Brief Communication: Is Variation in the Cranial Capacity of the Dmanisi Sample Too High To Be From a Single Species?

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ABSTRACT This study uses data resampling to test the null hypothesis that the degree of variation in the cranial capacity of the Dmanisi hominid sample is within the range variation of a single species. The statistical significance of the variation in the Dmanisi sample is examined using simulated distributions based on comparative samples of modern humans, chimpanzees, and gorillas. Results show that it is unlikely to find the maximum difference observed in the Dmanisi sample in distributions of female-female pairs from comparative single-species samples. Given that two sexes are represented, the difference in the Dmanisi sample is not enough to reject the null hypothesis of a single species. Results of this study suggest no compelling reason to invoke multiple taxa to explain variation in the cranial capacity of the Dmanisi hominids. Am J Phys Anthropol 127:263–266, 2005. © 2005 Wiley-Liss, Inc.

Variation in the hominid cranial sample from Dmanisi, Georgia (Gabunia et al., 2000; Vekua et al., 2002), has been the subject of a question often asked in paleoanthropology: does the sample represent more than one species? The researchers who reported on the first two crania discovered, D2280 and D2282, attributed them to a single species, *Homo ergaster* (Gabunia et al., 2000). However, the interpretation of the difference between these two crania ranged from that of two species (Schwartz, 2000) to that of two females of the same species (Wolpoff, 2002). With the discovery of another Dmanisi cranium, D2700 (Vekua et al., 2002), the cranial sample size of the Dmanisi hominids increased to three.[1] Although the newest additions to the sample prompted the discoverers to propose a new species, *Homo georgicus* (Gabunia et al., 2002), there was no change in their position that all the specimens in the Dmanisi hominid sample belonged to a single species.

The purpose of this paper is to test the null hypothesis that variation in the cranial capacity of the Dmanisi sample is within that expected from a sample consisting of a single species. Several mechanisms account for variation within a species: ontogeny, individual variation, sexual dimorphism, time, and geography (Eckhardt, 2000; Miller, 1991; Wood, 1976). Based on faunal remains and paleomagnetic evidence, the date of the hominids from Dmanisi is thought to be about 1.77–1.95 million years old (Vekua et al., 2002). Although these dates are not without controversy (Bräuer and Schultz, 1996; Dean and Delson, 1995), what remains undisputed is that the crania are from a time period of narrow span. As the Dmanisi cranial sample consists of adults (or near adults) of approximately the same geological age from one site, ontogeny, time, and geography can be ruled out. I examine sexual dimorphism and intrasexual individual variation as mechanisms that might explain the variation in the Dmanisi cranial sample.

MATERIALS

D2280 is a near-complete calvaria, and its endocranial volume of 775 cc was directly measured with seeds (Gabunia et al., 2000). Compared to D2282 (see below), D2280 has a larger cranial capacity and is more robust, suggesting male characteristics; however, some argue that it is a female specimen, based on morphological features (Wolpoff, 2002).

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[1]At the 72nd Annual Meeting of the American Association of Physical Anthropologists (April 2003), the discovery of a fourth hominid cranium from Dmanisi was announced. However, as the specimen has yet to be described, it is not examined in this paper.

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A subadult cranium, D2282, is thought to be female because of its small size and gracile morphology (Gabunia et al., 2000). The cranial capacity for D2282 cannot be measured directly because of postmortem deformation, and is estimated to be 650 cc (Gabunia et al., 2000). The D2700 cranium has partially erupted M^3s, and is reported to be a young individual. Its gracile morphology might be attributable to sex (female), although the researchers voice caution in the sex assessment due to the large crown size of the upper canines (Vekua et al., 2002). Because of its incomplete growth, the estimate of 600 cc for the endocranial capacity of D2700 may underestimate its adult endocranial volume.

The internal cranial sutures are closed in the two older specimens, D2280 and D2282 (Milford Wolpoff, personal communication); therefore, both individuals have completed growth in terms of cranial capacity, although they may have incomplete somatic growth. D2700 was reported to be equal to a 12–13-year-old modern human, based on dental development (Vekua et al., 2002). A subadult attains 93% growth of adult cranial capacity in modern humans, and 96–97% of adult cranial capacity, in chimpanzees, gorillas, and orangutans (Ashton and Spence, 1958). This study considers three cranial capacity values for D2700: 600 cc as reported, 618 cc under the assumption that 97% of cranial capacity growth is completed, and 645 cc under the assumption that 93% is completed.

Comparative cranial capacity data for modern humans, chimpanzees, and gorillas are from the Hamann-Todd Osteological Collection at the Cleveland Museum of Natural History (Todd, 1923). The modern humans are Americans of mixed ethnicity. Only adult specimens with complete crania were included in the data set, comprising 91 humans (51 males and 40 females), 34 chimpanzees (13 males and 21 females), and 34 gorillas (19 males and 15 females).

METHODS

The null hypothesis that the variation in the Dmanisi crania sample is within that expected from a single species was tested by examining whether the variation in the fossil sample exceeded that within three comparative samples, each consisting of a single species. However, the small size of the fossil sample ($n = 3$) limits the kind of statistical comparisons likely to yield valid results; and the uncertain sex diagnosis of the specimens (see Materials) complicates the assessment of sexual dimorphism.

This paper uses a simple ratio (the larger value divided by the smaller value) between all possible pairs of the three specimens from Dmanisi. The ratios are evaluated using data resampling with replacement of comparative data (Kramer et al., 1995; Lee, 1995, 1999, 2001; Lieberman et al., 1988; Richmond and Jungers, 1995). By directly comparing the ratio of the fossil sample to generated comparative distributions, the probability of the observed value or greater can be assessed for statistical significance.

TABLE 1. Pairwise cranial capacity ratios in Dmanisi sample

	D2280 (775 cc)	D2282 (650 cc)
D2280 (775 cc)		
D2282 (650 cc)	1.19	
D2700 (600 cc)	1.29	1.08
$D2700_{97}$ (618 cc)[1]	1.25	1.05
$D2700_{93}$ (645 cc)[1]	1.20	1.00

[1] $D2700_{97}$ refers to a hypothetical value under assumption that D2700 completed 97% of its brain size growth. Likewise, $D2700_{93}$ refers to a hypothetical value under assumption that D2700 completed 93% of its brain size growth.

To examine whether the difference among the Dmanisi crania is due to sexual dimorphism, I used the sex assessment of the original researchers and treated D2280 as a male and the other two (D2282 and D2700) females. The observed differences between D2280 and D2282, and D2700, respectively, were compared with the distribution of difference generated from the comparative samples of humans, gorillas, and chimpanzees. For each species, the distribution was generated as follows: 1) based on the individual record of sex, a pair of values consisting of one male and one female was sampled with replacement; 2) the sampled pair of values was then converted into a ratio of the male value divided by the female value; and 3) steps 1 and 2 were repeated 1,000 times to yield a distribution of ratios. The Dmanisi data were then compared to the generated distributions in order to assess how likely it is to observe such a difference from the comparative sample. Because the statistic of interest is how likely it is to observe a certain point or greater, this is a one-tailed test. Therefore, if less than 5% of the generated distribution is greater than the observed value, the null hypothesis is rejected.

With respect to variation among individuals of the same sex, the three Dmanisi crania yield three possible combinations of pairs from which ratios can be generated. The comparative distributions were generated using two single-sex samples. Each sampled pair of values was converted into a ratio between the larger value and the smaller value, and the procedure was repeated 1,000 times to generate a distribution of ratios for each sex sample of each species. The Dmanisi data were then compared to the generated distributions. As was the case for the sexual dimorphism hypothesis, the null hypothesis of individual difference of same sex is rejected if less than 5% of the generated distribution is greater than the observed.

RESULTS

Observed values in the Dmanisi sample are commonly found in the generated comparative distributions of male and female pairs. Assuming that D2280 is a male, and D2282 and D2700 females, pairwise ratio values are 1.19 and 1.29 (Table 1). The difference between D2280 and D2700, 1.29, was

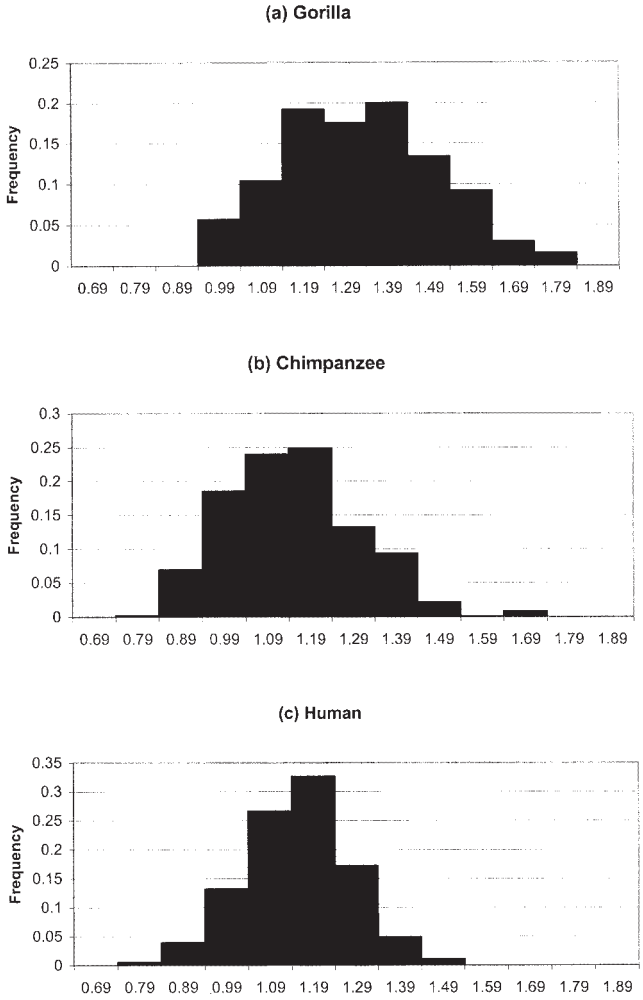

Fig. 1. Distribution of ratios from resampled male-female pairs of (**a**) gorillas, (**b**) chimpanzees, and (**c**) humans.

TABLE 2. Proportion of resampled distribution, male-female pairs

	1.29 or greater	1.25 or greater	1.20 or greater
Gorilla	0.47	0.54	0.64
Chimpanzee	0.12	0.18	0.25
Human	0.06	0.12	0.21

compared to distributions generated from resampled pairs of a male and a female (Fig. 1). For all three species, values greater than 1.29 were common: the observed value of 1.29 or greater comprised 47% of the gorilla distribution, 12% of the chimpanzee distribution, and 6% of the modern human distribution (Table 2). If D2700 can be assumed to have completed 97% of its cranial capacity growth (see Materials), the ratio of interest is 1.25. For all three species, values greater than 1.25 were common: 54% of the gorilla distribution, 18% of the chimpanzee distribution, and 12% of the modern human distribution showed values larger than 1.25 (Table 2). The ratio of interest (1.20) assuming D2700 completed

TABLE 3. Proportion of resampled distribution, male-male pairs

	1.29 or greater	1.25 or greater	1.20 or greater
Gorilla	0.12	0.16	0.29
Chimpanzee	0.08	0.17	0.25
Human	0.04	0.08	0.14

TABLE 4. Proportion of resampled distribution, female-female pairs

	1.29 or greater	1.25 or greater	1.20 or greater
Gorilla	0.02	0.08	0.15
Chimpanzee	0.03	0.06	0.15
Human	0.004	0.02	0.07

93% of its cranial capacity growth (see Materials) is found in even greater proportions from the generated distributions (Table 2).

The observed values in the Dmanisi sample are likely within the distributions of male and male pairs generated from gorillas or chimpanzees. If all three Dmanisi crania are male, pairwise ratios are 1.08, 1.19, and 1.29 (Table 1). The difference between D2280 and D2700, 1.29, was compared to distributions generated from resampled pairs of a male and a male. The largest value, 1.29, or greater comprises 12% of the gorilla distribution and 8% of the chimpanzee distribution. However, only 4% of the human distribution (Table 3) showed 1.29 or greater. If D2700 can be assumed to have completed 97% of its cranial capacity growth, the ratio of interest is 1.25. For all three species, values greater than 1.27 were not uncommon (Table 3). Results were similar in the hypothetical case of D2700 having completed 93% of its cranial capacity growth (Table 3).

The observed values in the Dmanisi sample are not likely to be found in distributions of female pairs generated from any of the three comparative taxa. If all three Dmanisi crania are female, pairwise ratios are 1.08, 1.19, and 1.29 (Table 1). The difference between D2280 and D2700, 1.29, was compared to distributions generated from resampled pairs of a female and a female. In all three species, less than 5% of the generated distributions showed a value of 1.29 or greater (Table 4). If D2700 can be assumed to have completed 97% of its cranial capacity growth, the ratio of interest is 1.25. Values greater than 1.25 were found in less than 5% in the comparative samples of chimpanzees or humans (Table 4). Under the second hypothetical scenario that D2700 completed 93% of its cranial capacity growth, ratios of 1.20 or greater were more common (Table 4).

DISCUSSION AND CONCLUSIONS

The results of this resampling study suggest that the largest difference between any two of the three Dmanisi endocranial volumes is often observed between male-female pairs of the comparative modern

humans, chimpanzees, and gorilla samples. The results were the same under two models of incomplete brain size growth. However, it is unlikely that such differences can be observed from intrasexual all-female pairwise differences.

These results need to be qualified in several ways. First, the data points of the fossil specimens may be in error. Only one value for each fossil specimen is reported as measured or estimated cranial capacity, without any error statements. For D2280, the cranial capacity is measured using seeds. However, this method was criticized for its unreliability and greater variation than lead shots (Gould, 1978). The reported cranial capacity for D2282 could be in error due to the effects of postmortem deformation and fragmentary preservation. The attempt to extrapolate to maturity the cranial capacity measurement of D2700 may have been incorrect. Another limitation of this study comes from the small sample size, by using the largest ratio possible from the three data points available.

Given the small sample size and the univariate nature of the analyses of this paper (Plavcan and Cope, 2001), definite conclusions cannot be drawn without further study. Variation comparable to that observed in the Dmanisi sample can easily be found in male-female pairs of modern humans, chimpanzees, and gorillas. On the other hand, it is quite unlikely that a pair of females can generate the level of difference in the Dmanisi sample. The results presented in this paper suggest that with respect to cranial capacity, the null hypothesis of a single species cannot be rejected.

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LITERATURE CITED

Ashton EH, Spence TF. 1958. Age changes in the cranial capacity and foramen magnum of hominoids. Proc R Soc Lond [Biol] 130:169–181.

Balter M, Gibbons A. 2002. Were "Little People" the first to venture out of Africa? Science 297:26–27.

Bräuer G, Schultz M. 1996. The morphological affinities of the Plio-Pleistocene mandible from Dmanisi, Georgia. J Hum Evol 30:445–481.

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

Eckhardt RB. 2000. Human paleobiology. Cambridge: Cambridge University Press.

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

Gabunia L, de Lumley M-A, Vekua A, Lordkipanidze D, de Lumley H. 2002. Découverte d'un nouvel hominidé à Dmanissi (Transcaucasie, Géorgie) [Discovery of a new hominid at Dmanisi (Transcaucasia, Georgia)]. C R Palevol 1:243–253.

Gould SJ. 1978. Morton's ranking of races by cranial capacity. Science 200:503–509.

Kramer A, Donnelly SM, Kidder JH, Ousley SD, Olah SM. 1995. Craniometric variation in large-bodied hominoids: testing the single-species hypothesis for *Homo habilis*. J Hum Evol 29: 443–462.

Lee S-H. 1995. Variability in *Australopithecus afarensis*: does sexual dimorphism explain the humeral variability in *Australopithecus afarensis*? Am J Phys Anthropol [Suppl] 20:132.

Lee S-H. 1999. Evolution of human sexual dimorphism: using assigned resampling method to estimate sexual dimorphism when individual sex is unknown. Ph.D. thesis. Ann Arbor: University of Michigan.

Lee S-H. 2001. Assigned resampling method: a new method to estimate size sexual dimorphism in samples of unknown sex. Przegl Anthropol 64:21–39.

Lieberman DE, Pilbeam DR, Wood BA. 1988. A probabilistic approach to the problem of sexual dimorphism in *Homo habilis*: a comparison of KNM-ER 1470 and KNM-ER 1813. J Hum Evol 17:503–511.

Miller JMA. 1991. Does brain size variability provide evidence of multiple species in *Homo habilis*? Am J Phys Anthropol 84: 385–398.

Plavcan JM, Cope DA. 2001. Metric variation and species recognition in the fossil record. Evol Anthropol 10:204–222.

Richmond BG, Jungers WL. 1995. Size variation and sexual dimorphism in *Australopithecus afarensis* and living hominoids. J Hum Evol 29:229–245.

Schwartz JH. 2000. Taxonomy of the Dmanisi crania. Science 289:55–56.

Todd TW. 1923. Cranial capacity and linear dimensions, in white and Negro. Am J Phys Anthropol 6:97–194.

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

Wolpoff MH. 2002. The species of humans at Dmanisi. Am J Phys Anthropol [Suppl] 34:167.

Wood BA. 1976. The nature and basis of sexual dimorphism in the primate skeleton. J Zool Lond 180:15–134.