1993). Also, it divides *H. erectus s. l.* into regionally based taxa including *H. erectus erectus* (Indonesia), *H. erectus pekinensis* (China), *H. erectus mauritanicus* (N. Africa), and African *H. erectus/ergaster* (referring to early Pleistocene *Homo* fossils from Africa). [Note: SK 15 was grouped with African *H. erectus/ergaster* based on its estimated age of 1.8–1.0 Ma (Susman et al., 2001 cited in Antón, 2003), while the Ternifine, Sidi Abderrahman, and Thomas Quarry material was given its own grouping, *H. erectus mauritanicus*, based on an estimated age of 400 ka (Hublin, 1985 cited in Antón, 2003) and its potential affinity with material referred to as *H. heidelbergensis* (Antón, 2003)]. We refer to this taxonomic hypothesis as the long taxonomy and believe that it presents meaningful comparisons for variation in the Dmanisi material as these comparative taxa, like Dmanisi, are more restricted in their temporal and spatial distribution.

Analysis of shape variation

Using the same four linear measurements of the mandibular corpora used in the analysis of size variation, shape variation was assessed using the following method. First, each linear measurement was divided by the geometric mean of all four measured variables (see above) to produce four shape variables (Jungers et al., 1995). To calculate a measure of shape variation between two mandibles, their average Euclidean distance (AED) was calculated using the following formula:

$d(a, b) = \sqrt{[1/n \sum (a_n - b_n)^2]}$, where a and b are individual mandibles and n is any number of shape variables (Sneath and Sokal, 1973). AED essentially provides a linear distance

between pairs of specimens in multidimensional shape space which can be used as a measure of shape difference (Aiello et al., 1999; Silverman et al., 2001). As in the analysis of size variation above, AEDs were calculated, using an exact resampling procedure, between all possible pairwise comparisons in a sample. The AED between D2600 and D211 was then compared to the distribution of AEDs for each extant hominoid sample. As above, comparisons of shape variation between Dmanisi and extant taxa were calculated with probability = $(D + 1)/(T + 1)$, where D is the number of times a pairwise AED in the comparative taxon exceeds that of the Dmanisi sample and T is the total number of pairwise AEDs in the comparative taxon. As above, we used a one-tailed test of significance with an alpha value of 0.05 (or 5%).

Results: size variation

Comparison with extant hominoid taxa

Table 1 lists the maximum ratios derived for each analysis and for each extant taxon, at both specific and subspecific levels, as well as the ratio of male mean and female mean. The Dmanisi ratios calculated for each analysis are also listed. Maximum ratios appearing in bold font indicate that the Dmanisi ratio is found in fewer than 5% of pairwise comparisons in the comparative sample; thus, the degree of size dimorphism at Dmanisi measured by the variable in question is unlikely to be seen in a random selection of any two individuals from the comparative taxon. The null hypothesis cannot be rejected in all other cases. As can be seen from Table 1, the results do not differ substantially regardless of whether comparisons of mandible dimorphism are made at the specific or subspecific level; therefore, based on larger sample sizes, the former will be presented in detail here.

Maximum pairwise ratios of overall mandibular size (GM of all variables) were higher than the Dmanisi ratio in all extant hominoid species except *P. paniscus* (note that the low maximum ratios for the subspecies *G. g. berengei* and *P. p. abelii* may be due to small sample sizes). However, in all hominoid species (except in *P. pygmaeus*, where $p = 0.051$) it is significantly unlikely to randomly select two individuals having as high a ratio as that of Dmanisi. The Dmanisi ratio is considerably larger than the ratios of mean male size to mean female size in the extant taxa (Table 1). Figure 1 shows the distributions of these pairwise ratios of hominoid species relative to the level of variation at Dmanisi (dashed line). Examining height and breadth variables separately suggests that this result is driven by the large difference in height between D2600 and D211. Dmanisi mandibular corpus and symphysis breadth measures exhibit a degree of size dimorphism consistent with all extant hominoid species, whereas height dimorphism differs significantly from these taxa.

The results of the extant comparison suggest that degree of overall size dimorphism present in the Dmanisi mandibles is rarely seen in any extant hominoid species or subspecies. In particular, the unusually high dimorphism in overall mandible size at Dmanisi is driven by extreme height dimorphism.

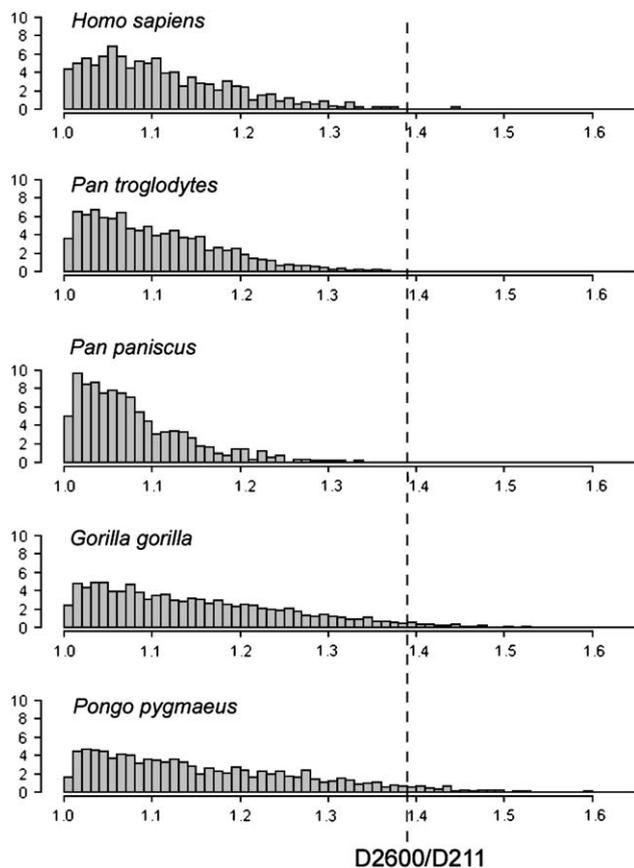


Fig. 1. Distributions of pairwise ratios in a comparison of overall mandible size variation for each extant hominoid species. Numbers along vertical axis indicate percent of cases; dashed vertical line indicates the Dmanisi ratio between mandibles D2600 and D211. The Dmanisi ratio is present in less than 5% of cases in all groups except *P. pygmaeus* ($p = 0.051$). See text for discussion and Table 1 for summary statistics.

Comparison with extinct hominin taxa

Table 2 lists the maximum ratios derived for each analysis of each hominin taxon under both short and long taxonomic hypotheses. Italicized values indicate that the maximum ratio of the Dmanisi mandibles exceeds that found in any pairwise comparison within a comparative hominin taxon (significance levels are provided for those taxa with 15 or more specimens).

Using a short, more conservative taxonomic hypothesis, the degree of size dimorphism in the Dmanisi mandibles is variably present among hominin taxa. The pattern is somewhat similar to the extant hominoid analysis in that analyses of GM and the two height variables produce maximum ratios that are rarely found in *Australopithecus* and *Paranthropus* taxa. However, the taxa *H. habilis s. l.* and *H. erectus s. l.* possess pairs of individuals who exhibit maximum ratios that exceed those between D211 and D2600 for most variables (Fig. 2). The degree of dimorphism in breadth measurements at Dmanisi appears as commonly in extinct hominin taxa (using the short taxonomy) as it does in extant hominoid taxa.

The results of using a long, more speciose taxonomic hypothesis highlight the influence of a taxon's fossil composition on the results of this type of analysis. When *H. habilis s. l.* is

split into *H. rudolfensis* and *H. habilis s. s.*, the maximum ratios derived for all analyses (with the exception of corpus breadth at M₁) fall below those seen at Dmanisi. This is because the large ratios derived within the short taxonomy stem from pairwise comparisons between large mandibles from Koobi Fora (e.g., KNM-ER 1483) and small mandibles from Olduvai (e.g., OH 13). A similar phenomenon occurs when *H. erectus s. l.* is split under the long taxonomy into five different taxa. In the short taxonomy, maximum ratios for *H. erectus s. l.* exceeded those at Dmanisi in all analyses (although the probability of getting a ratio as large as that seen in the Dmanisi mandibles is less than 5% for the two height variables). However, *H. erectus s. l.* spans roughly one million years in time depth and includes specimens from Africa, China, and Southeast Asia—a context that is quite different from that at Dmanisi. When the degree of size dimorphism is compared between more temporally and regionally restricted *H. erectus* taxa, *H. e. erectus* material from Sangiran possesses maximum ratios which exceed those at Dmanisi for most analyses (with the exception of the analysis of corpus height at M₁), whereas African *H. erectus/ergaster* and *H. e. pekinensis* only exceed Dmanisi for corpus breadth at M₁. *H. e. mauritanicus* does not exceed Dmanisi in any analysis.

The taxonomic composition of the Sangiran material has been debated since the 1940s when the discovery of the Sangiran 6 mandible prompted von Koenigswald (Weidenreich, 1944) to raise the new genus and species *Meganthropus paleojavanicus*, due to its morphology and overall great size when compared to other *Pithecanthropus* and *Sinanthropus* mandibles (e.g., Weidenreich, 1945; Jacob, 1973; Kramer, 1989, 1994; Tyler, 1991, 2001; Kaifu et al., 2005). That the large size of the Sangiran 6 mandible is driving the results of analyses for both *H. erectus s. l.* and *H. erectus erectus* is made apparent when it is removed from each taxon (see Table 2—taxa *H. erectus s. l.* and *H. e. erectus*: No Sangiran 6). After the removal of Sangiran 6 from *H. erectus s. l.*, the maximum ratios derived for analyses of GM and both height variables fall below those of Dmanisi (Table 2, Fig. 2). Similarly, after removal of Sangiran 6 from *H. e. erectus*, maximum ratios of all analyses, except corpus breadth at M₁, fall below Dmanisi.

In summary, results of comparison to extant hominoid taxa do not support the null hypothesis of moderate levels of size dimorphism at Dmanisi, but rather suggest that D2600 and D211 differ in size to a degree rarely seen in any extant hominoid taxon. Depending on the taxonomic classification applied to the hominin fossil record, the degree of dimorphism at Dmanisi can be seen as moderately to highly unlikely with respect to these taxa. It is also clear that it is the difference in mandibular corpus height that is unique between the Dmanisi mandibles and which is driving the results of our analyses.

Results: shape variation

Comparison with extant hominoid taxa

The analysis of size dimorphism between the Dmanisi mandibles highlights the fact that D2600 and D211 differ

Table 2
Comparison of maximum ratios between Dmanisi and extinct hominin taxa for different corpus size variables¹

TAXON	GM		SYMPHYSIS HEIGHT		SYMPHYSIS BREADTH		CORPUS AT M ₁ HEIGHT		CORPUS AT M ₁ BREADTH	
	Max (n)	<i>p</i>	Max (n)	<i>p</i>	Max (n)	<i>p</i>	Max (n)	<i>p</i>	Max (n)	<i>p</i>
Dmanisi (D211 and D2600)	1.39 (2)		1.59 (2)		1.25 (2)		1.66 (2)		1.14 (2)	
Short Taxonomy										
<i>A. anamensis</i>	1.21 (3)		1.00 (3)		1.31 (3)		1.46 (3)		1.18 (3)	
<i>A. afarensis</i>	1.38 (9)		1.39 (9)		1.47 (15)	ns	1.49 (23)	**	1.56 (23)	ns
<i>P. boisei</i>	1.26 (9)		1.43 (13)		1.46 (13)		1.67 (28)	**	2.06 (28)	ns
<i>H. habilis sensu lato</i>	1.49 (6)		1.60 (7)		1.39 (6)		1.49 (11)		1.59 (11)	
<i>H. erectus sensu lato</i>	1.72 (17)	0.095	1.62 (17)	*	2.01 (19)	ns	1.88 (27)	*	1.84 (27)	ns
<i>H. erectus s. l.</i> (No Sangiran 6) ²	1.33 (16)	*	1.45 (16)	**	1.69 (18)	ns	1.56 (26)	**	1.45 (26)	ns
Long Taxonomy ³										
<i>A. anamensis</i>	1.21 (3)		1.00 (3)		1.31 (3)		1.46 (3)		1.18 (3)	
<i>A. afarensis</i>	1.38 (9)		1.39 (9)		1.47 (15)	ns	1.49 (23)	**	1.56 (23)	ns
<i>P. boisei</i>	1.26 (9)		1.43 (13)		1.46 (13)		1.67 (28)	**	2.06 (28)	ns
<i>H. habilis sensu stricto</i>	1.13 (2)		1.16 (2)		1.06 (2)		1.21 (5)		1.24 (5)	
<i>H. rudolfensis</i>	1.21 (4)		1.25 (5)		1.23 (4)		1.27 (6)		1.35 (6)	
African <i>H. erectus/ergaster</i>	1.09 (5)		1.23 (5)		1.21 (6)		1.33 (9)		1.29 (9)	
<i>H. e. erectus</i> (Sangiran)	1.53 (5)		1.62 (5)		1.58 (5)		1.63 (6)		1.75 (6)	
<i>H. e. erectus</i> (No Sangiran 6) ²	1.19 (4)		1.45 (4)		1.12 (4)		1.31 (5)		1.32 (5)	
<i>H. e. pekinensis</i> (China)	1.14 (4)		1.25 (4)		1.10 (5)		1.33 (7)		1.36 (7)	
<i>H. e. mauritanicus</i> (Ternifine)	1.12 (3)		1.14 (3)		1.06 (3)		1.45 (5)		1.12 (5)	

¹ Sample sizes are given in parentheses after each ratio. Bold values indicate that the maximum ratio of the Dmanisi mandibles exceeds that found in any pairwise comparison within a comparative taxon. P-values are calculated for samples of 15 or more specimens: * = $p < 0.05$; ** = $p < 0.01$; ns = $p > 0.10$.

² Sangiran 6, under both short and long taxonomies, has a marked influence on the maximum ratio derived for each analysis (see Results).

³ Please note that values for *A. anamensis*, *A. afarensis*, and *P. boisei* are the same under both taxonomic classifications.

substantially in the relative height of their mandibular corpora and this can be considered as a difference in shape (i.e., the large difference in height of D2600 compared to D211 is not matched by a similar difference in breadth). The results of the analysis of shape variation based on AED distributions are presented in the right-hand column of Table 1. The degree of shape variation present at Dmanisi is significantly unlikely to be found in any of our extant hominoid taxa whether they are grouped as species (Fig. 3) or subspecies (with the notable exception of *Homo sapiens*). The results suggest that allometric trends in shape change are shared among extant hominoids and are not consistent with the pattern at Dmanisi. For example, shape differences between sexually dimorphic male and female orangutans and gorillas are not as extreme as that found between D2600 and D211.

The various components of shape difference between D2600 and D211 may be considered graphically in relation to the extant taxa and *H. erectus s. l.* (Fig. 4). Although D2600 is substantially larger than all modern human specimens and all *H. erectus s. l.* specimens except Sangiran 6 in this study (D2600 GM = 30.7, GM range for modern humans = 17.2 to 25.3, Sangiran 6 GM = 35.6, range of remaining *H. erectus s. l.* = 20.7 to 27.6), the shape of D2600 as measured by the four variables used in this study is most consistent with the shape of modern humans; D2600 also falls on the margins or outside the range of shape variation in *H. erectus s. l.* (Fig. 4). In contrast, the smaller D211 mandible (GM = 22.0) plots on the fringe or well outside the range of modern human shape variation in Figure 4, and is most similar in shape to African *H. erectus/ergaster*.

The most striking shape difference between D2600 and D211 is in relative corpus breadth at M₁: D2600 falls below the

H. erectus s. l. range (i.e., to the left), while D211 plots above (i.e., to the right). Thus, the disjunct in size dimorphism at Dmanisi (i.e., high dimorphism for overall size and heights, low dimorphism for breadths) is not primarily because relative heights are extremely different between D2600 and D211 (which would result in unusually high height size dimorphism), but rather because of the extreme difference in relative corpus breadth at M₁ (resulting in unusually low breadth size dimorphism) in conjunction with a more modest difference in relative heights. In fact, if D211 and D2600 were more similar in relative corpus breadth at M₁, absolute corpus breadth at M₁ would be more different between the two specimens and thus overall size (GM) would be more different, increasing the amount of size dimorphism present at Dmanisi above what is observed here.

Silverman and colleagues (2001) noted that taphonomic processes of erosion and expansion of fossil mandibles inflated the degree of variation present in *P. boisei*, particularly in breadth dimensions of the mandibular corpus. The Dmanisi mandibles do present breakage and missing fragments of their mandibular corpora; however, erosion and expansion (due to matrix infilling of cracks) do not appear to have substantially altered the breadth dimensions of these specimens. D211 and D2600 may represent individuals who differed significantly in age, and therefore in vivo changes to mandibular corpus dimensions remain a confounding factor in comparing these two mandibles (although the extant hominoid samples likely sample young adult and older adult specimens and should, therefore, account for potential age-related variation). While we believe our results to be robust, the potential significance of this source of variation should be explored in the Dmanisi sample.

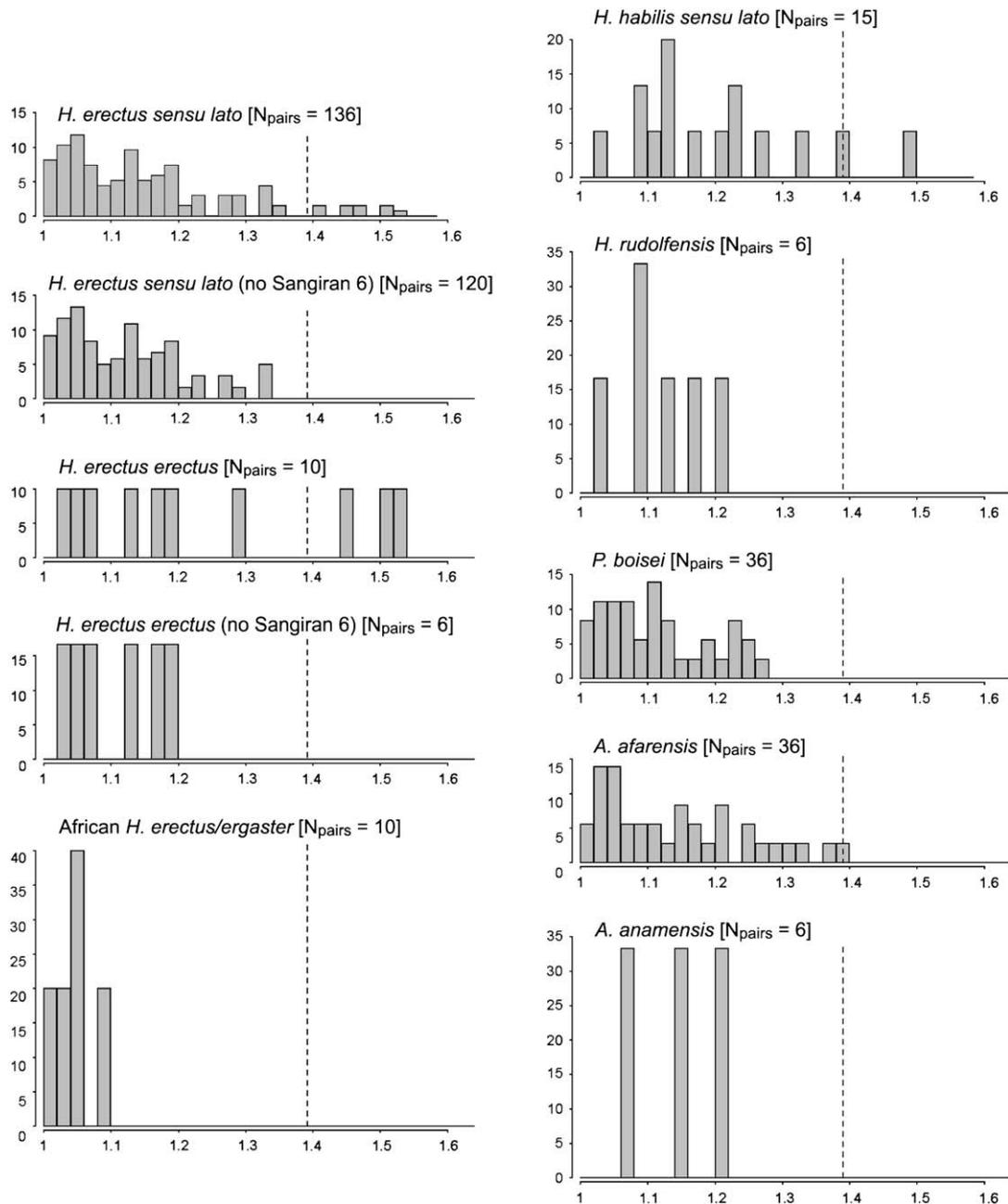


Fig. 2. Distributions of pairwise ratios in a comparison of overall mandible size variation for fossil hominin species. Numbers along vertical axis indicate percent of cases; dashed vertical line indicates the Dmanisi ratio between mandibles D2600 and D211. It is clear that the Dmanisi ratio of overall mandible size is rarely seen in fossil hominin taxa. The exceptions within *H. erectus s. l.* and *H. erectus erectus* are those comparing Sangiran 6 with smaller mandibles, and within *H. habilis s. l.* are those comparing large *H. rudolfensis* mandibles with small *H. habilis s. s.* mandibles. See text for discussion and Table 2 for summary statistics.

To summarize our analyses of size and shape variation, the pattern of variation for the Dmanisi hominins does not resemble that of any living species. Compared to modern humans they fall within the top end of shape variation but exhibit significantly more size variation. Compared to extant apes they have significantly more shape variation and significantly more size variation in corpus heights and overall mandible size (with the exception of *P. pygmaeus* for overall mandible size). When compared to fossil hominins they also appear to be aberrantly dimorphic in size, although taphonomic biases and small sample sizes suggest caution in interpreting the

significance of these latter comparisons. Additionally, the shape analysis suggests that differences in shape between D2600 and D211 may actually serve to reduce overall size dimorphism between the two specimens rather than increase it.

Discussion

One of the features characteristic of species of the genus *Homo* is lower levels of BSSD compared to *Australopithecus* species and some *Paranthropus* species attributed primarily to an increase in female body size (Wood and Collard, 1999;

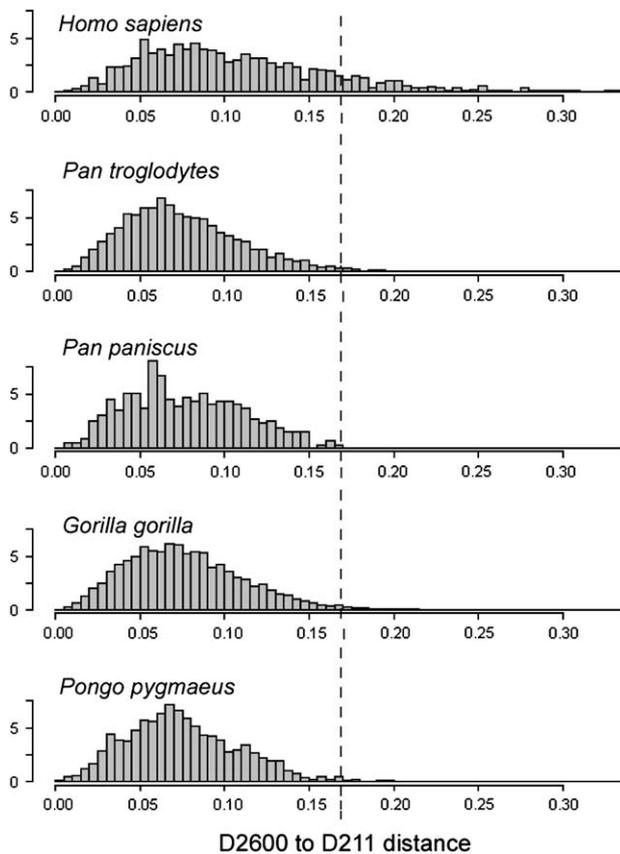


Fig. 3. Distribution of pairwise average Euclidean distances using four shape variables in a comparison of shape variation for each extant hominoid species. Numbers along vertical axis indicate percent of cases; dashed vertical line indicates the Dmanisi ratio between mandibles D2600 and D211. See text for discussion and Table 1 for summary statistics.

McHenry and Coffing, 2000; Skinner and Wood, nd; but see Susman et al., 2001 for a contrasting view of SD in South African *Homo*). Lockwood and colleagues (2000) examined variation in mandibular corpus size of *A. afarensis*. They concluded that *A. afarensis* possessed gorilla-like levels of sexual dimorphism and that there was a temporal trend towards increasing mandible size in *A. afarensis* which results in this taxon possessing overall levels of variation which can exceed *G. gorilla gorilla*. They also found a positive but non-significant trend for increasing mandibular corpus size over time in *P. boisei* and some evidence for levels of variation exceeding *G. gorilla gorilla* samples (using CV as a measure of variation yielded significant results but using Fligner-Killeen, which they describe as a more conservative test, did not suggest greater levels of dimorphism in *P. boisei*.). Examining craniofacial variation, Lockwood (1999) found that *A. africanus*, *H. habilis sensu lato* (i.e., specimens attributed by some to *H. rudolfensis* and *H. habilis sensu stricto*), and *P. boisei* all exhibited variation greater than that of modern humans and chimpanzees (to varying degrees) but less than that of modern gorillas (including specimens of both *G. g. gorilla* and *G. g. berengei*). Silverman and colleagues (2001), in their analysis of mandibular size variation, concluded that *P. boisei sensu stricto* possessed gorilla-like sexual dimorphism. Thus, if variation at Dmanisi is intraspecific, then our results support

the primitive retention of a relatively high BSSD in this Pleistocene *Homo* taxon. Indeed, it is noteworthy that the GM of D211 (22.0), which would be considered a female under a single species hypothesis, is the fifth smallest of all fossil hominin specimens included in our analysis.

We interpret the results of this comparative analysis of mandibular corpus size and shape as supporting two alternative hypotheses. First, the Dmanisi hominin hypodigm may sample a single species with unexpectedly pronounced size and shape variation due to either sexual dimorphism and/or temporal variation. Alternatively, the Dmanisi hypodigm may sample two hominin species, one smaller and one larger. Given these competing hypotheses, we examine more closely the geological context and provenience of the Dmanisi fossils to address their contemporaneity and the potential influence of temporal variation, as well as the qualitative morphological descriptions of D2600 and D211 mandibles.

Geological context

The Dmanisi hominins and fauna have been dated to ~1.75 Ma, but perhaps as young as ~1 Ma, based on geochronology (geomagnetic polarity and radioisotopes) and biogeographic indicators (macro- and microfauna) (Gabunia et al., 2000b, 2001, 2002). Importantly, the hominin-bearing sediments appear to have been deposited over a very short time interval, perhaps as little as 10–100 ka (Gabunia et al., 2001). Given the apparent rapid deposition of sediments and the fact that this level of intraspecific size variation is unmatched in most other hominin samples (which in all cases almost surely include significantly greater temporal and geographic ranges), temporal variation is not likely to have been a significant influence on size variation at Dmanisi.

The D2600 mandible is not contemporaneous (within a paleontological timeframe) with all of the other published hominin fossils in the same way that the latter are contemporaneous with each other. This stems from the fact that D2600 was recovered from the site's lowest stratigraphic layer (A1) which, along with the immediately underlying Masavera Basalt, expresses normal magnetic polarity, while the remaining hominin fossils were recovered from reversed polarity infills (deposited prior to the deposition of layer B1) present in the next overlying stratigraphic layer (A2) (Gabunia et al., 2001, Fig. 3). With regard to horizontal associations between the hominin remains, D2600 was discovered within ~2 square meters of the associated sub-adult individual (D2700/D2735) and the recently published edentulous male (D3444/D3900) (Vekua et al., 2002; Lordkipanidze et al., 2005). The other two crania (D2280 and D2282) and the other mandible (D211) were recovered ~15 meters away. Carnivore activity has been posited in the accumulation of hominin fossils (although diagnostic carnivore modification is not present) within the infills (Gabunia et al., 2000b; Gabunia et al., 2001). This might suggest different mechanisms by which D2600 and the other hominin fossils entered the site and highlights the importance of further analyses to determine the association between D2600 and the other Dmanisi fossils.

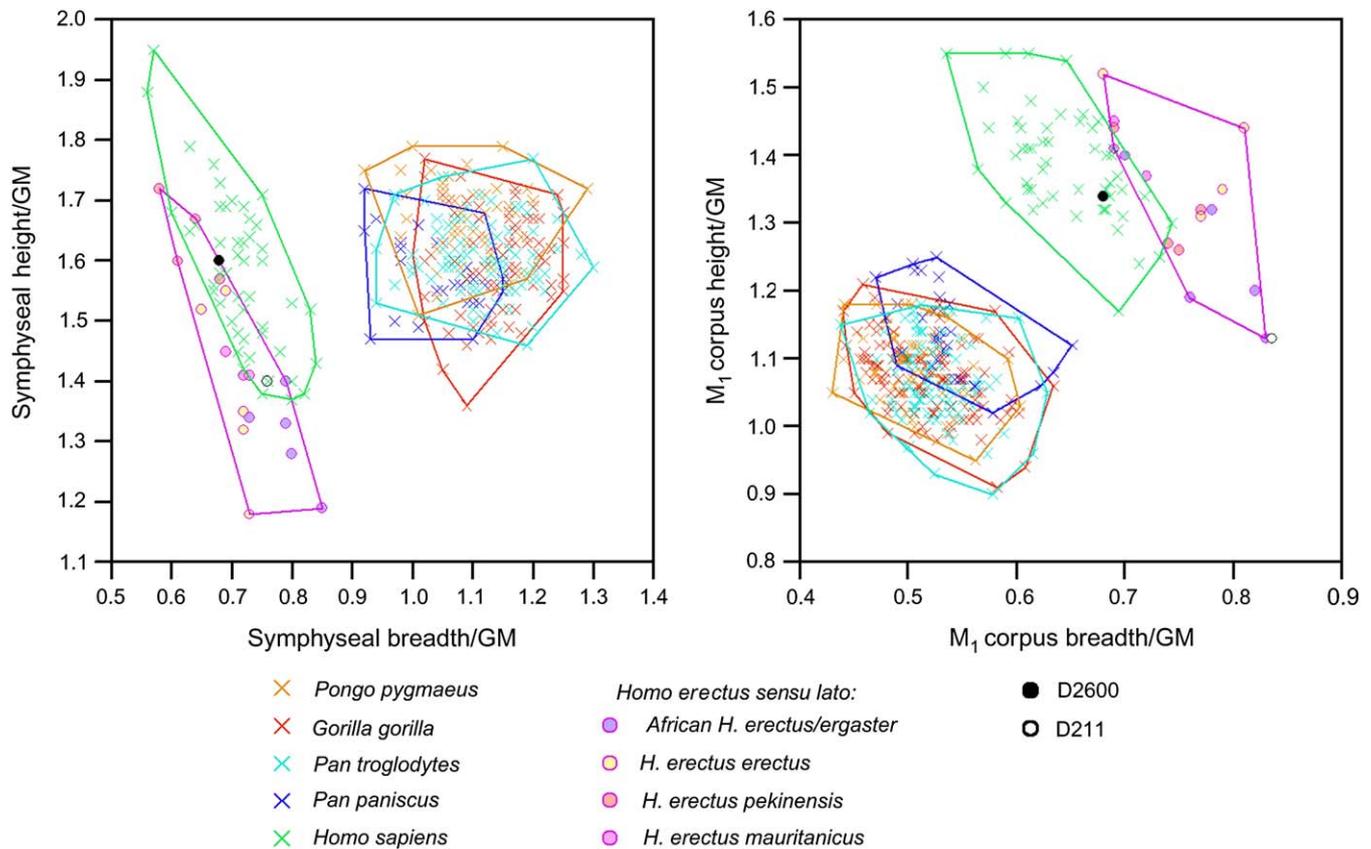


Fig. 4. Bivariate plots of shape variables in the symphysis and corpus at M_1 for extant hominoids, *H. erectus s. l.*, and Dmanisi hominins. Lines enclose all specimens for a particular species. *Homo* specimens exhibit a markedly different mandibular shape pattern than the great apes as shown by their separation from the ape cluster in both plots. For corpus shape at the mandibular symphysis, the Dmanisi fossil values fall within both the modern human and *H. erectus s. l.* ranges (left plot). This pattern differs for corpus shape at M_1 with the relative corpus breadth of D2600 falling within the modern human range and below the *H. erectus s. l.* range, while the relative corpus breadth of D211 is larger than all measured *H. erectus*, modern humans, and extant great apes.

Qualitative morphological evidence

Gabunia and colleagues (2002) note that D2600 and D211 share a number of morphological characters including a subvertical symphysis, a pronounced inferior marginal torus, a deep inter-toral sulcus, a mental foramen positioned at P_3 – P_4 , a U-shaped dental arcade, and a deep extramolar sulcus. The two mandibles are also described as differing in a number of morphological characters. The corpus of D2600 is relatively taller and narrower than that of D211, the shelving of the posterior face of the symphysis extends to P_4 , the canine juga are more pronounced, and the P_3 of D2600 is double-rooted while that of D211 is single-rooted. Previous studies have noted variation in P_3 root morphology in specimens of early *Homo* and *Pan* (Wood et al., 1988; Wood, 1993; Antón, 2003), and thus the variation present at Dmanisi may be intraspecific. Strong correlations between mandibular premolar absolute size and the presence of multiple roots have been found in modern humans (Shields, 2005) and may explain the variation present between D2600 and D211. The molars are absolutely larger and the molars of D2600 increase in size from M_1 – M_3 , whereas in D211 M_1 is the largest (Gabunia et al., 2002; Vekua et al., 2002). Whether these features are more consistent with sexual dimorphism or interspecific variation and how they compare to variation in other regional samples

of *Homo erectus s. l.* (e.g., Rosas and Bermudez de Castro, 1998) should be the focus of future analyses.

Estimates of dimorphism based on other skeletal evidence

To date, the large mandible is the only aberrantly large skeletal element published from the Dmanisi hypodigm. For example, the four crania, while exhibiting differences in cranial capacity, size, and shape can be accommodated within a single species of low-to-moderate sexual dimorphism (Vekua et al., 2002; Macaluso et al., 2004; Lee, 2005; Lordkipanidze et al., 2005). There is no current indication that the Dmanisi postcranial remains provide evidence for body size sexual dimorphism that exceeds that of other extant and extinct hominids.

Conclusion

In this paper, we presented the results of an analysis comparing mandibular size and shape dimorphism at Dmanisi (represented by two mandibles, D2600 and D211, and using four linear measurements of mandibular corpus size) to that present in pairwise comparisons of dimorphism within extant hominoid species and subspecies and within extinct hominin taxa. The results indicate that mandibular size dimorphism at

Dmanisi is most pronounced in the relative height of the mandibular corpus at both the symphysis and at the level of M₁. This degree of dimorphism in height, and its contribution to dimorphism in overall mandible size, is unlikely to be found in species and/or subspecies of *Pongo* and significantly unlikely to be found in species and/or subspecies of *Gorilla*, *Pan*, and *Homo sapiens*. Comparison to extinct fossil hominin taxa also indicates that the degree of size dimorphism at Dmanisi is rare and certainly exceeds that expected for a population belonging to the genus *Homo* (although this result is influenced by the taxonomic hypothesis applied to the hominin fossil record). The Dmanisi hominins also exhibit an unusually high level of shape dimorphism that is due in large part to the extremely high relative corpus breadth at M₁ in D211 as compared to that seen in living hominoids, modern humans, and D2600.

These results support two alternative hypotheses. First, the degree of sexual dimorphism in this Early Pleistocene *Homo* taxon exceeds expectations (Antón, 2003), thus highlighting the need to reconsider conclusions about its inclusion in, and/or the definition of, the genus *Homo*. Dmanisi may present a *Homo* taxon predating the increase in female body size that characterizes the low levels of BSSD present in other *Homo* taxa. The second hypothesis is that more than one taxon is present at Dmanisi. Given that D2600 is from a different stratigraphic layer than D211, possesses morphological features not seen in the other Dmanisi mandibles (e.g., different molar size gradient), and that the rest of the Dmanisi fossils do not provide strong evidence of a highly sexually dimorphic species,

the presence of a second hominin species, represented by D2600, should be considered (Rightmire et al., 2006). Applying similar methods to the postcranial elements would help to assess the level of variation and its meaning in this fossil sample.

Acknowledgements

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Appendix 1. Table of fossil hominin specimens used for comparative analysis grouped under both a short and long taxonomy

Specimen	Short Taxonomy	Long Taxonomy	Symp. Height	Symp. Breadth	Corp. @M1 Height	Corp. @M1 Breadth	GM	Detailed location of measured data	Reference
KNM-ER 31713	<i>A. anamensis</i>	<i>A. anamensis</i>	27	29	29	19.7	25.9	Midline and P4/M1	Ward et al., 2001
KNM-KP 29281 (AVG)	<i>A. anamensis</i>	<i>A. anamensis</i>	27	32.2	34	19.1	27.4	Midline and P4/M1	Ward et al., 2001
KNM-KP 29287	<i>A. anamensis</i>	<i>A. anamensis</i>	27	38	42.3	22.5	31.4	Midline and P4/M1	Ward et al., 2001
A.L. 145-35	<i>A. afarensis</i>	<i>A. afarensis</i>			27.8	21.1		M1	Kimbel et al., 2004
A.L. 198-1	<i>A. afarensis</i>	<i>A. afarensis</i>			31.1	15.8		M1	Kimbel et al., 2004
A.L. 207-13	<i>A. afarensis</i>	<i>A. afarensis</i>			28.4	18.1		M1	Kimbel et al., 2004
A.L. 228-2	<i>A. afarensis</i>	<i>A. afarensis</i>			31.8	16.3		M1	Kimbel et al., 2004
A.L. 266-1	<i>A. afarensis</i>	<i>A. afarensis</i>		21.1	31.5	21.7		Midline and M1	Kimbel et al., 2004
A.L. 277-1	<i>A. afarensis</i>	<i>A. afarensis</i>			37	17.9		M1	Kimbel et al., 2004
A.L. 288-1i	<i>A. afarensis</i>	<i>A. afarensis</i>	32.5	17.3	30	17.1	23.2	Midline and M1	Kimbel et al., 2004
A.L. 315-22	<i>A. afarensis</i>	<i>A. afarensis</i>		17.8	29.7	19.2		M1	Kimbel et al., 2004
A.L. 330-5	<i>A. afarensis</i>	<i>A. afarensis</i>		18.2	31.1	20.9		M1	Kimbel et al., 2004
A.L. 333w-12	<i>A. afarensis</i>	<i>A. afarensis</i>		18	30.6	17.4		I1/I2 and M1	Kimbel et al., 2004
A.L. 333w-1a + b	<i>A. afarensis</i>	<i>A. afarensis</i>			35.3	19.4		M1	Kimbel et al., 2004
A.L. 333w-32 + 60	<i>A. afarensis</i>	<i>A. afarensis</i>	45.2	21.9	38.4	23.6	30.8	Midline and M1	Kimbel et al., 2004
A.L. 400-1a	<i>A. afarensis</i>	<i>A. afarensis</i>	39.4	19.2	35.4	18.7	26.6	Midline and M1	Kimbel et al., 2004
A.L. 417-1a	<i>A. afarensis</i>	<i>A. afarensis</i>	38.2	17.7	36	18	25.7	Midline and M1	Kimbel et al., 2004
A.L. 433-1a, b	<i>A. afarensis</i>	<i>A. afarensis</i>			35	20.2		M1	Kimbel et al., 2004
A.L. 437-1	<i>A. afarensis</i>	<i>A. afarensis</i>	45.2	22.2	40	20	29.9	Midline and M1	Kimbel et al., 2004
A.L. 437-2	<i>A. afarensis</i>	<i>A. afarensis</i>	45	21.8	38.5	22.2	30.3	Midline and M1	Kimbel et al., 2004
A.L. 438-1(g)	<i>A. afarensis</i>	<i>A. afarensis</i>	39.6	25.5	41.3	24.7	31.9	Midline and M1	Kimbel et al., 2004
A.L. 444-2	<i>A. afarensis</i>	<i>A. afarensis</i>	45	24	41.2	23	31.8	I2 and M1	Kimbel et al., 2004
A.L. 620-1	<i>A. afarensis</i>	<i>A. afarensis</i>	43.2	22.9	36.2	20.5	29.3	I1/I2 and M1	Kimbel et al., 2004
LH-4	<i>A. afarensis</i>	<i>A. afarensis</i>		19.1	31.4	19.4		Midline and M1	Kimbel et al., 2004 (White, 1977)

(continued on next page)

Appendix 1 (continued)

Specimen	Short Taxonomy	Long Taxonomy	Symp. Height	Symp. Breadth	Corp. @M1 Height	Corp. @M1 Breadth	GM	Detailed location of measured data	Reference
MAK VP 1/12 (AVG)	<i>A. afarensis</i>	<i>A. afarensis</i>		21.5	30.5	18.7		I1/I2 and M1	Kimbel et al., 2004 (White et al., 2000)
DIK-2-1	<i>A. afarensis</i>	<i>A. afarensis</i>			38.5	21		M1	Alemseged et al., 2005, pers. Comm.
KGA-10-1 (AVG)	<i>P. boisei</i>	<i>P. boisei</i>			41.5	29		M1	Suwa et al., 1997
KNM-ER 1469	<i>P. boisei</i>	<i>P. boisei</i>		27	46	37		Midline and M1	Wood, 1991a
KNM-ER 15930	<i>P. boisei</i>	<i>P. boisei</i>			34.2	25.2		M1	Leakey and Walker, 1988
KNM-ER 1803	<i>P. boisei</i>	<i>P. boisei</i>			42	25		M1	Wood, 1991a
KNM-ER 3729	<i>P. boisei</i>	<i>P. boisei</i>			38	28		M1	Wood, 1991a
KNM-ER 3731	<i>P. boisei</i>	<i>P. boisei</i>			30	18		M1	Wood, 1991a
KNM-ER 3954	<i>P. boisei</i>	<i>P. boisei</i>			34	26		M1	Wood, 1991a
KNM-ER 403	<i>P. boisei</i>	<i>P. boisei</i>			47	30.5		M1	Wood, 1991a
KNM-ER 5877	<i>P. boisei</i>	<i>P. boisei</i>			44	29		M1	Wood, 1991a
KNM-ER 725	<i>P. boisei</i>	<i>P. boisei</i>		30	41	29.5		Midline and M1	Wood, 1991a
KNM-ER 726	<i>P. boisei</i>	<i>P. boisei</i>			46	30		M1	Wood, 1991a
KNM-ER 727	<i>P. boisei</i>	<i>P. boisei</i>			35	24		M1	Wood, 1991a
KNM-ER 728	<i>P. boisei</i>	<i>P. boisei</i>			37	26		M1	Wood, 1991a
KNM-ER 733	<i>P. boisei</i>	<i>P. boisei</i>			39.5	27		M1	Wood, 1991a
KNM-ER 805A	<i>P. boisei</i>	<i>P. boisei</i>			41	29		M1	Wood, 1991a
KNM-ER 810A	<i>P. boisei</i>	<i>P. boisei</i>		26	40	26		Midline and M1	Wood, 1991a
KNM-ER 818	<i>P. boisei</i>	<i>P. boisei</i>	57	30	50	36	41.9	Midline and M1	Wood, 1991a
OMO L7A-125 (AVG)	<i>P. boisei</i>	<i>P. boisei</i>	57	35	48.5	34.5	42.7	Midline and M1	Wood, 1991a
KNM-ER 3230 (AVG)	<i>P. boisei</i>	<i>P. boisei</i>	52	25	42	29	35.5	Midline and M1	Wood, 1991a
KNM-ER 1468	<i>P. boisei</i>	<i>P. boisei</i>	50	26	48	36	38.7	Midline and M1	Wood, 1991a
KNM-ER 1806 (AVG)	<i>P. boisei</i>	<i>P. boisei</i>	50	27	44.5	28.3	36.1	Midline and M1	Wood, 1991a
KNM-ER 3229	<i>P. boisei</i>	<i>P. boisei</i>	50		39	28		Midline and M1	Wood, 1991a
KNM-ER 5429	<i>P. boisei</i>	<i>P. boisei</i>	50		44	30		Midline and M1	Wood, 1991a
KNM-ER 729 (AVG)	<i>P. boisei</i>	<i>P. boisei</i>	50	32.5	44	28.3	37.7	Midline and M1	Wood, 1991a
Peninj 1 (AVG)	<i>P. boisei</i>	<i>P. boisei</i>	50	24	39.7	29	34.3	Midline and M1	Wood, 1991a
OMO L74A-21	<i>P. boisei</i>	<i>P. boisei</i>	47	26	43.5	25	34.0	Midline and M1	Wood, 1991a
KNM-ER 3889	<i>P. boisei</i>	<i>P. boisei</i>	45	28				Midline	Wood, 1991a
KNM-ER 801A	<i>P. boisei</i>	<i>P. boisei</i>	45		43.5	29.5		Midline and M1	Wood, 1991a
KNM-ER 16841	<i>P. boisei</i>	<i>P. boisei</i>	40	29.5	42.5	27	34.1	Midline and M1	Wood, 1991a (Leakey and Walker, 1988)
KNM-ER 819	<i>H. habilis s. l.</i>	<i>H. rudolfensis</i>			38	27		M1	Wood, 1991a
KNM-ER 1482 (AVG)	<i>H. habilis s. l.</i>	<i>H. rudolfensis</i>	36	22	31	20	26.5	Midline and M1	Wood, 1991a
KNM-ER 1483	<i>H. habilis s. l.</i>	<i>H. rudolfensis</i>	40	25	39.5	26.5	32.0	Midline and M1	Wood, 1991a
KNM-ER 1801	<i>H. habilis s. l.</i>	<i>H. rudolfensis</i>	32		34	20		Midline and M1	Wood, 1991a
KNM-ER 1802 (AVG)	<i>H. habilis s. l.</i>	<i>H. rudolfensis</i>	36	24.5	38	23	29.6	Midline and M1	Wood, 1991a
UR 501 (AVG)	<i>H. habilis s. l.</i>	<i>H. rudolfensis</i>	36.1	20.3	34.6	21.8	27.3	Midline and M1	Bromage et al., 1995
KNM-ER 1501	<i>H. habilis s. l.</i>	<i>H. habilis s. s.</i>			29	17		M1	Wood, 1991a
KNM-ER 1502	<i>H. habilis s. l.</i>	<i>H. habilis s. s.</i>			27	17		M1	Wood, 1991a
KNM-ER 1805	<i>H. habilis s. l.</i>	<i>H. habilis s. s.</i>			30	21		M1	Wood, 1991a
OH 13	<i>H. habilis s. l.</i>	<i>H. habilis s. s.</i>	25	18	26.5	18	21.5	Midline and M1	Wood, 1991a
OH 37	<i>H. habilis s. l.</i>	<i>H. habilis s. s.</i>	29	19	32	19.5	24.2	Midline and M1	Wood, 1991a
D2600	<i>H. georgicus</i>	<i>H. georgicus</i>	49.0	21.0	41.0	21.0	30.7	Midline and M1	Rightmire et al., 2006
D211	<i>H. georgicus</i>	<i>H. georgicus</i>	30.8	16.8	24.7	18.4	22.0	Midline and M1	Gabunia and Vekua, 1995
KNM-ER 730	<i>H. erectus s. l.</i>	African <i>H. erectus/ergaster</i>	32.7	17.7	32.3	19	24.4	Midline and M1	Day and Leakey, 1973
KNM-ER 992 (AVG)	<i>H. erectus s. l.</i>	African <i>H. erectus/ergaster</i>	37	21	31.5	20	26.5	Midline and M1	Wood, 1991a
KNM-BK 67 (AVG)	<i>H. erectus s. l.</i>	African <i>H. erectus/ergaster</i>	31	19.5	34	17	24.3	Midline and M1	Wood, 1991a
KNM-ER 731	<i>H. erectus s. l.</i>	African <i>H. erectus/ergaster</i>		20	27	19		Midline and M1	Wood, 1991a
KNM-BK 8518 (AVG)	<i>H. erectus s. l.</i>	African <i>H. erectus/ergaster</i>	30	21.5	30.2	20.7	25.2	Midline and M1	Wood, 1991a

Appendix 1 (continued)

Specimen	Short Taxonomy	Long Taxonomy	Symp. Height	Symp. Breadth	Corp. @M1 Height	Corp. @M1 Breadth	GM	Detailed location of measured data	Reference
OH 22	<i>H. erectus s. l.</i>	African <i>H. erectus/ergaster</i>	33.5	20	28.5	21	25.2	Midline and M1	Wood, 1991a
OH 23	<i>H. erectus s. l.</i>	African <i>H. erectus/ergaster</i>			33	21		M1	Wood, 1991a
OH 51	<i>H. erectus s. l.</i>	African <i>H. erectus/ergaster</i>			36	22		M1	Rightmire, 1993
SK 15	<i>H. erectus s. l.</i>	African <i>H. erectus/ergaster</i>			27.5	18.5		M1	Rightmire, 1993
Sangiran 1b (B/1937)	<i>H. erectus s. l.</i>	<i>H. erectus erectus</i>	32	17	36	16	23.7	Midline and M1	Wood, 1991a (von Koenigswald, 1937)
Sangiran 5 (<i>Pith. dubius</i>)	<i>H. erectus s. l.</i>	<i>H. erectus erectus</i>			38.5	19.3		M1	Weidenreich, 1945 (Table 6)
Sangiran 6 (Mega. A)	<i>H. erectus s. l.</i>	<i>H. erectus erectus</i>	47	25.5	48	28	35.6	Midline and MF(P4/M1)	Weidenreich, 1945 (Table 6)
Sangiran 8 (Mega. B)	<i>H. erectus s. l.</i>	<i>H. erectus erectus</i>	29	18	35.5	20	24.7	Midline and M1/M2	Wood, 1991a
Sangiran 9 (C)	<i>H. erectus s. l.</i>	<i>H. erectus erectus</i>	42	18	36	21.2	27.6	Midline and M1	Kaifu et al., 2005
Sangiran 22 (F) (AVG)	<i>H. erectus s. l.</i>	<i>H. erectus erectus</i>	36	16.1	29.4	17.1	23.2	Midline and M1	Kaifu et al., 2005
Zhoukoudian A II	<i>H. erectus s. l.</i>	<i>H. erectus pekinensis</i>			13.5	25.6	15.2	MF(P4/M1)	Weidenreich, 1945 (Table 6)
Zhoukoudian G I	<i>H. erectus s. l.</i>	<i>H. erectus pekinensis</i>	40.7	13.7	34	16.4	23.6	Midline and MF(P3/P4)	Weidenreich, 1945 (Table 6)
Zhoukoudian H I	<i>H. erectus s. l.</i>	<i>H. erectus pekinensis</i>	32.5	14	26	15.4	20.7	Midline and MF(P4/M1)	Weidenreich, 1945 (Table 6)
Zhoukoudian K1	<i>H. erectus s. l.</i>	<i>H. erectus pekinensis</i>	33.1	12.7	27.4	16	20.7	MF(P3/P4)	Weidenreich, 1945 (Table 6)
Lantian (PA 102)	<i>H. erectus s. l.</i>	<i>H. erectus pekinensis</i>	35	13.4	26.5	15.4	20.9	Midline and MF(P3/P4?)	Woo, 1964: 11
ZKD 1959.1 (PA 86)	<i>H. erectus s. l.</i>	<i>H. erectus pekinensis</i>			26.7	16.6		MF(P3/P4)	Wu and Poirier, 1995
Hexian (PA 831)	<i>H. erectus s. l.</i>	<i>H. erectus pekinensis</i>			32	20.7		M1/M2	Wu and Dong, 1982
Sidi Abderrahman	<i>H. erectus s. l.</i>	<i>H. erectus mauritanicus</i>			35	17.3		M1	Ennouchi, 1970
Ternifine 1	<i>H. erectus s. l.</i>	<i>H. erectus mauritanicus</i>	37	19	36	19	26.3	Midline and P4/M1	Arambourg, 1963
Ternifine 2	<i>H. erectus s. l.</i>	<i>H. erectus mauritanicus</i>	35	18	35	17	24.7	Midline and P4/M1	Arambourg, 1963
Ternifine 3	<i>H. erectus s. l.</i>	<i>H. erectus mauritanicus</i>	40	19	40	19	27.6	Midline and P4/M1	Arambourg, 1963
Thomas Quarry I	<i>H. erectus s. l.</i>	<i>H. erectus mauritanicus</i>			27.5	17		M1	Rightmire, 1993

Notes: Measurement definitions (from Wood, 1991a): *symphyseal height*—minimum distance between the base of the symphysis and infradentale; *symphyseal breadth*—maximum breadth, at right angles to symphyseal height; *corpus height at M1*—minimum distance between the most inferior point on the base and the lingual alveolar margin at the midpoint of M1; *corpus breadth at M1*—maximum breadth at right angles to corpus height at M1. All measurements taken from the literature and not all sources are primary. Measurements in italics are estimated due to poor preservation. (AVG) indicates that a mean value was calculated when right and left sides were present.

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