A Quantitative Assessment of Mandibular Variation in the Dmanisi Hominins

ADAM P. VAN ARSDALE
Department of Anthropology, 106 Central Street, Wellesley College, Wellesley, MA 02482, USA; avanarsd@wellesley.edu

DAVID LORDKIPANIDZE
Georgia National Museum, 3 Rustaveli Avenue, 0105 Tbilisi, GEORGIA; dLordkipanidze@museum.ge

ABSTRACT

The Lower Pleistocene locality of Dmanisi, Georgia, positioned at an important temporal and geographic junction in human evolution, has produced an abundant hominin fossil sample. The combination of derived and primitive characteristics within these hominins has provoked debate as to the evolutionary significance of Dmanisi for the early evolution of the genus *Homo* and the earliest dispersals of hominins outside Africa. Included within the Dmanisi hominin sample are four mandibular specimens, including one of the smallest Lower Pleistocene mandibles assigned to *Homo*, one of the largest assigned to *Homo*, and the earliest known edentulous hominin mandible. The range of variation displayed by this group of mandibles has been central to arguments regarding the taxonomic assessment of the Dmanisi remains. This paper tests the null hypothesis that variation in the Dmanisi mandibular sample is the result of sampling intraspecific variation, particularly age-related growth and skeletal size dimorphism, by using a quantitative metric approach. Utilizing both individual and nested resampling approaches, variation within the Dmanisi sample is compared to the patterns of variation seen in contemporary *Homo sapiens*, *Pan troglodytes*, and *Gorilla gorilla*. When individual trait comparisons are made, the results of these analyses suggest that in some metric characters the Dmanisi variation is greater than expected based on intraspecific variation in the comparative taxa. However, when the results for individual characters are considered jointly, the null hypothesis of a single hominin taxon at Dmanisi cannot be rejected. These results, alongside anatomical and geological assessments of the sample, support the hypothesis of a single Dmanisi hominin taxon. These results do raise interesting questions regarding baseline variation, including that associated with sexual dimorphism and development, in the Dmanisi hominins specifically, and early *Homo erectus* more broadly.

INTRODUCTION

The site of Dmanisi, located in southern Georgia, has yielded a rich assemblage of terminal Pliocene/early Pleistocene fossil hominins[1]. Excavations in 1991 yielded a hominin mandible (Gabunia and Vekua 1995) and excavations continuing to the present have uncovered well preserved cranial and post-cranial materials from multiple individuals derived from a tightly confined stratigraphic context (Ferring et al. 2011; Gabunia et al. 1999; Gabunia et al. 2000; Gabunia et al. 2002; Lordkipanidze et al. 2006; Lordkipanidze et al. 2007; Rightmire et al. 2008; Vekua et al. 2002). The fossil assemblage is placed at an important junction, both geographically and temporally, for understandings of the evolution of early *Homo* and the emergence of *Homo erectus* (Wood 2011). Included in the hominin sample from Dmanisi are four mandibles encompassing a large range of anatomical and metric variation. The variation within the mandibles has generated considerable discussion as to the proper interpretation of the Dmanisi hominins and the broader significance of the site for understandings of Lower Pleistocene *Homo* (Bräuer and Schultz 1996; Dean and Delson 1995; de Lumley et al. 2006; de Lumley and Lordkipanidze 2006; Gabunia and Vekua 1995; Gabunia et al. 2001; Gabunia et al. 2002; Jashashvili 2005; Meyer 2005; Pontzer et al. 2010; Rightmire et al. 2006; 2008; Rosas and Bermúdez de Castro 1998; Schwartz 2000; Skinner et al. 2006; Van Arsdale 2006). Establishing greater clarity regarding the variability within the Dmanisi hominin sample is necessary before the site can be properly placed within the broader context of Lower Pleistocene evolution. The mandibles, the most size-variable hominin element within the assemblage, are central to this challenge.

The goal of this paper is to test the null hypothesis of conspecificity within the Dmanisi hominin mandibular sample. This null hypothesis is first placed within the geological context of the site and comparative anatomy of the sample in order to assess whether it is the appropriate starting point for analysis. Finally, the results of the quantitative analysis will be considered with respect to the Dmanisi fossil assemblage as a whole and its relationship to other Plio-Pleistocene early *Homo* assemblages.

BACKGROUND

The Dmanisi sample is unique for the Lower Pleistocene hominin record in that it provides a rich fossil assemblage derived from a tightly constrained (both temporally and spatially) locality. These attributes give the assemblage tremendous potential to inform broader discussions of hom-

PaleoAnthropology **2012: 134–144.** **ISSN 1545-0031**
doi:10.4207/PA.2012.ART73

inin variability, dispersal, and ecology at the Pliocene/Pleistocene boundary (Dennell and Roebroeks 2005; Zhu et al. 2008). In particular, the Dmanisi assemblage, composed of multiple individuals with multiple preserved skeletal elements, should play a critical role in shaping discussions of sexual dimorphism, ontogeny, and other aspects of intraspecific variation at this time period. Before such analyses can be fully undertaken, however, a necessary first step is establishing a parsimonious explanation for the variability within the hominin remains, particularly whether or not the null hypothesis of a single species can be rejected.

Considerable debate exists on the taxonomic classification within the Dmanisi sample and it is worth examining whether a hypothesis of conspecificity is the appropriate starting point for analyzing the Dmanisi mandibular assemblage. Schwartz (2000), based on the early crania and original mandible recovered from the site, argues for multiple taxa at the site. Gabunia et al. (2002) use the D2600 specimen from Dmanisi to argue for the presence of a novel taxon, *Homo georgicus*, at the site. Skinner et al. (2006), using a quantitative approach, argue that the metric size variability of the Dmanisi mandibles exceeds that of relevant comparative taxa, and therefore a hypothesis of multiple taxa at the site should be given consideration (though see reply by Rightmire et al. 2008). The mandibles, particularly the large D2600 specimen and its contrasts with the enigmatic and more gracile D211 specimen, play critical roles in each of these arguments. Still others have argued on the basis of the cranial (Lee 2005; Lordkipanidze et al. 2005; Lordkipanidze et al. 2007; Rightmire et al. 2006; Rightmire and Lordkipanidze, 2009) and dental (Macaluso 2009; Martinon-Torres et al. 2008) remains for a single, highly variable taxon at the site, most readily identified as early *Homo erectus*.

The stratigraphic position of the mandibular materials within the site provide context of obvious relevance to considerations of the null hypothesis. Current understandings of the geology and sedimentological processes associated with the formation of the site suggest a narrow stratigraphic window for deposition of the Dmanisi remains, immediately straddling the Olduvai-Matuyama boundary at 1.78 Ma (Ferring et al. 2011; Lordkipanidze et al 2007; Mallol 2004; Rightmire et al. 2005). This has important implications for a hypothesis of conspecificity for the hominin remains. While a hominin presence is documented at the site from at least 1.81 Ma (Ferring et al. 2011), all of the mandibular remains are from the same stratigraphic feature within the site, currently designated as the B1 horizon. The B1 horizon represents sediment and fossil material associated with a rapid depositional event immediately following the Olduvai Matuyama reversal, conservatively dating from between 1.78–1.76 Ma. The hominin fossil material likely collected over a much shorter time period within this interval and has been excavated from a narrowly confined area within the site. This raises the possibility that the Dmanisi remains represent something close to a contemporaneous group of individuals, referred to by Lordkipanidze et al. (2006) as a single paleodeme. For the purposes of this study, it is important to note that the stratigraphic context does not provide any external evidence for the division of the Dmanisi hominin sample into multiple groups based on stratigraphic/temporal position within the site. Thus, an argument for multiple hominin taxa at the site is implicitly an argument for sympatric taxa.

The broader paleontological setting of Dmanisi is also important. Work by several researchers (see supplemental information, Lordkipanidze et al. 2007; Agustí and Lordkipanidze 2011) has documented the lack of similarity between the Dmanisi faunal assemblage, with a distinctly Eurasian faunal signal, and those from penecontemporaneous African localities such as the lower beds of Olduvai Gorge. The presence of multiple hominin taxa at Dmanisi therefore suggests a degree of ecological parallelism in the context of hominin ecology, niche development, and dispersal. Such a scenario—two closely related hominin taxa, occupying the same environment, following parallel dispersal paths, but maintaining reproductive isolation—appears unlikely, and certainly is not parsimonious in the absence of additional lines of evidence. The geology and setting of Dmanisi thus provide no evidence to reject the notion of a single hominin lineage at the site as an appropriate and parsimonious null hypothesis.

From an anatomical perspective, the Dmanisi mandibular sample displays a striking amount of variation (Figures 1 and 2). However, many of the most variable elements within the Dmanisi sample reflect traits that show a high degree of variation within and between other hominin taxa. The most variable aspects of the sample include measures of corpus height, dental root morphology, and distal molar size and morphology, all of which have been documented to show considerable levels of intraspecific variation (Abbott 1984; Antón 2003; Chamberlain and Wood 1985; Dean and Benyon 1991; Kaifu et al. 2005; Kupczik et al. 2005; Scott and Turner 1997; Spoor et al. 2007; Tobias 1995; Turner 1981; Weidenreich 1936; Wolpoff 1971; Wood 1992; Wood and Abbott 1983; Wood et al. 1988).

In contrast, several of the more consistent traits in the Dmanisi sample are either distinct to early *Homo* or unique to Dmanisi. Most notably, the Dmanisi specimens share a distinctive *torus mandibularis*, anteriorly-projecting *tuberculum marginale anteriori*, pattern and location of *foramina mentale*, orientation and shape of the *foramen mandibulare*, and shape of the dental arcade[2]. The *torus mandibularis* is manifest as a slight to moderate swelling on the lingual surface of the lateral corpus adjacent to P_4. This feature is most prominently expressed on D2735, but is visibly and palpably present on all of the Dmanisi mandibles (see Figure 2). The *tuberculum marginale anteriori*, particularly in D211 and D2600, exists as an anteriorly projecting phalange inferior to the canine along the basal margin (see Figure 1). This feature is present in many early *Homo* mandibles, but only in these two Dmanisi specimens does it exhibit such an extreme anterior orientation, creating the impression of a groove along its medial edge. Each of the Dmanisi specimens that preserves the *foramina mentale* do so with one prominent foramen on the right side, and two foramina—the second of which exists in smaller form distal and

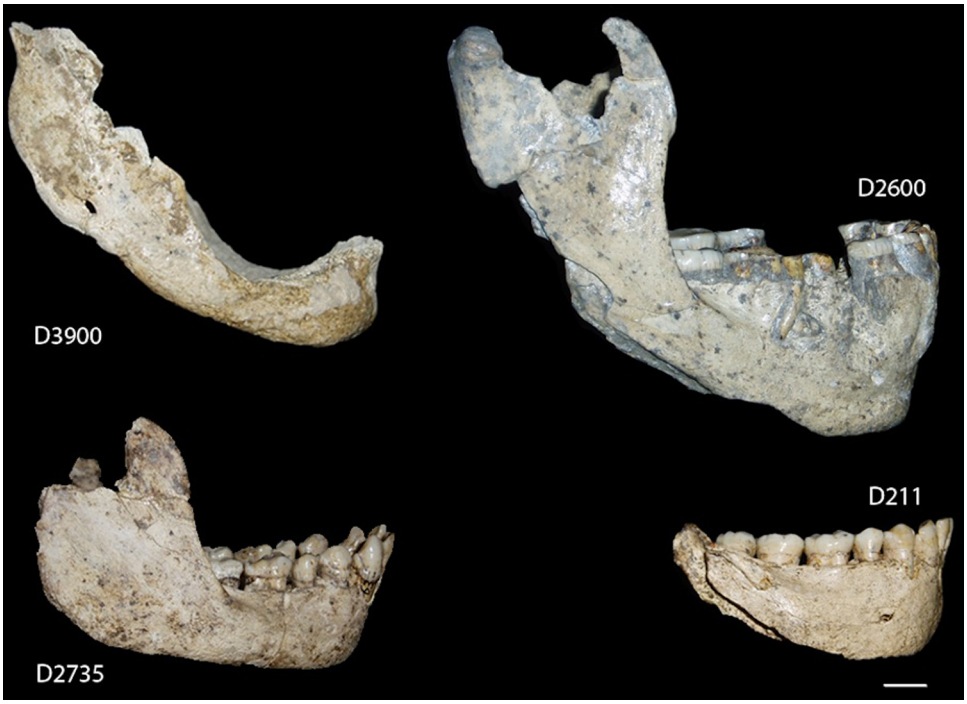

Figure 1. Dmanisi mandibles, lateral view.

inferior to the primary foramen—on the left side. D2600 and D2735 share an ovoid, horizontally oriented *foramen mandibulare*, a condition not shared with other early African *Homo* remains. These features suggest, despite the size variability within the sample, a high level of anatomical similarity (see Van Arsdale 2006 for more detail).

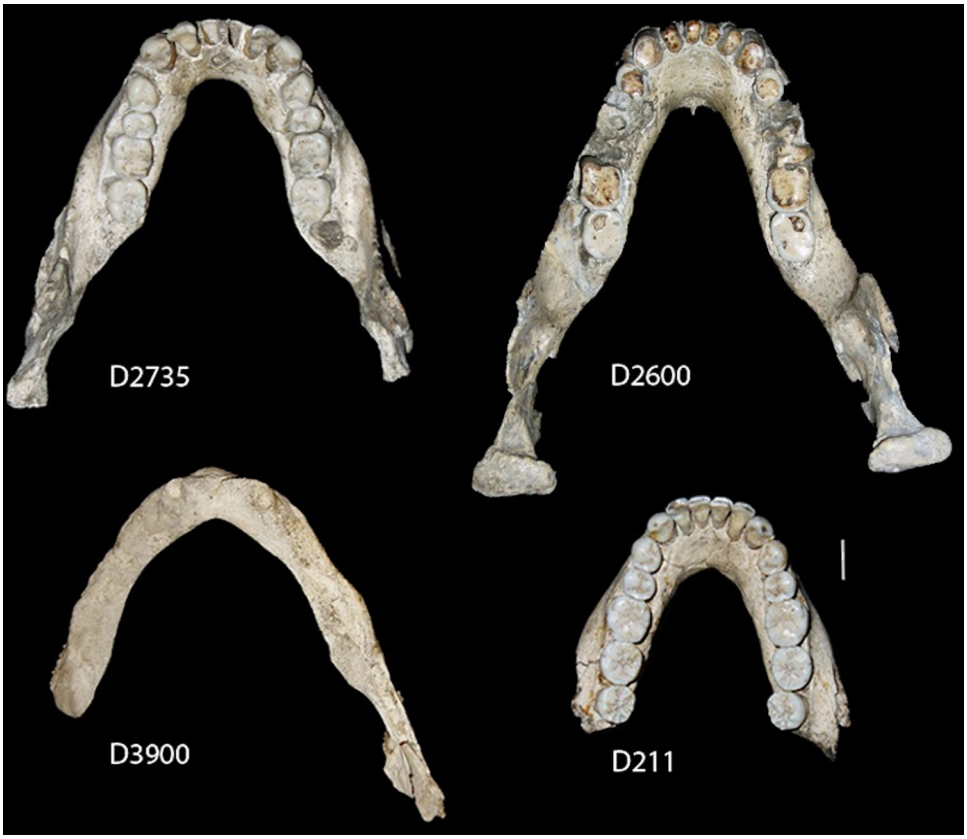

Figure 2. Dmanisi mandibles, superior view.

TABLE 1. COMPARATIVE EXTANT SAMPLE (total number of specimens including identifiable male, female, and unknown sex individuals).

	Total	Female	Male	Unknown
P. t. troglodytes	**100**	37	35	28
G. g. gorilla	**75**	39	34	2
H. sapiens	**86**	29	41	16

Therefore both the geology and the anatomy of the Dmanisi sample suggests that a null hypothesis of a single species, with variation associated primarily with differences in age-related growth and/or sexual dimorphism, is an appropriate starting point for analysis.

METHODS AND MATERIALS

To examine the hypothesis of conspecificity within the Dmanisi mandibular sample, a set of 31 linear measures covering aspects of corpus height, corpus breadth, tooth size, dental arcade dimensions, symphysis proportions, and ramus breadth were collected on the Dmanisi specimens as well as a sample of extant apes and recent humans (see Table 3 below). These measures were chosen on the basis of their preservation within the Dmanisi fossils and their ability to provide comparisons between the Dmanisi specimens. They were also chosen in order to provide as broad a coverage as possible of the mandibular morphology of these specimens, while limiting the level of morphological redundancy. All measurements were recorded by one of the authors (APV) directly on the original fossil and skeletal material.

The comparative samples used for these analyses are chimpanzees (*Pan trogolodytes*), gorillas (*Gorilla gorilla*) and recent humans (Table 1). The use of these species is intended to provide comparisons with the most closely related extant species as well as provide different models of size, dimorphism, and anatomy. The human sample is drawn from the Libben Osteological Collection, housed in the Department of Anthropology at Kent State University (Lovejoy et al. 1977). The *Pan troglodytes* and *Gorilla gorilla* samples are drawn from the Hamann-Todd collection, housed at the Cleveland Museum of Natural History, as well as the collections at the *Zoologische Staatssammlung München*, in Munich, Germany.

Tests of our null hypothesis were structured around a series of pairwise comparisons. For each of the 31 measurements used in this study, an index of relative difference (IRD) was calculated for each Dmanisi specimen pair that preserved the available measurement as the absolute value of the log difference between the two observed values:

$$x_{IRD} = abs\{ln(x_1)-ln(x_2)\}$$

These observed IRD values then served as the basis for hypothesis testing using a randomized resampling methodology. The use of a log difference has been shown to be an effective and parsimonious measure of dimorphism (Smith 1999) and the index is treated as an absolute value so that all comparisons are between positive values.

Each IRD value generated from an observed Dmanisi pair was compared to a distribution of expected values in order to assess whether the observed value was significantly greater than expected based on a hypothesis of conspecificity. The distribution of expected values was created by randomly sampling pairs of specimens with replacement, calculating the IRD value for the given pair and measurement, and repeating this process 1000 times for each of the three comparative groups. For example, in order to assess whether the observed IRD value of .1049 generated from the comparison of bi-mental breadth in D2600 (45.2mm) and D2735 (50.2mm) was significantly greater than expected (i.e., the two specimens are more different from each other than you would expect from an equivalent pair of human, *Pan troglodytes*, or *Gorilla gorilla* specimens), a distribution of expected IRD values for bi-mental breadth was generated. This distribution was established by randomly drawing a pair of specimens preserving this measure from one of the comparative samples, calculating an IRD value for the pair, and then repeating this process 1000 times. Comparing the observed IRD value in the illustration above to a randomly generated distribution based on measures of bi-mental breadth in the *Pan troglodytes* comparative sample, it can be shown that the observed Dmanisi value exceeds the expected value in 638 of 1000 cases. In other words, our observed IRD value for bi-mental breadth is not significantly different than expectations on the basis of comparisons with *Pan troglodytes*. This process was repeated for each of our 31 measurements, using each pairwise comparison available in the Dmanisi sample, and compared to each of our three analog taxa.

Together, these tests produce a complex set of univariate results for each comparative group, for each Dmanisi pair, and for the sample as a whole. One challenge in this approach is that it incorporates a large number of univariate tests in the evaluation of a single hypothesis. It would be advantageous not only to generate an expected distribution for each measurement IRD value, but also an expectation for the pattern of variability of the entire set of comparisons. In other words, if we compare 31 separate measures, how many might we expect to differ significantly just given the nature of our sampling strategy and the variability inherent to our comparative taxa? How many significant univariate results would constitute a significant rejection of

TABLE 2. NUMBER AND PERCENTAGE OF AVAILABLE MEASUREMENTS WITH SIGNIFICANT PAIRWISE DIFFERENCES (at the p=0.05 level).

	Pan t.t.		*Gorilla*		*Homo*	
Dmanisi Pair	S. Difs.	%	S. Difs.	%	S. Difs.	%
D211 / D2600	7/26	26.92	5/26	19.23	6/26	23.08
D211/ D2735	0/19	0.00	0/19	0.00	2/19	10.53
D2600 / D2735	4/25	16.00	2/25	8.00	4/25	16.00

our hypothesis in a multivariate context?

In order to incorporate the multiple univariate tests into a single hypothesis test, a nested resampling analysis was undertaken. This procedure is analogous to the resampling test described above, but instead of using the Dmanisi specimens as the basis for observation, a randomly drawn pair from the comparative sample serves the role of a simulated unknown sample (analogous to our observed Dmanisi fossil sample). The observed differences within this pair are then compared to the remainder of the sample to assess how many of the available measurement comparisons represent significant differences relative to the remaining sample. This entire procedure is then repeated 1000 times, each time randomly selecting a pair to serve as the simulated unknown sample. The product of this analysis is a distribution of the expected frequency of significant differences within each of our comparative taxa, making no *a priori* assumptions about the distribution of the data.

The nested resampling analysis can be viewed as a way of correcting for multiple univariate comparisons, free of the assumption of normality within the data and done explicitly within the sampling strategy utilized in the analysis. In comparing multiple univariate measures using a pairwise sampling approach, by chance alone, some traits might differ significantly even within a known group of conspecific specimens. This procedure allows for the quantification of the expected pattern of variability within each comparative sample given the limitations of the preserved fossil sample and the inherent variability within each comparative sample in order to better assess the significance of our results. If, for example, five of the 31 measurements examined show significant differences within the Dmanisi sample when compared to human standards, the nested resampling procedure provides a basis for evaluating whether this value is unexpected. The result is a multivariate test, based on univariate comparisons, of the null hypothesis. All analyses were conducted using code written for the Matlab software package.

RESULTS

The first set of results is based on the comparison of the Dmanisi sample to randomly drawn pairs of comparative specimens. Three observed pairwise comparisons were available within the Dmanisi sample for this set of tests—D211/D2600, D211/D2735, and D2600/D2735. Each of these three pairs, owing to the uneven preservation of homologous elements across the sample, allows for the comparison of a different set and number of measurements. The D211/D2600 pair preserves 26 of the 31 available measurements in common, D211/D2735 preserve 19 of the measurements, and D2600/D2735 preserve 25 measurements in common. The observed differences in each pair were compared to each of the three comparative model taxa (*Homo sapiens*, *Pan troglodytes*, *Gorilla gorilla*), producing nine sets of results in total.

Of the three Dmanisi pairs, the D211/D2735 combination produced the fewest number of significant comparisons. This is not a surprising result, as these two specimens are similar in both overall size and estimated dental age. When compared to a *Homo sapiens* model, only two of the 19 available measurements showed significant differences at the $p<0.05$ level (external corpus breadth at P_3 and anterior tooth row length), or 10.5% of the total traits examined. Compared with both the *Pan troglodytes* and *Gorilla gorilla* samples, no significant trait differences were observed within the set of measurements available for the pair.

Each of the pairings involving the D2600 specimen produced a greater number of significant differences relative to each of the three comparative taxa. The D211/D2600 comparison revealed six significant differences (23.08%) compared to a *Homo sapiens* model, seven significant differences (26.92%) compared to a *Pan troglodytes* model, and five significant differences (19.23%) compared to a *Gorilla gorilla* model (Table 2). The traits that showed significant differences, in all cases, were focused on aspects of corpus height and alveolar dental arcade dimensions (Table 3). Chord length between gnathion and M_3, corpus height at the canine, symphysis height, and distal tooth row length (M_2-M_3), were significantly more different within the Dmanisi pair than expected from any equivalent pair of specimens from each of the comparative groups.

The D2600/D2735 produced slightly fewer significant differences overall, but the differences that were observed still focus strongly on aspects of corpus height. Compared with both the *Homo sapiens* and *Pan troglodytes* samples, this pair displayed four significantly variable traits (16.00%), with only two significant differences compared to the *Gorilla gorilla* sample (8.00%). The two traits that were signifi-

cantly more variable than each of the three comparative models were corpus height at canine and corpus height at P_4.

In order to properly evaluate the above results, it is necessary to have a clear sense of the expected level of variability given the comparative models utilized in this study and sampling regime imposed by the fossil data. The nested resampling analysis serves this function by generating a distribution of expected significant differences given the number of univariate tests conducted and the nature of the comparative sample and sampling strategy.

In the 1000 randomized simulations examined, the human comparative model produced an average of 5.7% significant differences (approximately one or two out of 23 or 24 traits available for study) between randomly drawn pairs (Figure 3a). *Pan troglodytes* and *Gorilla gorilla* simulations produced similar results, with 6.04% (approximately one or two out of 27 or 28 traits available for study) and 6.40% (approximately one or two out of 26 or 27 traits available for study) of observed measurements displaying significant differences, respectively, within a randomly drawn pair (Figure 3b, 3c). It is not the average percentage of significant differences that is of interest, though, but where our observed results fit within the distribution of expectations. How frequently do the results of the nested resampling analysis exceed the variability observed within our Dmanisi-comparative taxon comparisons? For example, when compared to the *Gorilla gorilla* comparative sample, the Dmanisi pairings showed significant differences ranging from 0% (D211/D2735) to 19.23% (D211/D2600) of the compared measurements. Looking at the *Gorilla gorilla* distribution of expected differences generated by the nested resampling analysis, it can be seen that the greatest observed value (19.23%, generated from the D211/D2600 comparison) exceeded the simulated value in 899 of the 1000 trials. This makes it towards the high end of the distribution, but suggests our result is not significant when the aggregate perspective is taken into account. Given the measurements included in this analysis, a pairwise sampling approach, and the variability inherent to *Gorilla gorilla*, finding several significant differences is not unexpected. The variation observed within Dmanisi mandibular pairs does not exceed the expected level of variation in a *Gorilla* comparative model.

The results for *Pan troglodytes* and *Homo sapiens* were similar, though the Dmanisi 211/2600 comparison comes even closer to significance in these models of variation. The analysis of the D211/D2600 pair compared with a *Pan troglodytes* model of variation yielded seven significant differences, or 26.9% of our observations. This value exceed 937 of the 1000 simulated distributions in our nested resampling analysis, suggesting this value is unlikely, but not significantly so, given our comparison. Compared with humans we found six significant differences, or 23.1% of our observations, a value that exceeded 940 of 1000 simulated trials in our nested resampling analysis using the human comparative model.

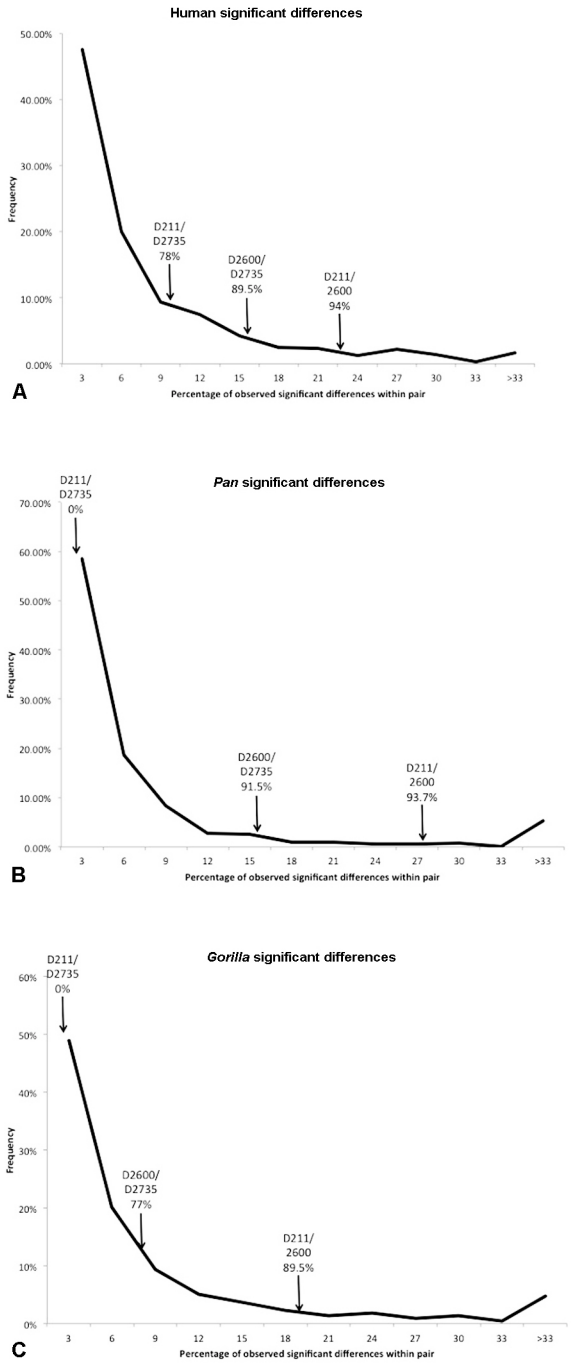

Figure 3. Nested resampling results (a,b,c: top to bottom) showing the expected distribution of significant differences in humans, Pan t.t. *and* Gorilla*, respectively. Each figure displays where in the distribution each of the analyzed Dmanisi pairs falls, including the percentile within the generated distribution of expected differences. The largest difference within the Dmanisi sample occurs between D211 and D2600, with the observed pattern of variation placing this pairing on the tail of all three distributions. Although it approaches significance when compared to humans and* Pan t.t.*, the results fail to reject the null hypothesis of a single Dmanisi hominin taxon.*

TABLE 3. COMPLETE LIST OF MEASUREMENTS USED FOR ANALYSIS AND UNIVARIATE RESAMPLING TEST RESULTS*.

		Corpus height				Corpus breadth			Mandibular breadth										Arcade dimensions										Other		
		CHSYM	CHM2	CHP4	CHC	CBSYM	CBP4	CBM2	BMENB	BCORB	BRBALV	BRBORG	BNOTB	XBI2C	XBC	XBP3	XBM2	XBM3	IBC	IBP3	IBM2	IBM3	I1CALV	P3P4ALV	M1M3ALV	CP4ALV	M2M3ALV	IP4M1ALV	IM3ALV	INFCOR	GNAM3	ORINC
D211		31	-	-	27.6	17.2	17.5	20.7	45.3	-	80	77.4	-	21.2	30.6	42.5	60.9	60.9	21.9	26.4	40.5	44.1	18.5	16.7	37.1	24.7	23.1	33.4	66.6	-	65.9	17.3
D2600		50	37.1	41.5	44.	22.7	21.9	21.8	45.2	107.5	94.1	85.8	107.5	24.7	36.8	48.8	69	71.6	22.3	32.3	44	47.1	21	19.2	44.9	28.6	30.7	39.7	78.4	14.3	84.2	24.6
D2735		34	21.2	24.4	26.2	16.1	19.4	22.7	50.2	89.4	81.8	81.1	89.4	25	34	49.8	61.3	-	24.9	31.1	40.5	-	24.9	17.8	-	29.1	-	39.5	-	94	-	17.3
D211/ D2600	*Homo*	**	-	-	**	ns	ns	ns	ns	-	ns	ns	-	ns	ns	ns	ns	*	ns	*	ns	ns	ns	ns	ns	ns	*	ns	*	-	**	ns
D211/ D2735	*Homo*	ns	-	-	ns	ns	ns	ns	ns	-	ns	ns	-	ns	ns	*	ns	-	ns	ns	-	-	**	ns	-	ns	-	ns	-	-	-	-
D2600/ D2735	*Homo*	*	*	**	**	*	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	-	ns	ns	ns	-	ns	ns	-	ns	-	ns	-	ns	-	ns
D211/ D2600	*Pan t. t.*	**	-	-	*	ns	ns	ns	ns	-	ns	ns	-	ns	ns	ns	ns	*	ns	ns	ns	ns	ns	ns	**	ns	**	ns	*	-	**	ns
D211/ D2735	*Pan t. t.*	ns	-	-	ns	ns	ns	ns	ns	-	ns	ns	-	ns	ns	ns	ns	-	ns	ns	-	-	ns	ns	-	ns	-	ns	-	-	-	-
D2600/ D2735	*Pan t. t.*	*	*	*	*	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	-	ns	ns	ns	-	ns	ns	-	ns	-	ns	-	ns	-	ns
D211/ D2600	*Gorilla g. g.*	*	-	-	*	ns	ns	ns	ns	-	ns	ns	-	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	*	ns	**	ns	ns	-	*	ns
D211/ D2735	*Gorilla g. g.*	ns	-	-	ns	ns	ns	ns	ns	-	ns	ns	-	ns	ns	ns	ns	-	ns	ns	-	-	ns	ns	-	ns	-	ns	-	-	-	-
D2600/ D2735	*Gorilla g. g.*	ns	ns	*	**	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	-	ns	ns	ns	-	ns	ns	-	ns	-	ns	-	ns	-	ns

*Measures of corpus height include corpus height at symphysis (CHSYM), at M_2 (CHM2), at P_4 (CHP4) and canine (CHC). Measures of mandibular corpus breadth include breadth parallel to the long axis of the symphysis (CBSYM), breadth at P_4 (CBP4), and M_2 (CBM2). Mandibular breadth measures include bi-mental breadth (BMENB), bi-coronoid breadth (BCORB), bi-ramus breadth at the alveolar margin (BRBALV), bi-ramus breadth at the origin on the lateral corpora (BRBORG), bi-notch breadth (BNOTB), external breadth at I_2/C midpoint (XBI2C), external breadth at the midpoint of the canine (XBC), external breadth at the midpoint of P_3 (XBP3), external breadth at the midpoint of M_2 (XBM2), and the external breadth at the midpoint of M_3 (XBM3). Measures of the alveolar arcade include the internal breadth at mid-canine (IBC), internal breadth at the midpoint of P_3 (IBP3), internal breadth at the midpoint of M_2 (IBM2) and the internal breadth at the midpoint of M_3 (IBM3). Additional measurements of the linear distance along the alveolar arcade include the distance from the mesial edge of I_1 to the distal edge of the canine (I1CALV), from the mesial edge of P_3 to the distal edge of P_4 (P3P4ALV), from the mesial edge of M_1 to the distal edge of M_3 (M1M3ALV), from the mesial edge of the canine to the distal edge of P_4 (CP4ALV), from the mesial edge of M_2 to the distal edge of M_3 (M2M3ALV), from *infradentale* to the midpoint of P_4/M_1 (IP4M1ALV), and from *infradentale* to the distal edge of M_3 (IM3ALV). Other measures include *infradentale* to the tip of the coronoid process (INFCOR), *gnathion* to the distal edge of M_3 (GNAM3), and *orale* to the posterior edge of the incisive plane (ORINC).

In the lower rows, the results of the re-sampling tests between the available measurements for each pair of Dmanisi specimens and the listed comparative sample are displayed. Dashes (-) indicate a lack of preserved measurements within the Dmanisi sample, 'ns' indicates a non-significant result, an asterisk (*) indicates a comparison significant at the p=0.05 level and a double asterisk (**) indicates a comparison significant at the p=0.01 level.

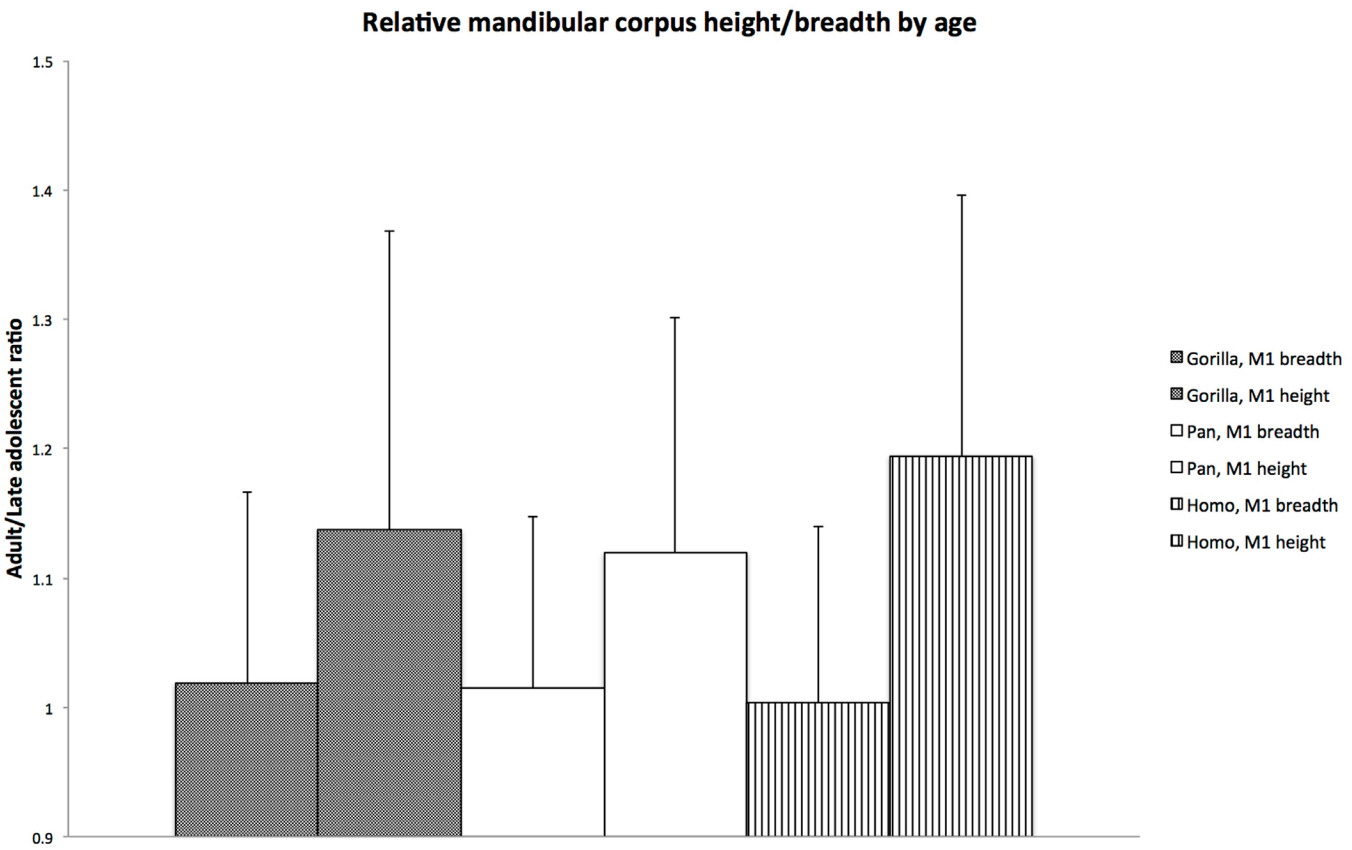

Figure 4. Ratio of adult/subadult height and breadth measures at M_1. Subadults are defined, in this case, as specimens in the process of M_3 alveolar eruption, comparable to the dental eruption stage bracketed by D2735 and D211. Whereas corpus breadth is largely equivalent between late adolescent and adult mandibles, adults show consistently taller corpora.

These results fail to reject our null hypothesis of a single Dmanisi hominin taxon. However, they do suggest the level of intraspecific variability within Dmanisi is consistently elevated, even when compared to *Gorilla gorilla*, a species with a high degree of sexual skeletal size dimorphism.

DISCUSSION

Our results support the conclusion of previous research on the cranial (Lee 2005; Rightmire and Lordkipanidze 2010; Rightmire et al. 2006) and dental (Macaluso 2009; Martinon-Torres et al. 2008) remains from Dmanisi in favor of a single Dmanisi hominin species. Despite the pronounced level of variation within the mandibular sample, our results fail to reject the null hypothesis of a single species. This conclusion also is consistent with parsimonious interpretations of the Dmanisi hominin assemblage supported by the geology of the site and comparative anatomy of the hominin mandibular remains.

These results do not, however, come without questions regarding the variation within the Dmanisi sample. That the results presented here show the observed level of variation to be near the high end of expected distributions of variation, even using *Gorilla gorilla* as a comparative taxon, raise important questions about the source of variability within this assemblage and for *Homo erectus* more broadly.

One important source of variation within the Dmanisi mandibular assemblage is certainly the difference in age, and subsequent age-related growth, across the sample. The mandible is one of the most dynamic skeletal elements throughout life and continues to undergo substantial changes even after primary skeletal growth has ceased, owing to changes and degradation of the dentition (Björk 1969; Enlow and Hans 2008). Within the Dmanisi sample, the two younger specimens (D211 and D2735) are both in the midst of M_3 alveolar eruption, the former just ending the process, with slight polishing wear on the M_3, and the latter likely slightly earlier in the process of eruption. Figure 4 displays the relative ratio between adult mandibles and "late adolescent" specimens, defined by actively being in the process of M3 alveolar eruption (similar to the time frame bracketed by D2735 and D211), of corpus height and breadth. Whereas corpus breadth has essentially reached peak dimensions by the time of M_3 eruption, corpus height, particularly in humans, is only 80-90% of full adult size on average. This suggests that some of the gross size differences between D2600 and the two younger Dmanisi specimens are the result of unachieved growth for each of the latter specimens. The morphology of these specimens—including the decline in corpus height distally in D2735, the lack of superficial structures on D2735 such as a *torus lateralis*, and the differences in inclination of the ramus between D2735 and D2600—also support the idea of age-related changes within the sample. Even accounting for the possible effects of growth, the difference between D2600 and

the remainder of the sample is exceptional. One element to note in this comparison is the high level of dental wear and attrition for the D2600 specimen, which has a higher molar wear gradient than any other Pleistocene *Homo* mandible (Rightmire et al. 2008; Van Arsdale 2006).

Finally, it is also possible that the variation within the Dmanisi sample reflects an elevated level of sexual dimorphism, particularly in comparison to recent humans and *Pan t.t.*. Estimating levels of sexual dimorphism in small fossil samples is notoriously difficult, however, and should be treated with caution. Additionally, dimorphism of the mandible remains a topic of debate (Loth 1996; Loth and Henneberg 2001; Franklin et al. 2007; Rosas et al. 2002). The Dmanisi remains are not alone in support of the idea of elevated sexual dimorphism within *Homo erectus* (Kramer 1993; Potts et al. 2004; Spoor et al. 2007; Wolpoff 1976). An interpretation of sexual dimorphism within the Dmanisi remains requires an acceptance of the conspecific nature of the remains, a situation that, given the results here, potentially lends itself to circularity. However, this interpretation is supported by a qualitative interpretation of the anatomy of the Dmanisi remains in addition to the quantitative study presented here. The presence of a number of synapomorphic features within the Dmanisi sample (relative to terminal Pliocene/early Pleistocene *Homo* mandibular assemblage) supports the interpretation of a single Dmanisi hominin taxon and an elevated expression of sexual dimorphism (Lordkipanidze et al. 2006; Van Arsdale 2006; Wood 1991). The close stratigraphic context of the remains, coupled with the early date and location of the Dmanisi site, adds logical support to this interpretation of the Dmanisi remains.

It would be naïve to think that the observed variation in living humans and two living great ape species adequately encompasses the variation across large samples of fossil hominids or other fossil primates (Kelley 1993; 1995; Kelley and Plavcan 1998). The comparative samples employed here display different combinations of morphological pattern (ape-like or human-like) and different degrees of sexual dimorphism (large or small). The one morphology-dimorphism combination that is not available among extant apes and humans is a human-like morphological pattern with large (or at least greater than living humans) levels of dimorphism. It is possible the Dmanisi sample, and early *Homo* or *Homo erectus* more broadly, represents such a combination. If this is the case, the ability to reliably assess conspecificity within such samples based solely on simple quantitative comparisons with extant taxa is limited, or at least must be interpreted with caution. Indeed, the identification of appropriate comparative models of both intraspecific and interspecific variation in sexual dimorphism poses a fundamental challenge in the interpretation of results for fossil studies, including the analyses presented here. Nevertheless, the pattern of variation within the Dmanisi mandibles supports the hypothesis of a single taxon with a moderate to high degree of sexual dimorphism (Cheverud et al. 1985; Kelley and Plavcan 1998; Plavcan 2001; Wood et al. 1991). The possibility of elevated levels of sexual dimorphism in the Dmanisi remains raises obvious questions for the interpretation of other early *Homo* remains from East and South Africa (Kramer et al. 1995; Lieberman et al. 1988; Lieberman et al. 1996; Wood 1993).

The Dmanisi mandibular sample presents an interesting case of a temporally and geographically constrained, anatomically similar, but highly size variable sample of early *Homo* fossil material. This analysis suggests that despite the large differences in size within the sample, the null hypothesis of a single species on the site cannot be refuted on the basis of the mandibular remains. The most parsimonious and best classification of the Dmanisi material thus remains that of a single, size variable taxon of early *Homo*.

ACKNOWLEDGEMENTS

We would like to thank the members of the Dmanisi team, including Teona Shelia, Gocha Kiladze, Reid Ferring, Martha Tappen, G. Philip Rightmire, Ana Margvelashvili, and Tea Jashashvili for their assistance in this work. In addition we would like to thank Milford Wolpoff and three anonymous reviewers for their helpful contributions and guidance.

ENDNOTES

[1] Our usage of Pliocene and Pleistocene will follow the Gradstein et al. (2004) definition of these terms, placing the Pliocene/Pleistocene boundary at approximately 1.8 Ma.

[2] Anatomical terminology follows Weidenreich (1936).

REFERENCES

Abbott, S.A. 1984. *A comparative study of tooth root morphology in the great apes, modern man and early hominids*. Ph.D. thesis, University of London.

Agustí, J. and Lordkipanidze, D. 2011. How "African" was the early human dispersal out of Africa? *Quaternary International* 30: 1338–1342.

Antón, S.C. 2003. Natural history of *Homo erectus*. *Yearbook of Physical Anthropology* 122(S37): 126–170.

Björk, A. 1969. Prediction of mandibular growth rotation. *American Journal of Orthodontics* 55(6): 585–599.

Bräuer, G. and Schultz, M. 1996. The morphological affinities of the Plio-Pleistocene mandible from Dmanisi, Georgia. *Journal of Human Evolution* 30*:* 445–481.

Chamberlain, A.T. and Wood, B. 1985. A reappraisal of variation in hominid mandibular corpus dimensions. *American Journal of Physical Anthropology* 66(4): 399–405.

Cheverud, J. M., Dow M. and Leutenegger W. 1985. The quantitative assessment of phylogenetic constraints in comparative analyses: sexual dimorphism in body weight among primates. *Evolution* 39(6): 1335–1351.

de Lumley, M.A., Gabunia, L., Vekua, A. and Lordkipanidze, D. 2006. Human remains from the Upper Pliocene — Early Pleistocene Dmanisi site, Georgia (1991-200). Part I: the fossil skulls (D2280, D2282, and D2700). *L'Anthropologie* 110*:* 1–110.

de Lumley, M.A. and Lordkipanidze, D. 2006. L'Homme de Dmanissi (*Homo georgicus*), il y a 1,810,000 ans. *Comptes Rendus Palevol* 5*:* 273–281.

Dean, M.C. and Beynon, A.D. 1991. Tooth crown heights, tooth wear, sexual
dimorphism and jaw growth in hominoids. *Zeitschrift für Morphologie und Anthropologie* 78: 425–440

Dean, D. and Delson, E. 1995. *Homo* at the gates of Europe. *Nature* 373*:* 472–473.

Dennell, R. and Roebroeks, W. 2005. An Asian perspective on early human dispersal from Africa. *Nature* 438: 1099–1104.

Enlow, D.H. and Hans, M.G. 2008. *Essentials of Facial Growth* (2nd edition). Philadelphia: W.B. Saunders Company.

Ferring, R., Oms, O., Agustí, J., Berna, F., Nioradze, M., Shelia, T., Tappen, M., Vekua, A., Zhvania, D. and Lordkipanidze, D. 2011. Earliest human occupations at Dmanisi (Georgian Caucasus) dated to 1.85–1.78 Ma. *Proceedings of the National Academy of Sciences* 108(20): 10432–10436.

Franklin, D., Oxnard, C.E., O'Higgins, P. and Dadour, I. 2007. Sexual dimorphism in the subadult mandible: quantification using geometric morphometrics. *Journal of Forensic Sciences* 52(1): 6–10.

Gabunia, L., Antón, S., Lordkipanidze, D., Vekua, A., Justus, A. and Swisher, C.C. 2001. Dmanisi and dispersal. *Evolutionary Anthropology* 10: 158–170.

Gabunia, L., de Lumley, M.A., Vekua, A., Lordkipanidze, D. and de Lumley, H. 2002. Discovery of a new hominid at Dmanisi (Transcaucasia, Georgia). *Comptes Rendus Palevol* 1: 243–253.

Gabunia, L. and Vekua, A. 1995. A Plio-pleistocene hominid from Dmanisi, East Georgia, Caucasus. *Nature* 373: 509–512.

Gabunia, L., Vekua, A. and Lordkipanidze, D. 1999. A hominid metatarsal from Dmanisi (Eastern Georgia). *Anthropologie* 37: 163–166.

Gabunia, L., Vekua, A., Lordkipanidze, D., Swisher, C.C., Ferring, R., Antón, S., Justus,A., Nioradze, M., Tvalchrelidze, M., Bosinski, G., Joris, O., de Lumley, M.A., Majsuradze, G. and Mouskhelishvili, A. 2000. Earliest Pleistocene hominid cranial remains from Dmanisi, Republic of Georgia: taxonomy, geological setting, and age. *Science* 288: 1019–1025.

Gradstein, F.M., Ogg, J.G. and Smith, A.G (eds.). 2004. *A Geologic Time Scale 2004*. Cambridge: Cambridge University Press.

Humphrey, L.T., Dean, M.C. and Stringer, C.B. 1999. Morphological variation in great ape and modern human mandibles. *Journal of Anatomy* 195: 491–513.

Jashashvili, T. 2005. *Hominid upper limb remains from the Paleolithic site of Dmanisi, a morphometrical comparison of taxonomic units and functional interpretations*. Doctoral thesis, Universita degli Studi di Ferrara, Ferrara.

Kaifu, Y., Baba, H., Aziz, F., Indriati, E., Schrenk, F. and Jacob, T. 2005. Taxonomic affinities and evolutionary history of the early Pleistocene hominids of Java: Dentognathic evidence. *American Journal of Physical Anthropology* 128(4): 709–726.

Kelley, J. 1993. Taxonomic implications of sexual dimorphism in *Lufengpithecus*. In *Species, Species Concepts and Primate Evolution*, W.H. Kimbel and L.B. Martin (eds.). New York: Plenum Press, pp. 429–458.

Kelley, J. 1995. Sexual dimorphism in canine shape among extant great apes. *American Journal of Physical Anthropology* 96: 391–417.

Kelley, J. and Plavcan, J.M. 1998. A simulation test of hominoid species number at Lufeng, China: implications for the use of the coefficient of variation in paleotaxonomy. *Journal of Human Evolution* 35: 577–596.

Kramer, A. 1993. Human taxonomic diversity in the Pleistocene: does *Homo erectus* represent multiple hominid species? *American Journal of Physical Anthropology* 91(2): 161–171.

Kramer, A., Donnelly, S.M., Kidder, J.H., Ousley, S.D. and Olah, S.M. 1995. Craniometric variation in large-bodied hominoids - testing the single-species hypothesis for *Homo habilis. Journal of Human Evolution* 29: 443–462.

Kupzcik, K., Spoor, F., Pommert, A. and Dean, M.C. 2005. Premolar root number variation in hominoids: genetic polymorphism vs. functional significance. In *Current trends in dental morphology research,* E. Zadzinska (ed.). Lodz: University of Lodz Press. Pp. 257–268.

Lee, S.-H. 2005. Is variation in the cranial capacity of the Dmanisi sample too high to be from a single species? *American Journal of Physical Anthropology* 127(3): 263–266.

Lieberman, D., Wood, B. and Pilbeam, D. 1996. Homoplasy and early *Homo*: An analysis of the evolutionary relationships of *H. habilis sensu stricto* and *H. rudolfensis*. *Journal of Human Evolution* 30: 503–511.

Lieberman, D.E., Pilbeam, D.R. and Wood, B.A. 1988. A probabilistic approach to the problem of sexual dimorphism in *Homo habilis*: a comparison of KNM-ER 1470 and KNM-ER 1813. *Journal of Human Evolution* 17: 503–511.

Lordkipanidze, D., Vekua, A., Ferring, R., Rightmire, G.P., Zollikofer, C., Ponce de León, M., Agustí, J., Kiladze, G., Mouskhelishvili, A., Nioradze, G. and Tappen, M. 2006. A fourth hominin skull from Dmanisi, Georgia. *The Anatomical Record* 288A: 1146–1157.

Lordkipanidze, D., Jashashvili, T., Vekua, A., Ponce de León, M.S., Zollikofer, C., Rightmire, G.P., Pontzer, H., Ferring, R., Oms, O., Tappen, M., Bukhsianidze, M., Agustí, J., Kahlke, R., Kiladze, G., Martinez-Navarro, B., Mouskhelishvili, A., Nioradze, M. and Rook, L. 2007. Postcranial evidence from early *Homo* from Dmanisi, Georgia. *Nature* 449: 305–310

Loth, S.R. 1996. *Sexual dimorphism in the human mandible: an evolutionary and developmental perspective*. Ph.D. thesis, University of Witswatersrand.

Loth, S.R. and Henneberg, M. 2001. Sexually dimorpic mandibular morphology in the first few years of life. *American Journal of Physical Anthropology* 115: 179–186.

Lovejoy, C.O., Meindl, R.S., Pryzbeck, T.R., Barton, T.S., Heiple, K.G. and Kotting, D. 1977. Paleodemography of the Libben Site, Ottawa County, Ohio. *Science* 198: 290–293.

Macaluso, P.J. 2009. Variation in dental remains from Dma-

nisi, Georgia. *Anthropological Science* 118(1): 31–40

Mallol, C. 2004. *Morphological observations from the archaeological sediments of 'Ubeidiya (Israel), Dmanisi (Georgia) and Grad Dolina-TD10 (Spain) for the reconstruction of hominid occupation contexts*. Ph.D. thesis, Harvard University, Cambridge.

Martinon-Torres, M., Bermúdez de Castro, J.M., Gómez-Robles, A., Margvelashvili, A., Prado, L., Lordkipanidze, D. and Vekua, A. 2008. Dental remains from Dmanisi (Republic of Georgia): morphological analysis and comparative study. *Journal of Human Evolution* 55(2): 249–273.

Meyer, M. 2005. *Functional biology of the Homo erectus axial skeleton from Dmanisi, Georgia*. Ph.D. thesis, The University of Pennsylvania, Philadelphia.

Plavcan, J.M. 2001. Sexual dimorphism in primate evolution. *Yearbook of Physical Anthropology* 44: 25–53.

Pontzer, H., Rolian, C., Rightmire, G.P., Jashashvili, T., Ponce de León, M.S., Lordkipanidze, D. and Zollikofer, C. 2010. Locomotor anatomy and biomechanics of the Dmanisi hominins. *Journal of Human Evolution* 58(6): 492–504.

Potts, R., Behrensmeyer, A.K., Deino, A., Ditchfield, P. and Clark, J. 2004. Small mid-Pleistocene hominin associated with East African Acheulean technology. *Science* 305: 75–78.

Rightmire, G.P., Lordkipanidze, D. and Vekua, A. 2006. Anatomical descriptions, comparative studies and evolutionary significance of the hominin skulls from Dmanisi, Republic of Georgia. *Journal of Human Evolution* 50(2): 115–141.

Rightmire, G.P., Van Arsdale, A.P. and Lordkipanidze, D. 2008. Variation in the mandibles from Dmanisi, Georgia. *Journal of Human Evolution* 54(6): 904–908.

Rosas, A. and Bermúdez de Castro, J.M. 1998. On the taxonomic affinities of the Dmanisi mandible. *American Journal of Physical Anthropology* 107: 145–162.

Rosas, A., Bastir, M., Martínez-Maza, C. and Bermúdez de Castro, J.M. 2002. Sexual dimorphism in the Atapuerca-SH hominids: the evidence from the mandibles, *Journal of Human Evolution* 42(4): 451–474.

Schwartz, J.H. 2000. Taxonomy of the Dmanisi crania. *Science* 289: 55–56.

Scott, G.R. and Turner II, C.G. 1997. *The anthropology of modern human teeth. Dental morphology and its variation in recent human populations*. Cambridge University Press, Cambridge.

Skinner, M.M., Gordon, A.D. and Collard, N.J. 2006. Mandibular size and shape variation in the hominins at Dmanisi, Republic of Georgia. *Journal of Human Evolution* 51: 36–49.

Smith, R.J. 1999. Statistics of sexual size dimorphism. *Journal of Human Evolution* 36: 423–459.

Spoor, F., Leakey, M.G., Gathogo, P.N., Brown, F.H., Antón, S.C., McDougall, I., Kiarie, C., Manthi, F.K. and Leakey, L.N. 2007. Implications of new early *Homo* fossils from Ileret, east of Lake Turkana, Kenya. *Nature* 448: 688–691.

Tobias, P.V. 1995. Root number in the maxillary third premolars: a very ancient polymorphism. In *Aspects of Dental Biology: Palaeontology, Anthropology and Evolution*. J. Moggi-Cecchi (ed.), Florence: International Institute for the Study of Man, pp. 283–290.

Turner II, C.G. 1981. Root number determination in maxillary first premolars for modern human populations. *American Journal of Physical Anthropology* 54: 59–62.

Van Arsdale, A.P. 2006. *Mandibular variation in early Homo from Dmanisi, Georgia*. Ph.D. thesis, University of Michigan, Ann Arbor.

Vekua, A., Lordkipanidze, D., Rightmire, G.P., Agustí, J., Ferring, R., Maisuradze, G., Mouskhelishvili, A., Nioradze, M., Ponce de León, M., Tappen, M., Tvalchrelidze, M. and Zollikofer, C. 2002. A new skull of early *Homo* from Dmanisi, Georgia. *Science* 297: 85–89.

Weidenreich, F. 1936. The mandibles of *Sinanthropus pekinensis*. *Paleontologia Sinica*, Series D *7*.

Wolpoff, M.H. 1971. Functional measure of tooth size. *Southwestern Journal of Anthropology 27:* 279–286.

Wolpoff, M.H. 1976. Some aspects of the evolution of early hominid sexual dimorphism. *Current Anthropology* 17: 579–606.

Wood, B.A. and Engleman, C.A. 1988. Analysis of the dental morphology of Plio-Pleistocene hominids. V. Maxillary postcanine tooth morphology. *Journal of Anatomy* 161: 1–35.

Wood, B.A. and Abbott, S.A. 1983. Mandibular molars, crown area measurements and morphological traits. *Journal of Anatomy* 136: 197–219.

Wood, B.A., Abbott, S.A. and Uytterschaut, H. 1988. Analysis of the dental morphology of PlioPleistocene hominids. IV. Mandibular postcanine root morphology. *Journal of Anatomy* 156: 107–139.

Wood, B.A. 1991. *Koobi Fora Research Project. Volume 4. Hominid Cranial Remains*. Oxford: Clarendon Press.

Wood, B. A., Li Y. and Willoughby C. 1991. Intraspecific variation and sexual dimorphism in cranial and dental variables among higher primates and their bearing on the hominid fossil record. *Journal of Anatomy* 174: 185–205.

Wood, B.A. 1992. Origin and evolution of the genus *Homo*. *Nature* 355: 783–790.

Wood, B.A. 1993. Early *Homo*: How many species? In *Species, Species Concepts, and Primate Evolution*, W.H. Kimbel and L.B. Martin (eds.). New York: Plenum, pp. 485–522.

Wood, B.A. and Aiello, L.C. 1998. Taxonomic and functional implications of mandibular scaling in early hominins. *American Journal of Physical Anthropology* 105: 523–538

Wood, B.A. 2011. Did early *Homo* migrate "out of" or "into" Africa? *Proceedings of the National Academy of Sciences* 108(26): 10375–10376.

Zhu, R.X., Potts, R., Pan, Y.X., Yao, H.T., Lü, L.Q., Zhao, X., Gao, X., Chen, L.W., Gao, F. and Deng, C.L. 2008. Early evidence of the genus *Homo* in East Asia. *Journal of Human Evolution* 55(6): 1075–1085.