Variation in dental remains from Dmanisi, Georgia

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Abstract Observable differences among craniomandibular specimens from Dmanisi, Republic of Georgia have resulted in controversy regarding the number of represented taxa. In this study, the hominin dental remains from Dmanisi are analyzed to help determine whether the variation present in the Georgian assemblage likely reflects interspecific or intraspecific variation, including sexual dimorphism. Metric variation is assessed with resampling methodology by comparing the Dmanisi teeth with reference samples of extant hominoids. Comparisons were also made between the variation observed in the Georgian sample and that of *Paranthropus boisei*. The results provide evidence for the taxonomic homogeneity of the D211/D2282 and D2735/D2700 skulls. Whether D2600 should be included within this sample or considered distinct is less clear as the distal molar crown dimensions of this robust specimen are notably larger than the other Georgian fossils. Nonetheless, it is argued that the metric size variation expressed by the Dmanisi dental sample, including D2600, is insufficient to reject the null hypothesis of a single species.

Key words: Intraspecific variation, Early *Homo*, Dental metrics, Randomization

Introduction

The stratified deposits at Dmanisi in the Georgian Caucasus have produced large quantities of well-preserved faunal remains, lithic artifacts, and hominin fossils. The hominin inventory from Dmanisi now includes four crania, four mandibles, and their associated teeth (Gabunia and Vekua, 1995; Gabunia et al., 2000, 2002a, 2002b; Vekua et al., 2002; Lordkipanidze et al., 2005, 2006), as well as numerous postcranial elements (Lordkipanidze et al., 2007). A combination of geological and paleontological evidence dates the fossil material to c. 1.77 million years ago (Rightmire et al., 2006; Lordkipanidze et al., 2007). Stratigraphic and sedimentological data seem to indicate that all of the Dmanisi fossils accumulated over a very short time interval, perhaps as little as 10 kyr (Gabunia et al., 2001; Lordkipanidze et al., 2006) or possibly during a single catastrophic event (de Lumley et al., 2008), and thus all the fossils may be regarded as essentially contemporary. However, a recent paleomagnetic study of the volcanic deposits suggests that although the age of the site could span several ten thousands of years, a much wider period of hundreds of thousands of years cannot be excluded (Calvo-Rathert et al., 2008).

In describing the cranial specimens from Dmanisi, Gabunia and colleagues (Gabunia et al., 2000; Vekua et al., 2002; Lordkipanidze et al., 2005) concluded that the observed variability is representative of a single hominin population

displaying size variation due to sexual dimorphism, as well as developmental and individual variation. A more comprehensive treatment of the hominin skulls provided a similar conclusion (Rightmire et al., 2006). Rightmire et al. (2006) demonstrated that although the Georgian hominins display variation related to growth status and sexual dimorphism, the individuals from Dmanisi represent one paleodeme. Statistical (randomization) analyses have also shown that the level of dimorphism displayed by the Dmanisi crania is not excessive relative to that observed in some extant apes and modern humans (Macaluso et al., 2004; Lee, 2005; Lorenzo et al., 2005).

These conclusions have not gone unchallenged, however, and other researchers have suggested that the morphological variation among the Dmanisi crania is excessive for a single species and reflects intertaxic rather than intrapopulational variation (Schwartz, 2000; Schwartz and Tattersall, 2003). Gabunia and colleagues (Gabunia et al., 2002a, 2002b) also discuss the significance of the morphological variation displayed among the Georgian mandibular remains. Although it has been suggested that the dissimilarity between D2600 and D211 reflects marked sexual dimorphism (Gabunia et al., 2002a), Gabunia and colleagues did not find this argument entirely convincing (Gabunia et al., 2002b). Furthermore, a recent study demonstrated that the Georgian mandibular specimens exhibit significantly more variation in several corpus size and shape variables when compared to extant great apes, modern humans, and extinct fossil hominin taxa (Skinner et al., 2006; but see Rightmire et al., 2008). Likewise, Martínón-Torres et al. (2008), in their descriptive and comparative study of Georgian teeth, suggest that the observed differences among the dental remains may indicate the presence of two distinct paleodemes at Dmanisi. Therefore, the results of these analyses, as well as the unclear geo-

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logical context associated with the hominin fossils, leave the interpretation of taxonomic homogeneity among the Georgian specimens in doubt.

Teeth are a valuable source of information for examining hominin morphological variation given that they develop early in life and change later only by breakage and wear, not remodeling, and thus their morphology expresses genetic information more directly than do other parts of the skeleton (Kieser, 1990; Brown and Walker, 1993; Henke, 1998; Gómez-Robles et al., 2007). Therefore, in this paper the hominin dental remains from Dmanisi are further analyzed to help determine whether the variation present in the Georgian assemblage likely reflects interspecific or intraspecific variation. The null hypothesis is that all the Georgian individuals represent one population and can therefore be subsumed within a single species. The degree of metric variation in the Dmanisi teeth was compared to that seen in reference samples of gorillas, chimpanzees, and modern humans using randomization methods. Comparisons were also made between the variation observed in the Georgian sample and that of *Paranthropus boisei*.

Materials and Methods

Samples

The Dmanisi dental sample utilized in this study includes the teeth associated with three mandibles and two crania, belonging to three individuals. The first individual consists of the D211 mandibular corpus with complete and little worn dentition, and the D2282 partial cranium, which retains the right P^4-M^1 and left M^1-M^2 . The second individual is represented by the reasonably complete D2600 mandible with severely worn teeth, including the I_1-P_3 on both sides, M_1-M_3 on the right, and M_2-M_3 on the left. The last individual consists of the well-preserved D2735 mandible with slightly worn teeth including P_3-M_2 antimeres, the largely complete D2700 cranium preserving in situ the right M^1-M^2 and the left P^4 and M^2 , as well as 12 isolated but associated teeth (Table 1). Data on the Dmanisi teeth were collected from the original specimens housed in the Georgian National Museum in Tbilisi, Georgia.

The comparative material used to assess variation within the Dmanisi sample consists of three extant, large-bodied hominine species: *Pan troglodytes troglodytes*, *Gorilla gorilla gorilla*, and *Homo sapiens*. The author collected dental data for all three samples from the Hamann-Todd Collection housed at the Cleveland Museum of Natural History. The modern human sample consists of African-American individuals drawn from this collection. The sample sizes for each dental dimension in each hominine species ranges from 37 to 50 individuals, with relatively equal numbers of males and females (Table 2). The comparative samples were chosen because they are the closest extant phylogenetic relatives of fossil hominins.

In addition to living hominines, *Paranthropus boisei* (*sensu stricto*) was included as a comparative fossil sample because its taxonomy is generally not contentious (Lockwood, 1999; Lockwood et al., 2000; Wood and Constantino, 2007; but see Groves, 1989). In addition, presumed members of both sexes have been collected, and the degree of dimorphism is

Table 1. Dmanisi dental sample

Specimen	Description
D211/D2282 skull	
D211	Mandibular corpus with right I_1-M_3 and left I_1-M_3
D2282	Partial cranium with right P^4-M^1 and left M^1-M^2
D2600	Mandible with right I_1-P_3 , M_1-M_3 and left I_1-P_3 , M_2-M_3
D2735/D2700 skull	
D2735	Mandible with right P_3-M_2 and left P_3-M_2
D2700	Cranium with right M^1-M^2 and left P^4 , M^2
D2677	Left I^2
D2678	Right C_1
D2710	Left M^1
D2711	Right M^3
D2719	Right P^4
D2720	Left M^3
D2723	Left C_1
D2732	Right C^1
D2736	Right I^1
D2854	Right I_2
D3672	Right P^3
D3698	Left I_2

probably high if the hypodigm is considered one species (Wood, 1991b; Lockwood, 1999; Lockwood et al., 2000). This fossil taxon is also useful for assessing variation in the Dmanisi sample because both groups have orthognathic faces and relatively small canines, which distinguish hominins from non-human apes (Wood, 1991b). Therefore, this sample provides important measures of the kinds of variation that can be expected to characterize an early hominin species. The composition of the *P. boisei* sample was modeled after that used by Wood et al. (1994). This sample was chosen to be as temporally and spatially restricted as possible, while maintaining a sufficient sample size, owing to the limited time depth and geographical range of the Dmanisi hominins. The specimens come from the Koobi Fora region and derive from deposits dated between 1.79 and 1.49 myr (Table 3). All *Paranthropus* data were obtained from published descriptions (Leakey and Walker, 1988; Wood, 1991a).

Measurements

The dental data evaluated in the randomization analyses (see below) includes buccolingual (BL) dimensions of many tooth classes, as well as corrected mesiodistal diameters (MD(C)) and measured crown areas (MCA) of the maxillary and mandibular postcanine teeth. Buccolingual diameters were taken with sliding calipers according to the methods outlined by Wood (1991a). For the postcanine teeth, mesiodistal diameters corrected for interproximal wear and measured crown areas were taken from standardized occlusal photographs following the methods outlined in previous studies (Wood and Abbott, 1983; Wood et al., 1983; Wood and Uytterschaut, 1987; Wood and Engleman, 1988; Bailey, 2004) with some modifications in image processing. Scaled photographs of occlusal surfaces were taken for individual teeth using a Nikon Coolpix 4300 digital camera with macro capabilities. The camera was mounted on a tripod and a level was used to ensure a consistent camera angle. Each tooth was positioned so that the plane of the cervical line was perpendicular to the optical axis of the camera. The tooth was

Table 2. Sample statistics for the extant hominine reference taxa^a

		<i>Homo sapiens</i>					<i>Pan troglodytes</i>					<i>Gorilla gorilla</i>				
		N	Mean	SD	Range	CV	N	Mean	SD	Range	CV	N	Mean	SD	Range	CV
I ₂ BL	M	23	6.7	0.61	5.9–8.5	9.03	19	9.8	0.53	8.5–10.8	5.41	16	10.3	0.70	9.1–11.5	6.74
	F	20	6.3	0.33	5.8–6.8	5.15	22	9.0	0.66	7.9–10.6	7.37	22	9.6	0.77	8.2–11.2	8.01
	C	43	6.5	0.52	5.8–8.5	8.03	41	9.4	0.73	7.9–10.8	7.82	38	9.9	0.82	8.2–11.5	8.31
C ₁ BL	M	23	8.2	0.60	7.3–9.9	7.27	22	13.3	1.26	11.0–16.8	9.47	21	17.8	1.14	15.4–19.6	6.38
	F	20	7.6	0.53	6.6–8.1	6.91	22	10.2	1.32	8.0–13.0	12.91	22	13.1	1.11	9.9–14.5	8.51
	C	43	8.0	0.64	6.6–9.9	8.03	44	11.7	2.00	8.0–16.8	17.00	43	15.4	2.65	9.9–19.6	17.19
P ₃ MD(C)	M	24	7.8	0.48	7.0–8.6	6.13	20	11.2	0.61	10.2–12.5	5.48	22	16.6	1.11	14.5–18.5	6.64
	F	25	7.6	0.46	7.0–8.8	6.02	24	10.9	0.75	9.7–12.6	6.91	23	14.6	0.54	13.6–15.7	3.67
	C	49	7.7	0.47	7.0–8.8	6.12	44	11.0	0.70	9.7–12.6	6.36	45	15.6	1.34	13.6–18.5	8.62
P ₃ BL	M	24	8.6	0.57	7.7–10.0	6.55	20	8.1	0.48	7.3–9.0	5.91	22	11.6	1.36	10.0–16.1	11.72
	F	25	8.2	0.53	6.9–9.2	6.52	24	7.5	0.57	6.7–8.8	7.54	23	10.3	0.66	9.2–11.5	6.39
	C	49	8.4	0.60	6.9–10.0	7.11	44	7.8	0.60	6.7–9.0	7.64	45	11.0	1.23	9.2–16.1	11.21
P ₃ MCA	M	23	48.9	6.57	39.8–65.9	13.45	20	68.5	6.68	60.3–88.8	9.76	22	153.6	20.19	117.4–198.3	13.14
	F	24	45.0	5.07	36.9–55.9	11.27	23	64.4	8.82	52.4–82.9	13.69	23	119.8	10.91	102.9–141.5	9.11
	C	47	46.9	6.11	36.9–65.9	13.02	43	66.3	8.07	52.4–88.8	12.18	45	136.3	23.38	102.9–198.3	17.15
P ₄ MD(C)	M	24	8.0	0.46	7.3–8.6	5.71	24	8.4	0.55	7.4–9.5	6.54	25	12.0	0.96	10.5–13.8	8.05
	F	23	7.7	0.42	6.9–8.8	5.51	24	8.0	0.38	7.4–8.8	4.73	25	11.5	0.55	10.5–12.9	4.81
	C	47	7.8	0.47	6.9–8.8	5.95	48	8.2	0.51	7.4–9.5	6.20	50	11.7	0.81	10.5–13.8	6.95
P ₄ BL	M	24	9.0	0.62	7.6–10.1	6.94	24	9.4	0.67	8.4–11.3	7.09	25	13.2	1.19	11.7–16.2	8.98
	F	23	8.4	0.45	7.7–9.6	5.31	24	8.6	0.66	7.5–10.1	7.63	25	12.3	0.78	10.9–13.5	6.30
	C	47	8.7	0.61	7.6–10.1	7.01	48	9.0	0.76	7.5–11.3	8.46	50	12.8	1.09	10.9–16.2	8.55
P ₄ MCA	M	24	54.1	6.18	45.0–65.5	11.43	24	62.3	7.14	50.8–81.8	11.46	25	126.4	17.47	97.1–152.8	13.83
	F	23	49.1	4.82	42.6–61.8	9.83	24	55.9	5.37	46.6–67.4	9.60	25	112.8	10.63	92.2–133.9	9.42
	C	47	51.6	6.05	42.6–65.5	11.72	48	59.1	7.03	46.6–81.8	11.89	50	119.6	15.87	92.2–152.8	13.27
M ₁ MD(C)	M	20	11.9	0.50	11.0–13.3	4.20	22	11.4	0.52	10.6–12.9	4.53	25	16.3	0.83	14.7–17.6	5.06
	F	23	11.7	0.46	10.5–12.4	3.90	25	11.1	0.62	9.7–12.2	5.63	23	15.5	0.71	14.0–17.0	4.58
	C	43	11.8	0.49	10.5–13.3	4.11	47	11.2	0.59	9.7–12.9	5.27	48	15.9	0.87	14.0–17.6	5.44
M ₁ BL	M	20	10.8	0.47	10.1–12.0	4.31	23	10.0	0.65	9.0–11.1	6.47	25	13.7	0.88	12.0–15.4	6.43
	F	23	10.5	0.53	9.4–11.4	5.06	25	9.6	0.55	8.7–10.5	5.71	23	13.0	0.69	11.4–14.4	5.26
	C	43	10.6	0.53	9.4–12.0	5.00	48	9.8	0.63	8.7–11.1	6.39	48	13.4	0.84	11.4–15.4	6.32
M ₁ MCA	M	20	103.9	7.49	92.4–123.5	7.21	22	96.0	9.08	81.9–115.4	9.46	24	182.0	19.41	154.4–221.0	10.67
	F	23	99.3	8.08	80.8–113.4	8.14	25	90.2	9.35	68.6–105.8	10.37	23	165.6	13.53	132.7–192.3	8.17
	C	43	101.4	8.07	80.8–123.5	7.96	47	92.9	9.59	68.6–115.4	10.32	47	174.0	18.57	132.7–221.0	10.67
M ₂ MD(C)	M	19	11.6	0.58	10.8–13.1	5.04	25	12.0	0.54	10.8–12.9	4.46	24	18.3	1.16	16.5–20.1	6.36
	F	23	11.5	0.52	10.2–12.2	4.51	25	11.5	0.51	10.4–12.4	4.49	24	17.1	0.73	15.4–18.7	4.26
	C	42	11.6	0.54	10.2–13.1	4.71	50	11.7	0.59	10.4–12.9	5.05	48	17.7	1.14	15.4–20.1	6.43
M ₂ BL	M	19	11.0	0.54	10.2–12.2	4.89	25	10.9	0.71	9.9–12.8	6.47	24	15.7	0.99	13.8–17.5	6.30
	F	23	10.5	0.40	9.9–11.3	3.78	25	10.2	0.60	8.9–11.2	5.90	24	14.5	0.57	13.2–15.3	3.94
	C	42	10.7	0.51	9.9–12.2	4.78	50	10.6	1.75	8.9–12.8	7.11	48	15.1	1.02	13.2–17.5	6.77
M ₂ MCA	M	19	103.8	7.56	93.5–122.8	7.28	25	110.5	12.05	92.4–135.7	10.90	24	233.1	27.75	183.2–280.9	11.91
	F	23	98.4	8.20	79.5–112.6	8.33	25	100.3	9.83	77.0–119.7	9.80	24	203.0	15.36	167.2–226.2	7.57
	C	42	100.8	8.27	79.5–122.8	8.20	50	105.4	12.04	77.0–135.7	11.42	48	218.0	26.90	167.2–280.9	12.34
M ₃ MD(C)	M	19	11.8	0.82	10.5–13.4	6.96	21	11.4	0.55	10.6–12.6	4.83	22	18.0	1.27	15.9–20.3	7.05
	F	20	11.4	1.01	9.3–13.9	8.91	21	10.8	0.53	9.7–11.8	4.89	21	16.7	0.89	14.4–18.0	5.32
	C	39	11.6	0.94	9.3–13.9	8.12	42	11.1	0.62	9.7–12.6	5.60	43	17.4	1.29	14.4–20.3	7.42
M ₃ BL	M	19	10.9	0.63	9.9–12.1	5.80	21	10.5	0.61	9.1–11.6	5.81	22	15.3	1.20	12.9–17.8	7.88
	F	20	10.7	0.53	9.5–11.8	4.97	21	9.8	0.60	8.7–10.9	6.08	21	14.2	0.85	11.5–15.5	5.97
	C	39	10.8	0.59	9.5–12.1	5.43	42	10.1	0.68	8.7–11.6	6.75	43	14.8	1.17	11.5–17.8	7.92
M ₃ MCA	M	18	101.8	10.77	83.2–118.1	10.57	21	99.9	9.43	81.0–117.5	9.49	22	216.7	29.09	162.7–262.3	13.42
	F	20	95.6	12.08	72.5–121.5	12.64	21	88.1	8.90	73.1–105.3	10.11	21	188.5	17.62	143.1–216.9	9.35
	C	38	98.5	11.76	72.5–121.5	11.93	42	94.0	10.86	73.1–117.5	11.55	43	202.9	27.85	143.1–262.3	13.72
P ⁴ MD(C)	M	22	7.2	0.45	6.5–7.8	6.23	20	7.6	0.63	6.3–8.9	8.32	23	11.3	0.77	9.9–12.6	6.82
	F	21	7.2	0.45	6.3–8.4	6.31	25	7.5	0.53	6.6–8.5	7.04	25	10.8	0.62	9.5–12.1	5.71
	C	43	7.2	0.45	6.3–8.4	6.20	45	7.5	0.57	6.3–8.9	7.63	48	11.0	0.74	9.5–12.6	6.74
P ⁴ BL	M	22	9.8	0.51	9.1–10.8	5.16	20	10.4	0.80	8.5–11.9	7.77	23	14.9	0.97	12.9–16.4	6.54
	F	22	9.5	0.46	8.3–10.3	4.87	25	10.0	0.56	9.3–11.5	5.67	25	14.1	0.59	12.8–15.2	4.21
	C	44	9.7	0.51	8.3–10.8	5.28	45	10.1	0.70	8.5–11.9	6.91	48	14.5	0.89	12.8–16.4	6.13
P ⁴ MCA	M	21	54.0	5.02	47.7–63.9	9.30	20	62.7	9.13	44.7–81.4	14.57	22	129.5	17.75	97.4–160.2	13.71
	F	22	53.8	7.18	41.6–68.4	13.35	25	59.4	6.29	51.7–73.9	10.59	24	118.3	12.82	94.3–147.0	10.84
	C	43	53.9	6.16	41.6–68.4	11.41	45	60.8	7.77	44.7–81.4	12.77	46	123.7	16.22	94.3–160.2	13.11
M ¹ MD(C)	M	17	11.3	0.70	9.9–12.6	6.16	22	10.8	0.63	9.7–12.3	5.84	23	15.5	0.82	14.1–17.0	5.25
	F	23	11.0	0.54	9.7–12.0	4.85	25	10.4	0.56	9.5–11.7	5.34	23	14.7	0.65	13.5–15.5	4.41
	C	40	11.2	0.62	9.7–12.6	5.54	47	10.6	0.61	9.5–12.3	5.75	46	15.1	0.85	13.5–17.0	5.63

Table 2. (continued)

		<i>Homo sapiens</i>					<i>Pan troglodytes</i>					<i>Gorilla gorilla</i>				
		N	Mean	SD	Range	CV	N	Mean	SD	Range	CV	N	Mean	SD	Range	CV
M ¹ BL	M	17	11.7	0.56	10.9–13.1	4.77	22	11.8	0.69	10.9–13.0	5.41	23	15.5	1.00	13.9–17.2	6.47
	F	23	11.4	0.46	10.5–12.2	4.02	25	11.2	0.73	10.0–12.7	6.47	23	14.7	0.66	13.3–15.8	4.50
	C	40	11.5	0.51	10.5–13.1	4.41	47	11.5	0.74	10.0–13.0	6.48	46	15.1	0.93	13.3–17.2	6.18
M ¹ MCA	M	16	103.2	11.19	85.8–128.4	10.85	22	104.8	10.54	89.8–127.2	10.06	22	183.9	20.00	142.4–218.9	10.88
	F	22	98.6	7.82	83.4–113.7	7.93	25	96.6	10.04	78.2–114.8	10.40	22	167.1	15.99	133.0–201.5	9.57
	C	38	100.5	9.52	83.4–128.4	9.47	47	100.4	10.99	78.2–127.2	10.94	44	175.5	198.1	133.0–218.9	11.29
M ² MD(C)	M	18	10.9	0.86	9.6–12.8	7.84	22	11.0	0.63	9.9–12.5	5.77	24	17.1	1.20	15.0–19.2	7.02
	F	25	10.9	0.65	9.7–12.5	5.92	25	10.4	0.64	9.4–11.9	6.14	25	15.8	0.76	14.2–16.8	4.82
	C	43	10.9	0.73	9.6–12.8	6.71	47	10.7	0.69	9.4–12.5	6.43	49	16.4	1.17	14.2–19.2	7.09
M ² BL	M	18	12.5	0.71	11.3–13.6	5.66	22	1.2	0.79	10.9–13.6	6.42	24	16.5	1.02	14.7–18.8	6.20
	F	25	11.8	0.49	10.9–12.7	4.17	25	11.5	0.71	10.4–13.0	6.17	25	15.4	0.81	13.5–17.0	5.26
	C	43	12.1	0.66	10.9–13.6	5.48	47	11.8	0.83	10.4–13.6	6.96	49	15.9	1.06	13.5–18.8	6.67
M ² MCA	M	16	103.1	12.00	84.4–126.4	11.69	22	108.6	10.38	88.8–130.5	9.56	23	211.3	28.11	161.9–272.9	13.30
	F	24	99.9	8.99	82.2–122.1	9.00	25	98.4	10.87	77.2–118.4	11.06	24	187.9	13.89	156.5–210.3	7.39
	C	40	101.1	10.27	82.2–126.4	10.15	47	103.1	11.72	77.2–130.5	11.37	47	199.4	24.80	156.5–272.9	12.44

^a MD(C) = mesiodistal corrected; BL = buccolingual; MCA = measured crown area; M = males; F = females; C = combined sex.

Table 3. *Paranthropus boisei* (*sensu stricto*) sample^a

Specimen	Description	Age (myr) ^b
KNM-ER 729	Mandible	1.49–1.55
KNM-ER 733	Mandible/skull fragments	1.49–1.55
KNM-ER 801	Mandibular fragment	1.56–1.60
KNM-ER 802	Isolated teeth	1.56–1.60
KNM-ER 810	Mandibular fragment	1.77
KNM-ER 818	Mandibular fragment	1.55–1.65
KNM-ER 1171	Isolated teeth	1.56–1.60
KNM-ER 1467	Isolated teeth	1.49–1.55
KNM-ER 1509	Isolated teeth	1.56–1.60
KNM-ER 1804	Maxillary fragment	1.77
KNM-ER 1816	Mandibular fragments/teeth	1.56–1.60
KNM-ER 1820	Mandibular fragment	1.67–1.70
KNM-ER 3230	Mandible	1.56–1.60
KNM-ER 3737	Isolated teeth	1.56–1.60
KNM-ER 3885	Isolated tooth	1.77–1.79
KNM-ER 3890	Isolated tooth	1.56–1.60
KNM-ER 5877	Mandibular fragments	1.49–1.55
KNM-ER 15930	Mandibular fragment	1.77
KNM-ER 15940	Isolated teeth	1.77

^a Data from Wood (1991a); Leakey and Walker (1988).

^b Ages taken from Wood and Constantino (2007).

situated in the center of the image seen through the camera's LCD monitor to minimize parallax error (Bailey et al., 2004). A scale was included in each photograph and placed parallel to the tooth in the same horizontal plane as the occlusal surface. The digital photos were transferred to the computer, calibrated, and measured on-screen using Photoshop 7.0 software (© Adobe Systems, Inc.). Each measurement was taken three times and the mean value recorded for the specimen. Intraobserver measurement error was consistently less than 1%, comparable to other investigations of crown occlusal areas (e.g. Wood and Abbott, 1983; Bermúdez de Castro and Nicolás, 1995; Bromage et al., 1995; Bermúdez de Castro et al., 1999, 2001; Kondo and Townsend, 2006). The variables employed are limited to those that are present in at least two of the Georgian individuals. The mesiodistal and buccolingual measurements obtained for the Dmanisi teeth in this study (Table 4) do not

differ considerably (generally less than 0.3 mm) from those provided in earlier papers (Rightmire et al., 2006; Martínón-Torres et al., 2008). However, several dimensions (such as those of the maxillary second molar and mandibular third premolar) do display more substantial variation—most likely due to differences in measurement technique, including corrections for interproximal wear, and observer error. When tooth antimeres are available, the average of both sides is used to represent the specimen in the randomization analyses.

Statistical tests

Systematic resampling (randomization) of skeletal dimensions is a powerful and useful method for assessing variation in small samples (Lockwood et al., 1996; Reno et al., 2003) and has been employed in a number of analyses concerning fossil hominins (e.g. Kramer et al., 1995; Richmond and Jungers, 1995; Grine et al., 1996; Lockwood et al., 1996, 2000; Arsuaga et al., 1997; Lorenzo et al., 1998, 2005; Aiello et al., 1999; Lockwood, 1999; Bermúdez de Castro et al., 2001; Silverman et al., 2001; Reno et al., 2003; Dobson, 2005; Villmoare, 2005; Skinner et al., 2006). In this study, exact randomization methodology (Manly, 1997) is used to evaluate the degree of variation in the Dmanisi dentition when only two individuals are available for analysis. This method involves computing all possible pairwise size ratios of metric variables (larger value divided by smaller value) in a comparative sample. A previous analysis, however, demonstrated that utilizing the entire sample available for a fossil assemblage presents a more conservative assessment of variation than that provided by pairwise comparisons using exact randomization, even when the fossil sample includes only three individuals (Lockwood et al., 1996). Therefore, for the remaining variables in which more than two Georgian specimens are available for study, bootstrapping methodology (Manly, 1997) is employed. This method consists of simulating 1000 random samples from a comparative taxon, keeping sample size comparable to the Georgian assemblage ($n = 3$). The maximum ratio (largest value divided by smallest value) of each random sample is then calculated.

Table 4. Measurements (mm) of the Dmanisi dentition^a

Variable	Side	D211	D2282	D2600	D2700 ^b	D2735 ^c
P ⁴ MD(C)	Right	—	8.6	—	7.0	—
	Left	—	—	—	—	—
P ⁴ BL	Right	—	10.8	—	11.6	—
	Left	—	—	—	—	—
P ⁴ MCA	Right	—	71.7	—	65.5	—
	Left	—	—	—	—	—
M ¹ MD(C)	Right	—	12.8	—	13.4	—
	Left	—	12.7	—	13.1	—
M ¹ BL	Right	—	12.8	—	13.1	—
	Left	—	12.9	—	13.0	—
M ¹ MCA	Right	—	135.0	—	144.0	—
	Left	—	130.1	—	138.5	—
M ² MD(C)	Right	—	—	—	12.9	—
	Left	—	13.0	—	13.1	—
M ² BL	Right	—	—	—	13.1	—
	Left	—	12.4	—	13.1	—
M ² MCA	Right	—	—	—	136.1	—
	Left	—	126.4	—	134.0	—
I ₂ BL	Right	6.4	—	—	—	7.2
	Left	6.4	—	—	—	7.5
C ₁ BL	Right	8.2	—	—	—	9.2
	Left	8.3	—	—	—	9.2
P ₃ MD(C)	Right	8.9	—	9.5 ^d	—	9.7
	Left	9.1	—	—	—	9.9
P ₃ BL	Right	9.6	—	11.9 ^d	—	10.1
	Left	9.4	—	—	—	10.1
P ₃ MCA	Right	63.6	—	85.4 ^d	—	73.0
	Left	63.6	—	—	—	73.4
P ₄ MD(C)	Right	8.2	—	—	—	7.7
	Left	8.2	—	—	—	7.8
P ₄ BL	Right	9.7	—	—	—	9.3
	Left	9.7	—	—	—	9.3
P ₄ MCA	Right	65.6	—	—	—	60.0
	Left	66.2	—	—	—	57.9
M ₁ MD(C)	Right	13.3	—	—	—	13.3
	Left	13.4	—	—	—	13.2
M ₁ BL	Right	12.5	—	—	—	11.6
	Left	12.4	—	—	—	11.2
M ₁ MCA	Right	133.3	—	—	—	132.0
	Left	134.2	—	—	—	120.4
M ₂ MD(C)	Right	12.3	—	13.9	—	13.6
	Left	12.2	—	13.8	—	13.2
M ₂ BL	Right	11.6	—	13.4	—	10.7
	Left	11.6	—	13.0	—	10.5
M ₂ MCA	Right	122.1	—	157.0	—	120.0
	Left	124.0	—	153.6	—	114.5
M ₃ MD(C)	Right	11.6	—	15.7	—	—
	Left	11.2	—	15.0	—	—
M ₃ BL	Right	10.6	—	13.3	—	—
	Left	10.5	—	12.5	—	—
M ₃ MCA	Right	98.7	—	176.3	—	—
	Left	96.1	—	161.0	—	—

^a MD(C) = mesiodistal corrected; BL = buccolingual; MCA = measured crown area.

^b Includes specimens: D2710 (left M¹) and D2719 (right P⁴). The left P⁴ is not included in the analyses as this tooth is pathologically deformed.

^c Includes specimens: D2678 (right C₁), D2723 (left C₁), D2854 (right I₂), and D3698 (left I₂).

^d The severity of occlusal wear does not allow for an accurate estimation of crown dimensions in the unworn state, and thus measurements represent only minimum values.

For both resampling procedures, the maximum ratio for the Dmanisi sample is then compared against the distribution of ratios generated for the comparative sample to determine the likelihood of sampling a pair of specimens from a reference species that exhibit size differences greater than those present in the Dmanisi assemblage. If the result is a low probability ($P < 0.05$) in comparison to the species with a high degree of dimorphism (e.g. gorillas), this would suggest the presence of multiple species in the Georgian sample (Lockwood, 1999). Low probabilities when compared to less dimorphic chimpanzees and humans would suggest that size variation, and by inference sexual dimorphism, in the Dmanisi sample is higher than in those taxa (Lockwood, 1999).

Because multiple comparisons are made (26 for each reference taxon), the sequential Bonferroni correction (Holm, 1979; Rice, 1989) was used to protect against Type I errors and maintain an α level of 0.05 for each comparative group (across all 26 variables). However, within the biological sciences there is substantial debate concerning the application of the Bonferroni correction. A number of researchers note that there is no formal consensus for when, or how, adjustments for multiple testing are to be performed (e.g. Feise, 2002; Moran, 2003; Nakagawa, 2004), while others feel that the increase in Type II errors associated with this procedure is unacceptable (e.g. Rothman, 1990; Perneger, 1998; Moran, 2003; Nakagawa, 2004). In addition, some researchers feel that the Bonferroni correction is an inappropriate method for this type of data, because the separate dimensions do not constitute independent tests (Kramer et al., 1995; Lockwood, 1999; Lockwood et al., 2000). Therefore, significant values at unadjusted 0.05 α levels are also reported.

The comparison of size variation at Dmanisi to that of *P. boisei* involved an assessment of whether, for each dental dimension, the maximum ratios found in this fossil sample exceeded that of the Georgian assemblage. These comparisons included a similar set of metric variables as that utilized in the randomization analyses with the extant hominine taxa; only maxillary P4 dimensions have been excluded, as the restricted australopithecine sample does not preserve the minimum of two individuals needed for comparison.

Results

The results of the randomization analyses for the Dmanisi dentition are presented in Table 5. In analyses that include only D211/D2282 and D2735/D2700, the Dmanisi dentition does not display excessive size variation compared with the distributions of the extant reference samples. Nearly all of the maxillary teeth analyzed show low levels of variation in which the probability of finding a maximum ratio in the comparative taxa greater than that of the Dmanisi sample is relatively high. Only one variable measured for the Dmanisi sample exceeds the size variation present in the highly dimorphic gorilla sample [P⁴ MD(C); $P = 0.025$]. However, this P -value is not significant after the sequential Bonferroni correction is applied. As for the mandibular teeth, no dental dimension is significantly more variable among the Dmanisi hominins than in the three reference samples.

Slightly different results are obtained when D2600 is included in the analyses along with D211 or both D211 and

Table 5. Probabilities of obtaining maximum ratios in extant hominine samples greater than those that characterize the Dmanisi dentition^a

Variable	Comparison	Ratio	<i>n</i>	Humans	Chimpanzees	Gorillas
I ₂ BL	D2735/D211	1.156	2	0.152	0.205	0.180
C ₁ BL	D2735/D211	1.115	2	0.327	0.658	0.653
P ₃ MD(C)	D2735/D211	1.089	3	0.626	0.597	0.785
P ₃ BL	D2600/D211	1.253	3	0.068	0.069	0.225
P ₃ MCA	D2600/D211	1.343	3	0.206	0.208	0.430
P ₄ MD(C)	D211/D2735	1.051	2	0.562	0.543	0.590
P ₄ BL	D211/D2735	1.043	2	0.665	0.723	0.709
P ₄ MCA	D211/D2735	1.117	2	0.500	0.428	0.553
M ₁ MD(C)	D211/D2735	1.008	2	0.919	0.949	0.891
M ₁ BL	D211/D2735	1.096	2	0.196	0.178	0.304
M ₁ MCA	D211/D2735	1.060	2	0.585	0.700	0.675
M ₂ MD(C)	D2600/D211	1.130	3	0.158	0.206	0.361
M ₂ BL	D2600/D2735	1.245	3	0.000	0.077	0.053
M ₂ MCA	D2600/D2735	1.324	3	0.050	0.181	0.233
M ₃ MD(C)	D2600/D211	1.351	2	0.009	0.000	0.003
M ₃ BL	D2600/D211	1.217	2	0.009	0.036	0.085
M ₃ MCA	D2600/D211	1.749	2	0.000	0.000	0.003
P ^d MD(C)	D2282/D2700	1.229	2	0.060	0.055	0.025
P ^d BL	D2700/D2282	1.074	2	0.344	0.455	0.410
P ^d MCA	D2282/D2700	1.095	2	0.550	0.597	0.634
M ¹ MD(C)	D2700/D2282	1.039	2	0.622	0.637	0.651
M ¹ BL	D2700/D2282	1.016	2	0.835	0.901	0.837
M ¹ MCA	D2700/D2282	1.066	2	0.613	0.693	0.712
M ² MD(C)	D2700/D2282	1.000	2	0.963	0.959	0.974
M ² BL	D2700/D2282	1.056	2	0.489	0.600	0.581
M ² MCA	D2700/D2282	1.069	2	0.656	0.694	0.673

^a MD(C) = mesiodistal corrected; BL = buccolingual; MCA = measured crown area. The maximum ratios for the Dmanisi sample are calculated using the average value for tooth antimeres, when available. **Boldface** *P*-values indicate that Dmanisi ratios are significantly greater than those of the comparative samples ($P < 0.05$). **Boldface and italic** *P*-values indicate that Dmanisi ratios are significantly greater than those of the comparative samples after the sequential Bonferroni adjustment.

Table 6. Comparison of maximum ratios between Dmanisi and *Paranthropus boisei*^a

Variable	Dmanisi			<i>Paranthropus boisei</i>		
	Comparison	Ratio	<i>n</i>	Comparison	Ratio	N
I ₂ BL	D2735/D211	1.156	2	KNM-ER 3230/ER 801	1.209	2
C ₁ BL	D2735/D211	1.115	2	KNM-ER 729/ER 3230	1.021	2
P ₃ MD(C)	D2735/D211	1.089	3	KNM-ER 729/ER 1816	1.120	3
P ₃ BL	D2600/D211	1.253	3	KNM-ER 3230/ER 1816	1.171	3
P ₃ MCA	D2600/D211	1.343	3	KNM-ER 729/ER 3230	1.024	2
P ₄ MD(C)	D211/D2735	1.051	2	KNM-ER 1171/ER 3885	1.287	8
P ₄ BL	D211/D2735	1.043	2	KNM-ER 3230/ER 1816	1.146	8
P ₄ MCA	D211/D2735	1.117	2	KNM-ER 3230/ER 802	1.220	7
M ₁ MD(C)	D211/D2735	1.008	2	KNM-ER 3230/ER 1820	1.111	8
M ₁ BL	D211/D2735	1.096	2	KNM-ER 729/ER 15930	1.250	8
M ₁ MCA	D211/D2735	1.060	2	KNM-ER 3230/ER 3890	1.197	7
M ₂ MD(C)	D2600/D211	1.130	3	KNM-ER 3230/ER 1816	1.185	5
M ₂ BL	D2600/D2735	1.245	3	KNM-ER 3230/ER 15930	1.297	6
M ₂ MCA	D2600/D2735	1.324	3	KNM-ER 3230/ER 1816	1.366	5
M ₃ MD(C)	D2600/D211	1.351	2	KNM-ER 5877/ER 810	1.441	8
M ₃ BL	D2600/D211	1.217	2	KNM-ER 5877/ER 15930	1.333	10
M ₃ MCA	D2600/D211	1.749	2	KNM-ER 729/ER 810	1.460	6
M ¹ MD(C)	D2700/D2282	1.039	2	KNM-ER 733/ER 1804	1.061	2
M ¹ BL	D2700/D2282	1.016	2	KNM-ER 733/ER 1804	1.024	2
M ¹ MCA	D2700/D2282	1.066	2	KNM-ER 733/ER 1804	1.005	2
M ² MD(C)	D2700/D2282	1.000	2	KNM-ER 1171/ER 1804	1.050	2
M ² BL	D2700/D2282	1.056	2	KNM-ER 1804/ER 1171	1.040	2
M ² MCA	D2700/D2282	1.069	2	KNM-ER 1804/ER 1171	1.071	2

^a MD(C) = mesiodistal corrected; BL = buccolingual; MCA = measured crown area. The maximum ratios are calculated using the average value for tooth antimeres, when available. **Boldface** values indicate that the maximum ratio of the Dmanisi dentition exceeds that found in any pairwise comparison in *P. boisei*.

D2735. The maximum ratios of the Dmanisi teeth for third premolar and second molar dimensions are commonly exceeded in random samples of extant hominines. Of these eight dental dimensions analyzed in the Dmanisi sample, two display more variation than is present in modern humans (M_2 BL, M_2 MCA; $P \leq 0.05$), and only crown width ($P = 0.000$) is significant after the sequential Bonferroni correction is applied.

However, as the measurements of the third premolar recorded for D2600 represent only minimum values, the maximum ratios provided for the Georgian third premolars almost certainly underestimate the size variation among these hominins. In the Georgian dentition, the M_3 appears to be the most variable tooth. All three dental dimensions of the Dmanisi assemblage have maximum ratios that are rarely, or never, exceeded in pairwise comparisons of either modern humans or chimpanzees ($P \leq 0.036$). Crown length and area of the third molar are also more variable than in the gorilla sample ($P = 0.003$). The P -values for the gorilla sample are not significant, however, after the sequential Bonferroni adjustment.

The results of the comparison of maximum ratios for the Dmanisi and *P. boisei* samples are given in Table 6. These results indicate that there is a fair amount of size variation in the *P. boisei* sample. In relation to the Dmanisi assemblage, the *P. boisei* sample possesses larger maximum ratios for a majority of variables, including dimensions of the mandibular P_4 , M_1 , and M_2 . As with the Dmanisi assemblage, the M_3 appears to be the most variable tooth in the *P. boisei* sample. The maximum ratios for *P. boisei* exceed those of Dmanisi for M_3 crown length and breadth diameters, although the Georgian sample is more variable for M_3 crown area. In addition, the Dmanisi dentition possesses maximum ratios that exceed those of *P. boisei* for several mandibular canine and third premolar crown dimensions. For the maxillary teeth, the maximum ratios for the two fossil hominin samples are roughly equal for most dimensions.

Discussion

The results from the randomization analyses reveal that the Dmanisi sample is characterized by a lower level of maxillary dental size variation than all extant comparative taxa. Likewise, size variation in the mandibular dimensions of the Dmanisi dentition is exceeded in the comparative samples much of the time. As nearly all of these comparisons are between D211/D2282 and D2735/D2700, the results of the analyses provide evidence for the taxonomic homogeneity of these two individuals. This is consistent with a recent morphological analysis of the Dmanisi dental remains (Martínón-Torres et al., 2008), as well as earlier studies concerning the associated mandibles and crania (Vekua et al., 2002; Rightmire et al., 2006).

Interestingly, among the Dmanisi mandibular teeth a couple of M_3 dimensions display significantly greater size variation (using unadjusted significance levels) compared to the highly dimorphic *Gorilla* sample. These comparisons include teeth associated with the large and somewhat distinct D2600 mandible. However, the results of the randomization analyses using Bonferroni-adjusted significance levels indi-

cate that the size variation observed in the Dmanisi sample for all dental dimensions, including the third molar, is not significantly greater than in the gorilla sample, and thus provide no support for a multiple-species hypothesis. For the additional variables in which D2600 was included in the comparisons (such as P_3 and M_2 dimensions), the variation exhibited by the Dmanisi specimens is also not significant, supporting a single-taxon solution. However, the values recorded for D2600, particularly for the third premolar, are affected by occlusal wear, and as a result, the degree of variation among the Georgian hominins for this tooth is almost certainly underestimated. Therefore, when compared to extant reference taxa, the degree of metric variation within the Dmanisi dental sample provides equivocal evidence concerning the taxonomic association of D2600 with the other Georgian specimens.

The Dmanisi hominins also appear less variable than *P. boisei*, a fossil taxon whose integrity as a single species has been confirmed by a number of studies (e.g. Wood, 1991b; Silverman et al., 2001; Wood and Lieberman, 2001). On the whole, the *P. boisei* sample displays larger maximum ratios than does the Dmanisi assemblage. This includes ratios for several M_2 and M_3 dimensions that were significantly more variable compared to the extant reference taxa. These results suggest that the size variation within the Dmanisi dental sample, including that of the M_3 , is not excessive for a fossil hominin group dated to the Early Pleistocene. However, the high variability displayed by *P. boisei* may be due, in part, to the effects of time (Lockwood et al., 2000). Although the *P. boisei* sample was chosen to be as temporally and geographically restricted as possible, a time depth up to 250 ka is associated with the specimens included in the size comparisons; and even a few tens of thousands of years may generate an additional source of variation in fossil collections (Pilbeam, 1978; Lieberman et al., 1988; Wood and Xu, 1991; Wood, 1993). Nonetheless, the diversity within the *P. boisei* sample employed in this study must reflect, to a certain extent, the considerable range of size variation previously observed for this taxon (e.g. Blumenberg and Lloyd, 1983; Wood, 1991b; Lockwood et al., 2000; Silverman et al., 2001; Moggi-Cecchi, 2003). Therefore, the metric size variation observed within the Dmanisi dental sample is insufficient to reject the null hypothesis of a single species, assuming that the variation displayed by the *P. boisei* sample sets an appropriate upper limit by which to judge the Georgian assemblage.

Although metric analyses provide valuable evidence regarding the taxonomic homogeneity of a fossil sample, a more robust evaluation also includes information concerning the level of morphological variation. However, the tooth crowns of D2600 are appreciably worn, prohibiting a comprehensive assessment of the morphological dental variation displayed by the Dmanisi hominins. Nonetheless, one morphological feature that can be observed in this specimen is mandibular premolar root form. The expression of premolar root form within the Dmanisi sample was among the features that prompted Gabunia and colleagues (Gabunia et al., 2002b) to question the taxonomic association of D2600 and D211. Among the Georgian specimens, the lower premolars of D211 are single-rooted, whereas in D2600 these teeth ex-

hibit two completely separate roots (mesial and distal). In D2735, the P_3 s have a Tomes' root form, while the P_4 s are single-rooted (Macaluso, 2006). However, mandibular premolar root form among other early *Homo* groups is also quite variable, with expression varying from a single root, via Tomes' root form, to teeth with separate mesial and distal roots (Wood, 1991a, 1993, 1994; Antón, 2003; Kaifu et al., 2005). In addition, modern human populations are also polymorphic in mandibular premolar root form (Abbott, 1984; Eckhardt, 2003). Furthermore, a recent study of post-canine mandibular root form among modern humans has demonstrated that males with larger teeth have a significantly higher proportion of multi-rooted premolars (Shields, 2005). Wood (1993) also demonstrated that the P_3 roots of *Pan* are somewhat sexually dimorphic, with females exhibiting a higher frequency of single-rooted teeth (46%) compared to that of males (20%). Assuming that these relationships also apply to Plio-Pleistocene *Homo*, the variation observed in the postcanine subocclusal morphology of the Dmanisi hominins may be attributed to sexual dimorphism. Therefore, based on these comparisons, it is not unreasonable to presume that the polymorphism in premolar root form within the Dmanisi sample is the result of normal intraspecific variation.

In summary, the majority of metric dimensions do not exhibit a significant level of variation compared to extant and extinct hominines. In addition, the evidence for interspecific variation among the Georgian M_3 crowns and premolar roots is not conclusive. Therefore, the results presented above provide tentative support for the acceptance of the single-species hypothesis for the current dental sample. If it is accepted that all of the Dmanisi hominins, including the large D2600 mandible, belong to a single taxon, then sexual dimorphism is one explanation for the observed differences between specimens (Gabunia et al., 2002a; Lordkipanidze et al., 2006; Rightmire et al., 2008).

Conclusions

When the results of the randomization analyses and comparisons of premolar root form are considered, the case for taxonomic heterogeneity within the Georgian dental sample is finely balanced. For most variables, the range of size among the specimens from Dmanisi can be accommodated within models of dimorphism based on extant and extinct analogues. As the comparisons frequently incorporate D211/D2282 and D2735/D2700, these specimens can be grouped together without reservation. This result is consistent with previous studies pertaining to the observable variation among the associated cranial and mandibular remains (Vekua et al., 2002; Macaluso et al., 2004; Rightmire et al., 2006). Whether the D2600 mandible should be included within this sample or considered distinct is perhaps more questionable as the dentition of this robust specimen differs from the other Georgian fossils in proportions of the distal cheek teeth and its premolar root form. Nonetheless, it is argued that the size range and variation in premolar root form expressed by the Dmanisi dental sample, including D2600, is presently insufficient to reject the null hypothesis of a single species.

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