Mandibular Variation in early *Homo* from Dmanisi, Georgia

by

Adam Paul Van Arsdale

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Doctoral Committee:

Professor Milford H. Wolpoff, Chair
Professor Steven A. Goldstein
Professor Philip D. Gingerich
Professor John D. Speth

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ABSTRACT

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Adam Paul Van Arsdale

Chair: Milford H. Wolpoff

The Plio-Pleistocene locality of Dmanisi, Georgia, has produced an abundant hominid fossil sample, including four mandibular specimens. These fossils are noteworthy for their outstanding preservation within confined sedimentary deposits and the large range of variation they present. Included within this mandibular sample are two subadult and two adult mandibles; including one of the smallest Lower Pleistocene mandibles assigned to *Homo*, one of the largest assigned to *Homo*, and the earliest known edentulous hominid mandible. This dissertation attempts to describe and test explanatory hypotheses for the mandibular variation.

The anatomy of the Dmanisi sample is systematically described and compared with other Plio-Pleistocene hominid mandibles. Within the Dmanisi sample, a combination of similarities and differences are found. The mandibles share several distinctive characters to the exclusion of other Plio-Pleistocene hominid samples, including features of the lateral corpus, medial corpus, anterior symphysis, dental arcade, and foramina. Most notable among the characters that differ within the sample are the

overall difference in size, especially noteworthy in aspects of corpus and ramus height, and the size of the posterior teeth.

The morphology of the Dmanisi specimens, together with their context, suggest an appropriate null hypothesis is that the variation in the sample is the result of a process of sampling different age and different sex individuals from a single evolutionary group. Specifically, the large D2600 mandible is proposed to be an adult male, the small edentulous D3900 mandible an adult female, and the remaining two mandibles, D211 and D2735, subadult females.

This hypothesis is tested through a series of comparative analyses with extant humans and great apes using a random resampling procedure. This procedure is designed to directly address the likelihood of observing the pairwise differences found within the Dmanisi sample (i.e. male/female, adult/subadult) relative to known comparative models of variation while operating within the constraints posed by a small sample size. The results of these analyses suggest that the Dmanisi variation is greater than expected based on a model of sampling different age and different sex individuals using a low dimorphism, human or chimpanzee comparative model. In particular, the differences seen in corpus height and posterior tooth size within the Dmanisi group are exceptional relative to these comparative models. However, the results are consistent with a high dimorphism model of intraspecific variation found in gorillas.

An alternative hypothesis that the variation is the result of mixed-taxa sample is also quantitatively examined. Building on the previous analysis, a novel nested re-sampling procedure is developed to test whether or not the magnitude or profile of variation observed in the Dmanisi sample are consistent with that of a mixed-taxa sample.

For each of three possible mixed-taxa pairings (Human-Chimpanzee, Human-Gorilla, Chimpanzee-Gorilla) and three underlying comparative models (Human, Chimpanzee, and Gorilla), this procedure generates a distribution of the expected number of significant trait differences and a distribution of which traits are expected to differ. These simulated distributions allow for a test of whether the observed Dmanisi pattern of variation is consistent with an expected mixed-taxa sample. The results of this analysis suggest the pattern of variation seen in the Dmanisi sample does not likely represent a mixed-taxa sample.

Taken together, these results and the observed anatomy of the Dmanisi mandibular sample support the notion of single hominid taxon at Dmanisi, but one with greater variation than could be reasonably sampled from either extant humans or chimpanzees. This conclusion is reinforced when comparisons are made between the observed range of variation in the Dmanisi sample and that of *Australopithecus boisei*, a penecontemporaneous hominid with a high level of dimorphism. The impact of this conclusion for Dmanisi and for the broader issue of early *Homo* evolution are considered.

CHAPTER 1

Introduction

> A great deal of misunderstanding in judging primitiveness of a given mandible has been caused by the tendency already mentioned above to consider all peculiarities apparent in a mandible of high geologic antiquity as peculiarly characteristic for the entire stage of evolution concerned…Furthermore, it is overlooked that a great variation also occurs in recent man and that most of the variations are not confined to a special race but are identical for mankind as a whole. (Weidenreich, 1936, p. 122)

The Plio-Pleistocene is a time period of rich inquiry in the study of hominid evolution. Abundant fossil evidence from East and Southern Africa, and more recently from Eurasia, provides a large sample on which to address questions of hominid evolution. Furthermore, the Plio-Pleistocene is the period of human evolution when the production of stone tools is first observed (Asfaw *et al*., 1999), body size expands into the range of modern humans for the first time (Walker and Leakey, 1993), significant encephalization beyond that of any previously recorded fossil primate is observed (McHenry, 1976; Martin, 1981; Aiello and Wheeler, 1995; Potts, 1998), and the first evidence of hominid expansion out of Africa is recorded (Tchernov, 1987; Gabunia and Vekua, 1995). It is also the time period during which the human genus, *Homo*, first appears on the evolutionary landscape (Leakey *et al*., 1964; Hill *et al*., 1992; Schrenk *et al*., 1993; Bromage *et al*., 1995).

This dissertation is an attempt to systematically address a narrow question regarding the evolution of early *Homo* during this time period. The site of Dmanisi, located in southern Georgia, is the earliest known hominid site outside of Africa and in the course of excavations during the past 15 years has produced a rich assemblage of fossil material (Gabunia and Vekua, 1995; Gabunia *et al*., 1999; Gabunia *et al*., 2000b Gabunia *et al*., 2002; Vekua *et al*., 2002; Jashashvili, 2005; Meyer, 2005). Included in the hominid sample are four mandibles encompassing a large range of variation. The variation within the mandibles has generated considerable discussion as to the proper interpretation of the Dmanisi hominids and the significance of the site (Dean and Delson, 1995; Gabunia and Vekua, 1995; Bräuer and Schultz, 1996; Rosas and Bermúdez de Castro, 1998; Schwartz, 2000; Gabunia *et al*., 2001; Gabunia *et al*., 2002; de Lumley *et al*., 2006).

The goal of this dissertation is to systematically describe and examine the variation within this mandibular sample through a series of hierarchically structured hypotheses based on comparisons with closely related extant and fossil taxa. The Dmanisi sample is somewhat unique in that it provides a relatively confined, temporally and geographically, though rich, fossil assemblage. Furthermore, as the earliest known hominid site outside of Africa, dated to approximately 1.77 MA, the significance of the site for understanding the biogeography and behavior of early *Homo* is clear. Before detailed questions regarding the significance of Dmanisi can be considered, a parsimonious explanation for the variability within the hominid remains must be established.

Properly understanding the hominid variation from Dmanisi has important consequences not only for interpretations of Dmanisi, but also for the larger understanding of this critical time period in human evolution. As the most variable element within the Dmanisi sample (and the most abundant element within the greater Plio-Pleistocene hominid sample), the mandibles provide an important avenue into the development of a greater understanding of the site, and subsequently, broader issues pertaining to the evolution of early *Homo*.

Chapter two presents a detailed outline of the main question of this work; how is the Dmanisi mandibular variation best understood? Following this is a presentation of the methods and rationale used to collect the primary and comparative data. In addition to the Dmanisi mandibles, data were recorded from a large set of hominid fossils, gorillas, chimpanzees, and recent humans. This chapter also presents the theoretical basis for the questions and approach employed in the course of the dissertation. Finally, chapter two briefly outlines the analytical methods used in the chapters to follow.

Chapter three provides a background to the site of Dmanisi and the hominid mandibular sample recovered up to, and including the 2005 excavation season. A brief history of the excavations conducted at Dmanisi is presented, including the medieval archaeological work conducted at the site since the 1930s which are responsible for the initial discovery of Plio-Pleistocene age sediments. Following this, a brief description of the current understanding of the site's geology, age, formation process, and stratigraphic context is presented. Finally, detailed anatomical descriptions of the individual Dmanisi mandibles are made. As fairly new discoveries, most of the Dmanisi material has received only a minimal published description. This chapter provides the first systematic

and complete description of all of the Dmanisi mandibular specimens. The goal of this chapter is present the basic data, both regarding the context of the site and the anatomical character of the mandibles, upon which the remaining analyses of the dissertation are conducted.

Chapter four further elaborates on the anatomical description of the Dmanisi mandibular material by providing detailed comparisons among the mandibles and with other relevant hominid fossils. The comparisons made in this chapter are intended not as a statement of the taxonomic affinity of the Dmanisi material, but rather as further clarification of the similarities and differences observed within the Dmanisi group as well as with other fossil hominid material. A null hypothesis for the observed Dmanisi variation is presented on the basis of these anatomical descriptions and comparisons. This hypothesis states that the Dmanisi variation is the product of resampling different age and different sex individuals from within a single evolutionary group.

Chapter five presents a series of analyses related to testing the null hypothesis of variation within the Dmanisi mandibular sample. This chapter focuses on mandibular variation associated with sexual dimorphism, age and growth, and the combined effects of sex and age. A review is presented of the significance of these factors in understanding fossil samples and their particular importance for understanding the Dmanisi mandibular variation. The observed variation within a wide set of mandibular metrical characters found in the Dmanisi sample is quantified relative to relevant comparative model taxa through a randomized, probability based approach. These tests are designed to answer the question of whether the observed variation within the Dmanisi sample can be explained by the expected levels of variation associated with underlying

sex and/or age factors in each of the comparative taxa. Finally, the null hypothesis is reevaluated in light of the results produced from the above analyses.

Chapter six presents two alternative hypotheses for understanding the Dmanisi variation; the possibility of two, sympatric and distinct hominid taxa within the Dmanisi assemblage and the possibility of a single species which exceeds the expected levels of variation observed in some extant, comparative models. A brief review of approaches to dealing with mixed-taxa samples is presented. The first of these alternative hypotheses is tested using a novel, nested resampling methodology, developed as a logical outgrowth of the previous analyses. The two alternative hypotheses are considered in the context of these nested random resampling results. Finally, these results and their significance for understanding the Dmanisi hominids are further considered with regards to observed variation in a large mandibular sample taken from *Australopithecus boisei,* another Plio-Pleistocene fossil hominid taxon.

Chapter seven presents a synthesis and discussion of the descriptions, analyses, and results of the dissertation. Chapter seven reintroduces the initial problem, that of systematically assessing the variation in a temporally and geographically confined sample, and outlines the procedures and rationale for the approach taken here. A complete summary and interpretation of the analyses is undertaken, including the final conclusions of the work. Included in this is a discussion of the importance of the Dmanisi mandibles for understanding the site as whole, potential implications of this revised understanding of the site, and potential areas of future inquiry that might provide additional understanding on the specific topic of Dmanisi and the broader topic of the evolution of early *Homo*.

CHAPTER 2

Methods and Materials

The purpose of this chapter is to present the theoretical framework, methods of data collection, comparative samples, and analytical methodology employed in this work. The theoretical approach and underlying hypothesis structure are first discussed. The data used to address these hypotheses and the research design involved in collecting these data are then presented. This includes a summary of the comparative samples from which the data are derived, including recent extant apes and humans as well as fossil hominids. Finally, a basic outline of the analytical approach used to address the hypotheses in question is discussed.

Theoretical Approach:

The problem of this work, as presented in the chapter one, is how the variation within the Dmanisi hominid mandibular sample is parsimoniously understood in an evolutionary context. The Dmanisi mandibular sample presents a large range of metric and anatomical variation (see Appendix A for complete pictures) (Gabunia and Vekua, 1995; Gabunia *et al*., 2002; Vekua *et al*., 2002; Lordkipanidze *et al*., 2005). Of all of the Dmanisi hominid elements, the mandibles present the largest range of variation in size and non-metric features. Given the potential significance of the site to the understanding

of the evolution of early *Homo* and early hominid dispersal out of Africa, developing an understanding of this variation is of critical importance.

The tight stratigraphic context of the Dmanisi site, discussed in greater detail in chapter three, provides a unique opportunity to explore the question of variation at a refined, microevolutionary scale. Rather than begin the analysis of the Dmanisi variation with the question of whether or not multiple species are present, the tight association between the Dmanisi remains and their excellent preservation allows for a more basic consideration of what factors may parsimoniously account for the observed variation. These include aspects of variation associated with both age and sex, in addition to possible phylogenetic variation. As discussed below and in greater detail in chapters three and four, this approach is also grounded in an appreciation for the anatomy of the Dmanisi individuals.

Beginning the analysis with hypotheses regarding intraspecific sources of variation has a scientific appeal, as well. One of the difficulties in beginning an analysis of variation at the level of the species is that any *post hoc* attempt to examine hypotheses related to issues of age and sex (or any other kinds of intraspecific variation) will be affected largely by the either implicit or explicit assumptions regarding models of development or sexual dimorphism in the initial species-level model of variation. Thus, any appraisal of intraspecific variation after specific distinctions have been made will be based largely on untestable assumptions. This may not be a problem if taxa are easily distinguishable, but when dealing with the possibility of closely-related taxa within the hominid clade, this problem is real. By beginning with hypotheses of intraspecific

variation, it is theoretically possible to progress through a series of hierarchically constructed hypotheses, moving to higher and higher orders of variation.

The process of understanding fossil variation in an evolutionary context is thereby a multi-step process. The first step in this process is a detailed and clear description of what that variation is and how, on a general scale, it relates to variation seen in relevant comparative groups. While initial descriptions of the Dmanisi mandibular material are available (Gabunia and Vekua, 1995; Bräuer and Schultz, 1996; Gabunia *et al*., 2002; Vekua *et al*., 2002; Rightmire *et al*., 2005), formal and complete documentation of their anatomy has not yet been carried out. This will be the focus of the next two chapters, providing a background of the Dmanisi site and a complete anatomical description of the hominid mandibular sample.

Once an effective description of the anatomical variation is available, the second step of the process is rigorously testing hypotheses that might account for the observed variation. In paleoanthropology, inherently a comparative discipline, the bases of such hypotheses are often predictions generated from comparative explanatory models of variation. Closely related extant taxa or other fossil taxa may provide such comparative explanatory models. Once the variation is parsimoniously explained and the strengths and weaknesses of competing models are discussed, questions of the broader evolutionary context of the problem can be addressed.

Identifying a Null Hypothesis:

A challenge in paleoanthropological studies is where and how to begin a hypothesis testing structure. A common approach is to present "sameness" as a null

model. However, “sameness” can be classified at multiple levels (i.e. species or sex). Numerous sources of variation can be proposed as likely causes of an observed set of variation. It is worthwhile to consider both what these sources are and also how they can be logically sorted and dealt with parsimoniously.

Within a species, individuals vary along several identifiable and somewhat regular vectors. These include, but are not limited to, variation associated with age (the consequence of growth), sex (the consequence of sexual dimorphism), and geographic or population affinity (the consequence of population structure). These elements of variation, how they are patterned and how they relate to each other define the anatomical bounds that describe the species. Therefore, in considering a question of variation, it is possible to construct a hierarchical and logically driven hypothesis testing structure, beginning with the most basic units of intraspecific variation and proceeding into higher order interspecific patterns of variation (Albrecht and Miller, 1997; Miller *et al*., 1998).

One alternative approach would be to begin by addressing higher order hypotheses of variation, such as the issue of single or multiple species, and only afterwards consider intraspecific sources of variation (Tattersall, 1986; Tattersall, 1992). The most significant problem with this approach is that in order to address a hypothesis of species-level differences, one must *a priori*, either implicitly or explicitly, assume a model of intraspecific variation regarding such factors as development and sexual dimorphism. Any attempt then to *post hoc* analyze these factors will be, in part, predetermined by the assumptions inherent in the initial species-level hypotheses.

A critic of the approach involving examination of intraspecific variation first, followed by interspecific variation might suggest that, in effect, such an approach makes

a priori assumptions about the species classification of the material in question. However, utilizing this approach, the initial *a priori* assumption can then itself become an independent, testable hypothesis. For example, the approach in this work will focus on variation associated with age, sex, and the combined effects of age and sex, and only then will address potential specific differences in the Dmanisi sample. Any consideration of the taxonomic integrity of the sample includes an appreciation of how variation associated with age and sex might be structured within the sample.

The stratigraphic context of the Dmanisi material allows the issue of geographic and temporal variation in the sample to be effectively ignored. Thus it is possible to begin with an initial question of whether the observed variation can be accounted for by a model of expectations for age (growth) related changes within a species. If this hypothesis cannot be rejected and the results are reasonable on the basis of the observed anatomy, there is no need to re-evaluate and test the assumption of species uniformity. If instead the hypothesis is rejected, the question moves on to ask whether or not the observed variation can be accounted for by a model of sexual dimorphism. Again, if the hypothesis cannot be rejected and the results appear appropriate given the anatomical makeup of the sample, the process of evaluating the variation is complete and conclusions can be considered. If the hypothesis is rejected, the variation can be considered in a model in*corpora*ting the combined effects of age and sex. Finally, only if this explanation is rejected, is it reasonable to address hypotheses of species differences within the sample. The presence of variation which is unaccountable under the tested models of intraspecific variation suggests the initial assumption of a single species may be inappropriate and should be addressed with testable hypotheses.

A few cautions regarding this structure are necessary. First, while Dmanisi is remarkable in that the fossil material all appear to come from a narrow window of time and space, this is often not the case in fossil studies. In other contexts, where fossils are scattered across a wide geographic area and derive from stratigraphic contexts with large temporal ranges, an approach which begins by asking questions of possible population-level sources of variation such as age and sex will more likely be problematic. The complicating factor of temporal uncertainty makes testing hypotheses on the basis of recent extant comparative samples more difficult. In these instances, while hypotheses are being directed at material potentially spanning long time gaps, the basis for the hypotheses tests themselves comes from material which is confined to recent history. The relationship between variation across time and comparative variation across space remains untested. Also, the Dmanisi fossils are, whatever their phylogenetic relationship, the product of recent, shared ancestry. If the fossil sample is composed of elements whose shared evolutionary ancestry is more distantly removed, testing single models of growth and development becomes more problematic.

Another caution would be to carefully consider the conclusions drawn from hypotheses in the context of the fossil anatomy. If the test of a single variable rejects any intraspecific model of variation, is this enough evidence to constitute specific difference? This is an issue that is hard to address in any general manner but must be considered in the context of specific examples. In some cases, the uniqueness of a trait may be enough to form such an argument. In other cases, the pattern of variation, across a series of traits may be a more relevant basis on which to draw conclusions. Again, the bases for the hypotheses examined in this work are the observed variation in recent extant apes and

humans. It would be naïve to think these samples cover the entire possible range of variation in hominoid evolutionary history. The results of the quantitative hypothesis tests conducted here will considered with respect to the specifics of the Dmanisi anatomical variability.

The value of a detailed understanding of the anatomy is also apparent in the context of such a hypothesis structure. The generation of specific hypotheses for any given sample is the outgrowth of a detailed anatomical understanding in the context of broader, comparative knowledge of the material. Such an examination is undertaken in chapters three and four and constitutes the basis of the null hypothesis of this work.

Data:

The data I have collected for this work consists of descriptive anatomical assessments and linear measurements. 3-D landmark data for future research were also collected for all of the specimens using a Microscribe 3DX, but will not be utilized in this work. The anatomical descriptions are based largely on the mandibular terminology employed by Weidenreich (1936). In nearly all cases anatomical descriptions were based on an extended examination of the original material and included detailed sketches, notes, and photographs. In the minority of cases in which the original fossil material was not examined by the author, discussion is based on photographs, casts, and published descriptions of the material.

Linear measurements consisted of a large set of standard and non-standard measurements. These measurements are designed to not only span the entire mandibular morphology, but to also allow for comparisons of fragmentary material. As a result, the

complete set of measurements is intentionally redundant in its coverage (See Appendix B for measurement list and data). For individual analyses, subsets of this complete data set were chosen in a manner as to allow for as extensive comparisons as possible within the Dmanisi group, while partially minimizing redundancy. The measurements themselves were recorded using a sliding caliper and recorded to the nearest 0.1 mm. Accuracy of the calipers was assessed by first comparing its results with a measure of known value. Plastic calipers were used in order to minimize damage to the fossil and skeletal specimens. The complete set of measurements was taken in triplicate so as to assess the measurement error associated with each measurement. These measurement errors ranged from a standard error of approximately 0.03 for some of the smaller measures (~ +/- 0.1-0.2 mm), to a standard error of approximately 0.25 for some of the larger measures (+/- 1.0-1.5 mm). In the case of the Dmanisi specimens, measurements were also repeated on separate occasions so as to assure consistency between viewings of the specimens. Measurement values used in the analyses represent the average value recorded for each trait.

Materials:

The comparative samples used come from recent and fossil humans, chimpanzees, and gorillas. The use of these species is intended to both examine the most closely related extant species to fossil hominids and provide different models of size, dimorphism, and anatomy (see table 2.1). The comparative samples are chimpanzees (*Pan troglodytes trogolodytes*), gorillas (*Gorilla gorilla gorilla*) and recent humans (*Homo sapiens*). In these samples, *Pan* and recent *Homo* are generally recognized as

having relatively low levels of sexual dimorphism in both body mass and related skeletal traits. In contrast, *Gorilla* is known for having the largest observed levels of dimorphism amongst the living great apes (Wolpoff, 1976b; Wolpoff, 1976a; Hall, 1982; Cheverud *et al*., 1985; Clutton-Brock, 1985; Leutenegger and Cheverud, 1985; Dean and Benyon, 1991; Kelley, 1995; Daegling, 1996; Loth, 1996; Plavcan, 2001; German and Stewart, 2002; Plavcan, 2002). By covering a range of observed levels of size dimorphism, these comparative samples allow for comparisons to be made against different models of size, growth, and sexual dimorphism. These comparative specimens also provide a range of overall mandibular morphological patterns. To varying extents, the details of fossil hominid mandibles intermediate between those of living humans and great apes. Living great ape mandibles can easily be distinguished from human specimens by many traits, including their expanded canines, parallel teeth rows, and obliquely oriented symphyses. In addition to providing a range of dimorphism models, these comparisons also provide a range of different morphological patterns. Comparisons were also made with an extensive array of fossil hominids across both time and space, with an emphasis on Plio-Pleistocene mandibles from East and South Africa.

Table 2.1 – Comparative Sample

	Total	Female	Male	Unknown	Dimorphism	Morphology
P. t. troglodytes	61	26	23	12*	Small	Ape
G. g. gorilla	54	31	22	1*	Large	Ape
H. sapiens	90	30	41	20*	Small	Human

Table 2.1 – Comparative extant sample. Total number of specimens, broken down by sex, level of dimorphism, and mandibular morphological pattern. (* - specimens of unknown sex represent individuals which are too young to have been reliably sexed)

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

collection is ideal for such a study for several reasons. First, the remains come from a pre-modern dentistry population and show dental wear patterns broadly consistent with wear patterns seen in fossil hominids. Many osteological samples are derived from anatomy donations collected within the last two centuries and display evidence of modern dental and eating practices inconsistent with observed patterns in the fossil record (Brace, 1962; Brace and Mahler, 1971). Additionally, the Libben sample consists of associated skeletal remains, allowing age and sex to be determined on both the basis of the large number of individuals present and the different skeletal elements within each individual. This allows for a very accurate assessment of age and sex.

The chimpanzee sample is from the Hamann-Todd collection, housed at the Cleveland Museum of Natural History. This sample consists of infant to old adult specimens, generally well-sexed (with uncertainties mainly found in young individuals), and well preserved. The bulk of the sample comes from Cameroon and is generally believed to represent *Pan troglodytes troglodytes*.

The gorilla sample is also from the Hamann-Todd collection in Cleveland. It too consists of infant to adult specimens and is clearly sexed. Again, most of this sample consists of wild-shot gorillas from Cameroon and is thought to be entirely *Gorilla gorilla gorilla*. A few additional gorilla remains are taken from the *Naturmuseum Senckenberg* in Frankfurt, Germany, and are also *G. g. gorilla*.

Fossil specimens come from a variety of institutions and represent several hominid taxa.

Method:

One of the challenges in analyses of fossil samples is the statistical problem posed by small sample sizes and fragmentary individuals. Most fossil samples are ill suited for hypothesis testing or analysis by traditional, distribution-based statistical methods. In samples of three or four individuals, the statistical robusticity of traditional sample measures such as the mean and standard deviation is extremely limited. The removal or addition of a single individual to such a sample can produce dramatic differences in results from traditional statistics, with significant implications for the interpretation of such results. Even worse, in many cases fossil samples are single individuals, often assumed to represent the population or sample mean in their characters, with no information as to the variability of such characters. When the question of interest for a given fossil sample is whether or not it has greater variation than can be expected for a given hypothesis and comparative sample single specimen samples are not useful.

The coefficient of variation has long been advocated as a robust and useful measure of the statistical variation of a sample (Simpson *et al.*, 1960, Cope and Lacy, 1992; Kramer, 1993; Cope and Lacy, 1995; Donnelly and Kramer, 1999; Lockwood *et al*., 2000). However, approaches using this, or related metrics, necessarily rely on the comparison of assumed distribution-based statistics (i.e. mean and standard deviation) and thus do not escape the problem of small samples sizes posed by fossils (Lee, 2001). An approach to small samples which has become increasingly common is the use of random resampling strategies (Lockwood *et al*., 1996; Aiello *et al*., 2000; Lockwood *et al*., 2000; Lee, 2001; Ahern *et al*., 2002). These strategies have the advantage of not relying on an assumed distribution with uniform properties. Instead, random resampling

strategies utilize the inherent properties of the sample in question (sample size, defined categorical makeup of sample) to establish particular hypothesis tests.

Consider the case of the seemingly simple question of whether a particular fossil sample is more or less variable than a given comparative sample of known properties. A simple approach might be to compare the range of variation of the fossil and comparative samples. If the fossil sample fits within the range of the comparative sample, or has an equivalent range, the hypothesis of greater variation can be rejected. However, as Cope and Lacy showed (1995), range statistics are both extremely sensitive to small sample sizes and differences in underlying size between the two samples. If one of the samples has larger individuals, a similar degree of variation will produce a greater absolute range of variation. Alternatively, one might compare the coefficient of variation between the two samples as a way to distinguish greater and lesser amounts of variation. However, again the problem of small sample sizes makes establishing the significance of such a comparison highly sensitive to the addition or subtraction of a single specimen.

The advantage of a random resampling approach is that it incorporates the potential sample size problem into the hypothesis testing structure. For example, if the fossil sample in question consists of five individuals, the limitations of that size become part of the question. Using a random resampling approach, the question is not whether the sample is more variable than a given comparative sample, but instead what is the likelihood of randomly drawing a sample of five individuals from the comparative sample with greater or lesser variation than that observed in the initial fossil sample. Furthermore, under this approach, the actual test statistic used to measure variability can be modified to whatever is most appropriate given the specifics of the problem involved

(Cope and Lacy, 1995; Lockwood *et al*., 1996; Donnelly and Kramer, 1999). In the case of the analyses presented here, many of the hypotheses will be structured based on the expected difference between representatives of pre-determined or hypothesized binary categories such as sex (male-female) and age (adolescent-adult). Therefore, in the context of the quantitative analyses presented in chapters five and six, the discussion of Dmanisi mandibular variation is really a discussion of the likelihood of sampling an index of pairwise difference (i.e. male/female) from a comparative sample rather than a true assessment of the variability of the Dmanisi sample. Given the nature of the Dmanisi, this is both a more convenient and more effective approach to addressing hypotheses of age, sex, or species difference within the sample. Rather than merely asking the question of whether or not the Dmanisi sample is more variable than a comparative sample of humans or chimpanzees, using a random resampling approach allows for the quantitative assessment of the likelihood of finding the observed fossil pairwise index within each of the comparative samples. Such an approach is both specific to the hypothesis and conservative with regards to the limitations of the sample in that the small sample size is built into the hypothesis testing framework.

Summary:

Dmanisi provides both a well preserved and stratigraphically confined hominid sample. Within this sample, the four mandibles provide the most dramatic representation of the hominid variation at the site. The nature of the site allows for a detailed assessment of the anatomy of the individual specimens as well as a hypothesis testing approach which attempts to differentiate between intraspecific and interspecific sources

of variation. Rather than assuming a model of growth and/or sexual dimorphism, these two possible sources of variation can be directly tested. Thus, the null hypothesis addressed in this work will be based upon intraspecific sources of variation. Only if this null hypothesis is rejected will hypotheses of taxonomic distinctions within the Dmanisi mandibles be addressed.

Fossil samples pose characteristic problems for addressing hypotheses of variation. First among these is the issue of small sample sizes. Most traditional statistical approaches are ill-suited for the hypotheses and available sample sizes found in fossil hominid studies. The analyses undertaken here utilize a random resampling methodology which is advantageous in that it minimizes the number of distributional assumptions. In this context, the question of the Dmanisi mandibular variation becomes one of assessing the likelihood of randomly drawing a greater amount of variation from an equal number of individuals taken from a comparative sample. The measure of variation used here is a measure of pairwise difference on the basis of hypothesized differences (i.e. old/young, male/female). The comparative samples through which the Dmanisi variation will be understood consist of recent and fossil humans, chimpanzees, and gorillas.

The following chapters use the above-outlined approach to address questions regarding the variation within the Dmanisi hominid mandibular sample. The goal of this approach is to address questions at the Dmanisi variation as thoroughly and systematically as possible. This begins with a thorough understanding of the anatomy in order to provide as strong a foundation as possible from which to make comparisons, both quantitative and qualitative. Chapters three and four provide an explication of the

background to Dmanisi, the anatomy of the Dmanisi mandibles, and comparisons with other fossils. Chapters five and six quantitatively assess the variation within the Dmanisi sample relative to comparative groups of *Homo*, *Pan*, and *Gorilla*, using a randomized resampling based approach. This approach has the advantage of minimizing the number of assumptions applied to the data in order to quantitatively test hypotheses. Issues of sample size, particularly problematic for fossil samples, are minimized in resampling strategies. The limitations of such sample sizes are built into the hypotheses tested. This work will specifically employ such an approach to examine hypotheses of both intraspecific variation, in the form of sexual dimorphism and growth (chapter five), and interspecific variation (chapter six).

CHAPTER 3

The Dmanisi Site and the Mandibular Sample

The following chapter is intended as an introduction to the site of Dmanisi, including aspects of the sites history, location, geological context, age, and a brief introduction to some of the materials recovered in excavations through the 2005 field season. Following this introduction, a thorough description of the four individual mandibles is presented. Chapter four presents detailed comparisons within the Dmanisi sample and with other fossil hominid mandibles.

Site history and locality:

The site of Dmanisi is located 85 km southwest of Tbilisi (44°20'N, 41°20'E), in the Kvemo-Kartli region of the Republic of Georgia (see figure 1) (Gabunia and Vekua, 1995; Bräuer and Schultz, 1996; Gabunia *et al*., 2000a; Gabunia *et al*., 2001). The excavation area is in the midst of ruins from the ancient settlement of Dmanisi, a prosperous citadel and trading town situated on the Silk Road and dating to between the 6th and 13th century. The small village of Patara Dmanisi sits adjacent to the area today.

Figure 3.1 – Map of Georgia and the Dmanisi site

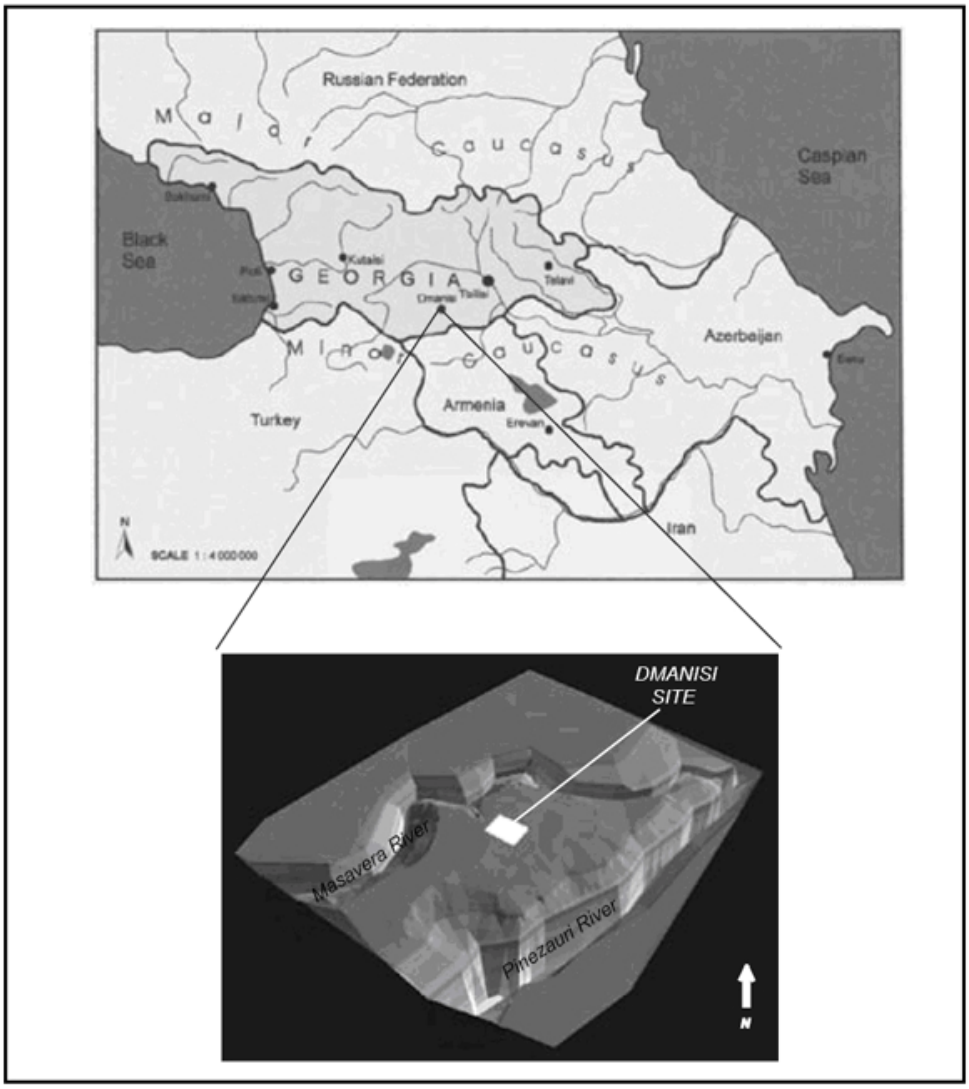


Figure 3.1 – Map of the Kvemo Kartli region in Georgia and the location of the Dmanisi site (from Mallol 2005, modified from Gabunia *et al*, 2000).

Archaeological excavations of the historic citadel and town complex began in 1936-1937, led by Levan Muskhelishvili, and have continued at various intervals over the last several decades (Jashashvili, 2005). By 1982, the focus of the archaeological work had extended beyond the larger citadel complex to include the details of the settlement itself, including the many associated buildings situated north of the citadel. During the 1982 season, the excavation of a medieval cellar revealed a set of mammalian fossils,

including the remains of *Dicerorhinus etruscus etruscus*, an extinct Villefranchian species of rhinoceros. Identified by paleontologists Leo Gabunia and Abesalom Vekua, these finds gave the first indication of fossiliferous, Plio-Pleistocene age sediments underlying the medieval site.

Full scale excavations of the paleo-sediments began in 1991 with a joint project conducted by the Archaeological Research Center of the Georgian Academy of Sciences and the *Römisch-Germanisches Zentralmuseum* of Mainz (Bosinski *et al*., 1989a; Bosinski *et al*., 1989b; Dzaparidze, 1989; Majsuradze *et al*., 1989; Vekua and Gabunia, 1989). Amongst the material recovered during the initial season of excavation was a hominid mandibular fragment (D211), sparking increased interest in the Dmanisi paleo-sediments and their potential significance for hominid evolution (Gabunia *et al*., 1991; Dean and Delson, 1995; Gabunia and Vekua, 1995). Excavations between 1991 and 1998 focused on three main areas now identified as Area I, Area II, and Room XI, in addition to several test soundings labeled M1-M6 (see figure 3.2). These excavations yielded abundant faunal and archaeological material (Gabunia, 1992; Gabunia and Vekua, 1995; Bräuer and Schultz, 1996; Gabunia *et al*., 2000a), but only a single additional hominid fossil (Gabunia *et al*., 1999).

Figure 3.2 – Map of Dmanisi excavations

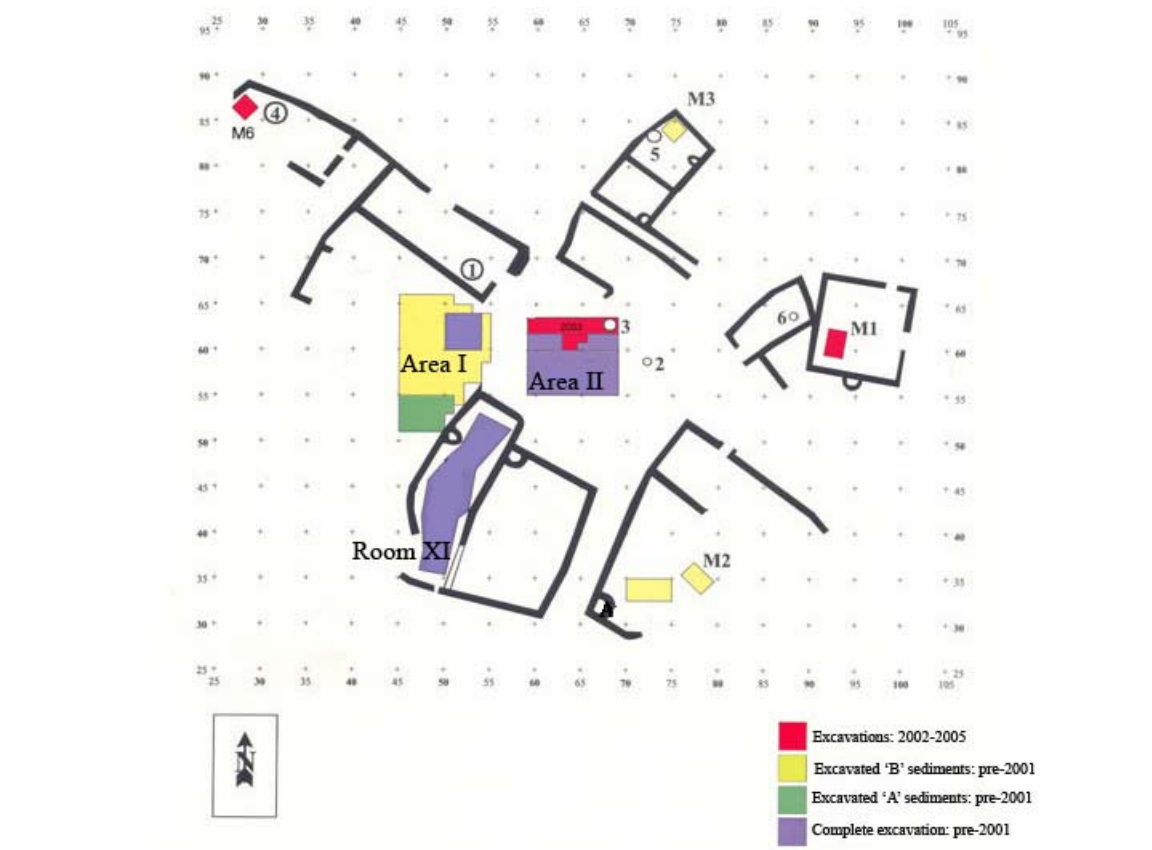


Figure 3.2 – Dmanisi excavation plan, 1991-2005. (modified from Jashashvili, 2005)

Since 1999, the excavations have been carried out by an international team, led by the Georgian State Museum and directed by David Lordkipanidze and, until his death in 2003, Leo Gabunia. Excavations during this period have uncovered numerous hominid fossil remains in addition to an increasing collection of archaeological and faunal material (Gabunia *et al*., 2000b; Gabunia *et al*., 2001; Gabunia *et al*., 2002; Vekua *et al*., 2002; Mallol, 2004; Garcia, 2005; Jashashvili, 2005; Lordkipanidze *et al*., 2005; Meyer, 2005; Rightmire *et al*., 2005). Aside from the recovery of new material, the primary goals of the recent excavations (1999-2005) have been the confirmation and clarification of the early age of the site, a re-evaluation of the geological setting and stratigraphic sequence, and an examination of the taphonomic processes that led to the deposition and

fossilization of the recovered material. As of 2005, roughly 175m^2 have been excavated, producing some 7,000 bone fragments, 6,000 stones, and nearly sixty hominid remains.

Geological Setting and Age:

Dmanisi is located at an altitude of just under 1000m in the foothills of the Lesser Caucasus of southern Georgia. The surrounding region is dominated by Plio-Pleistocene volcanogenic sediments including the Masavera basalt, a large lava flow up to 80m thick which extends throughout the Masavera paleo-valley and forms the base of the Dmanisi sequence, and associated overlaying ashes (Bosinski *et al*., 1989b; Gabunia *et al*., 2001; Mallol, 2004; Garcia, 2005; Jashashvili, 2005). The site is situated on an outcropping, Cretaceous prominence, approximately 100m above the confluence of the Masavera and Pinezauri rivers.

The Dmanisi paleo-sediments consist of between 1-5m of volcanoclastic alluvium and are dominated by a strong calcrete presence (Ferring and Lordkipanidze, 2003). Veins of calcrete penetrate the sediments to varying degrees, most prominently in the form of a dense laminar calcium carbonate layer, or 'kerki', up to 50 cm thick, which runs through the middle of the stratigraphic sequence. Initial attempts to assess the stratigraphy divided the sediments into six, horizontally bedded units, identified as layers 1-6 (Bosinski *et al*., 1989b; Gabunia and Vekua, 1995; Bräuer and Schultz, 1996; Gabunia *et al*., 2001; Garcia, 2005). Subsequent geologic work by Ferring *et al*. altered this scheme to one consisting of two principle layers, A and B, corresponding to separate, periodic ashfalls onto the underlying Masavera basalt (see figure 3.3) (Gabunia *et al*., 2001; Ferring and Lordkipanidze, 2003). Additionally, the revised stratigraphy has

corrected a significant error from the earlier scheme of treating the 'kerki' as a true depositional layer, rather than the post-depositional diagenic artifact, likely resulting from a period of water table fluctuation (Mallol, 2004).

Figure 3.3 – Dmanisi stratigraphic sequence

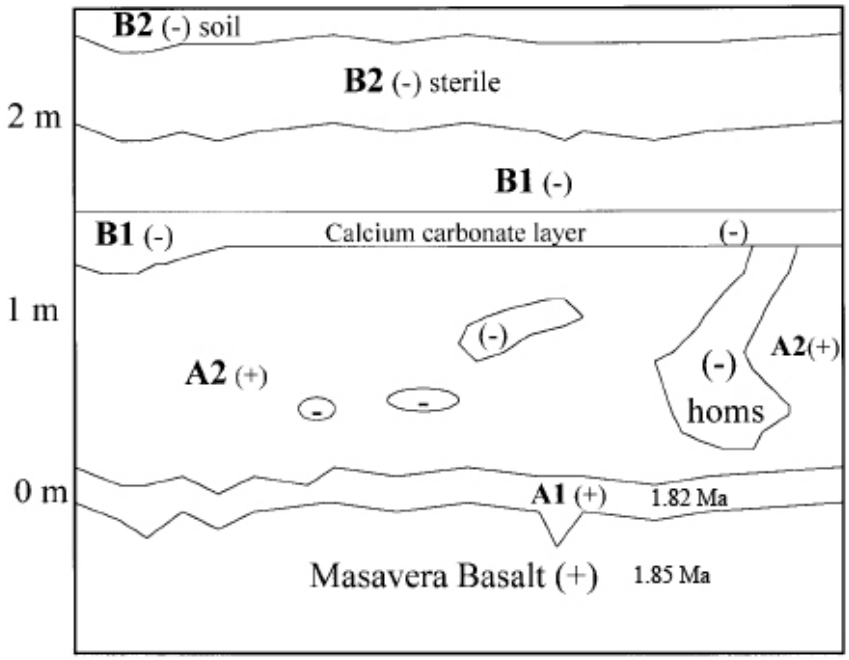


Figure 3.3 – Simplified Dmanisi stratigraphic sequence. The sequence consists of A (normal polarity) and B (reverse polarity) ash layers, typically separated by a dense calcium carbonate, or 'kerki', layer. Archaeological and fossil material are found throughout the sequence, although as of 2005, hominids have only been preliminarily identified in infill features in within the A layers. (modified after Gabunia *et al*, 2005)

Part of the initial difficulty involving the stratigraphy, and in particular, in correctly identifying the 'kerki' layer, owes to the carbonate layer's situation within the stratigraphic sequence. When the 'kerki' entered the sequence, it did so opportunistically, calcifying within the stratigraphy at weak points in the soil column (Ferring and Lordkipanidze, 2003; Mallol, 2004). As a result, the 'kerki' layer is most commonly observed at the junction of the A and B soil layers, a natural weak point in the sequence, and thereby imitating a true depositional layer. At numerous locations,

however, the ‘kerki’ layer can be seen to transect different stratigraphic units of both the A and B layers as well as occasionally transecting fossil materials themselves. The ‘kerki’ is also of interest for its relationship with the fossils of the site. While fossil material is found throughout all of the Dmanisi deposits, the preservation of fossil materials found below the level of the ‘kerki,’ including most of the hominid remains as of 2005, is often extraordinary. This is of obvious benefit in anatomical analyses.

The current scheme also recognizes a complex series of overlying erosional and microstratigraphic features, particularly in the area of Area II (Mallol, 2004). Work by Mallol (Mallol, 2004) and Ferring (Ferring and Lordkipanidze, 2003), as well as others, has attempted to address the sedimentary context in which the Dmanisi material may have accumulated. Their preliminary results suggest a series of ashfall events, associated with brief, non-depositional interruptions. Following the deposition of the initial A ashes, a brief period of soil formation appears to have existed, as evidenced by micromorphological and stratigraphic assessments of the A-B contact, which includes trace biotic elements as well as preserved erosional features. The exact temporal length of this gap is unknown, but appears to have been brief, possibly on the scale of decades rather than extended geologic time (Mallol, 2004). The B sediments represent at least two periods of soil formation, erosion, and renewed deposition. Although a hominid presence at the time of the initial deposits cannot be ruled out, the A-B contact and the soil horizons in the B layer likely represent the occupational horizons for the Dmanisi hominids.

Prominent in the erosional sequence and depositional environment at Dmanisi is the presence of underground pipe features (Ferring and Lordkipanidze, 2003). These

features presumably would have initially formed as the result of subterranean water flow. The size of these features is variable, but at places their exposed margins have a diameter in excess of 1.5m, suggesting they may have quite large. These piping features are of particular interest as they are abundantly filled with fossil remains, including many of the hominid specimens.

A major uncertainty which remains to be clarified is how and when the fossil material came to end up in these features. It is likely several vectors played a role in the total fossil accumulation (Tappen and Vekua, 2003). Some of this material likely represents a resampling of the overlying A-B and B horizons through post-depositional erosion processes. However, some of the material may have accumulated as a result of active vectors during the initial A-B occupation horizon. Amongst the potential active vectors are carnivores that may have intermittently used these structures as dens. *Canis etruscus*, a small wolf-like species is present amongst the fossil remains in large numbers. Hyena (*Pachycrocuta perrieri*), widely identified as a source of bone accumulations in many African paleo-settings (Brain, 1981), is also present, although with a much lesser frequency than the canids. A diverse group of additional carnivores (see table 3.1 for complete faunal list), both large and small, may also have played a role. It is also possible hominids may have acted as a vector of accumulation. Archaeological materials, although present in much greater quantities in the B deposits, are found within the erosional and piping features in the A deposits.

Table 3.1 - Dmanisi Faunal List

Reptilia	
	Bufo viridis
	Anura indet.
	Testudo graeca
	Lacerta gr. *L. viridis*
	Sauria indet
	Elaphe quatuorlineata
	Colubines indet.
	Serpentes indet.
Aves	
	Struthio dmanisiensis
	Gallus dmanisiensis
	Strix gigas
Mammalia	
	Sorex sp.
	Ochotona cf. *largerli*
	Hypolagus cf. *brachygnathus*
	Rodentia
	Sciuridae
	Marmota sp.
	Apodemus aff. *dominans*
	Cricetus sp.
	Cricetulus nov. sp.
	Mimomys tornensis
	Mimomys ostramocensis
	Mimomys pliocenicus
	Gerbillus sp.
	Parameriones aff. *ubeidiyensis*
	Kowalskia sp.
	Hystrix sp.
	Canis ertuscus
	Vulpes alopecoides
	Ursus etruscus
	Ursus sp.
	Martes sp.
	Meles sp.
	Pachycrocuta perrieri
	Pachycrocuta sp.
	Lynx issiodorensis
	Panthera gombaszoegensis
	Meganthereon meganthereon
	Homotherium cernatidens
	Mammuthus meridionalis
	Equus stenonis
	Equus sp. aff. *altidens*

Table 3.1 - Dmanisi Faunal List (continued)

Dicerorhinus etruscus etruscus
Cervus perrieri
Cervus sp. (ex. gr. *Arvernoceros ardei*)
Eucladoceros aff. *senezensis*
Cervus (Dama) cf. *nestii major*
Palaeotragus sp. (= *Giraffidae cf. Paleotraginae*)
Dmanisibos georgicus (= *Bison (Eobison) georgicus*)
Galogoral meniginii sicenbergii
Capra sp. nov. sp.
Sorgelia sp. (= *Sorgelia* cf. *minor*)
Ovibovini gen.et sp. indet
Gazella sp. (= *Antilopini* gen.et sp. indet.)
Antilopini gen.et sp. indet.
Homo sp. indet. aff. *erectus* (= *H. ergaster*)

Table 3.1 – Faunal list of Dmanisi fossils (after Jashashvili, 2005)

Correlating the stratigraphic position of particular fossil remains and artifacts between the earlier and revised stratigraphy is a source of confusion and difficulty. In some cases, particularly with materials initially removed from Room XI and Area I of the excavations between 1991-1998, an exact correlation between the two stratigraphic interpretations is impossible. In the area of Area II, where much of the work has been conducted to revise the stratigraphy, it is usually possible to make some estimate as to what stratigraphic unit particular specimens, originally identified by the old stratigraphy, are derived from. Generally, materials initially labeled as coming out of layer 2 derive from one of the 'B' ashfall horizons, while materials labeled as coming from layers 4 and 5 most likely belong to some form of the A2 layer (the reworked 'A' ashfall deposits). Materials removed from layer 3 (the 'kerki' layer), generally fall in close association with the A-B contact zone, and may come from either the A2 of B layers. Ongoing work at Dmanisi continues to refine the view of the exact depositional and stratigraphic sequence, thus promising additional revisions of the stratigraphy in the future.

Dating of the site was initially quite controversial owing to the unique stratigraphic context and morphological ambiguity of the D211 mandible discovered in 1991 (Gabunia, 1992; Dean and Delson, 1995; Gabunia and Vekua, 1995; Bräuer and Schultz, 1996; Rosas and Bermúdez de Castro, 1998). From the beginning, the presence of Villefranchian age fossil mammals indicated the possibility of a late Pliocene-early Pleistocene age for the deposits (Vekua and Gabunia, 1989). Additionally, the age of the Masavera basalt was well established early in the excavations at approximately 1.85 MA by direct radiometric dating (Bosinski *et al*., 1989b; Majsuradze *et al*., 1989; Gabunia *et al*., 2001). However, the morphology of the D211 mandible, especially the presence of reduced M_3s and a distinctive *mentum osseum* (discussed in greater detail in the following chapter), coupled with prevailing thoughts about the role of the Caucasus region as a refugia throughout much of the Pleistocene, led many observers to speculate the hominid materials from the site were from later Middle, or even Upper Pleistocene deposits. Paleomagnetic dating further clouded the picture by showing the fossiliferous deposits yielded a combination of reserve and normal polarity sediments, making it unclear if the fossils derived from the Olduvai (> 1.77 MA) or Matuyama chron (1.77-1.07 MA) (Dean and Delson, 1995; Gabunia and Vekua, 1995; Goguitchaichvili and Parés, 2000; Gabunia *et al*., 2001; Garcia, 2005).

Additional work and an improved recognition of the stratigraphic sequence have greatly aided the understanding of the dates for the site. ^{40}Ar-^{39}Ar and K-Ar dating of both the underlying basalt (~1.85 MYA), and the lowest A1 ashes (~1.82 MYA) have yielded dates consistent with a terminal Pliocene-Lowest Pleistocene age (de Lumley *et al*., 2002; Garcia, 2005; Lordkipanidze *et al*., 2005; Rightmire *et al*., 2005). The

combination of normal and reverse polarity sediments appears to suggest the time period of deposition straddled the Olduvai-Matuyama subchron divide. Evidence for deposition rates based on soil micromophology suggests, however, that much of the sedimentation occurred very rapidly and therefore, likely did not occur over a greatly extended period of time (Mallol, 2004). Additionally, the identification of a similar sedimentary profile at the nearby locality of Zemo Orozmani, sandwiched between the Masavera basalt and an overlying basalt preliminarily dated to 1.76 MYA, provide a potential capping date for the Dmanisi sediments (Mallol, 2004). Therefore, the current consensus holds that all of the hominid materials come from a tightly controlled time period sometime between 1.77-1.76 MYA, with a possible hominid presence both before and after this date.

Early environmental reconstructions of the Dmanisi site suggest that the climate was likely similar to modern Mediterranean habitats, with generally warm, semi-arid conditions (Gabunia *et al*., 2000a; Gabunia *et al*., 2001). Temperature would have been moderated to a degree by the presence of the large Black-Caspian Sea (Pontian Sea-Lake) to the North, although may have been subject to some degree of seasonal shifts. The initial flow of the Masavera basalt was also responsible for the creation of a temporary paleo-lake in what is today the Pinezauri valley (R. Ferring, personal communication). The lake was likely a temporary feature on the landscape, and although in close proximity to the site of current excavations, current evidence suggests the lake's margin likely never reached them. The diverse assemblage of fauna, representing both forest and grassland habitats, suggests the presence of a heterogeneous mixture of environments and an occupation of the site contemporary with the lakes existence.

Archaeology:

In addition to fossil material, an abundant assortment of archaeological materials have been recovered (Bosinski *et al*., 1989a; Gabunia *et al*., 2001; de Lumley *et al*., 2005). Stone tools, like the fossils, exist throughout the Dmanisi stratigraphic sequence. However, unlike the faunal remains, which are present in larger numbers in the lower sediments and smaller numbers in the higher deposits, the reverse is true of stone artifacts. All of the stone tools present have thus far been described as either basic Oldowan (Bosinski *et al*., 1989a; Gabunia *et al*., 2001) or, more recently, pre-Oldowan in nature (de Lumley *et al*., 2005), consisting largely of cores and flakes manufactured out of locally derived raw materials (see figure 3.4). There is a preference for fine-grained basalt pebbles. Thus far, no identifiable differences serve to distinguish the archaeological materials derived from the A and B layers.

Hominid Material:

As of the 2005 field season, excavations at Dmanisi have yielded as many as sixty hominid fossils, including five crania, the four mandibles described here, several isolated teeth, and numerous post-cranial remains (Gabunia and Vekua, 1995; Gabunia *et al*., 1999; Gabunia *et al*., 2000b; Gabunia *et al*., 2002; Jashashvili, 2005; Lordkipanidze *et al*., 2005; Meyer, 2005; Rightmire *et al*., 2005).

Figure 3.4 – Dmanisi archaeological material

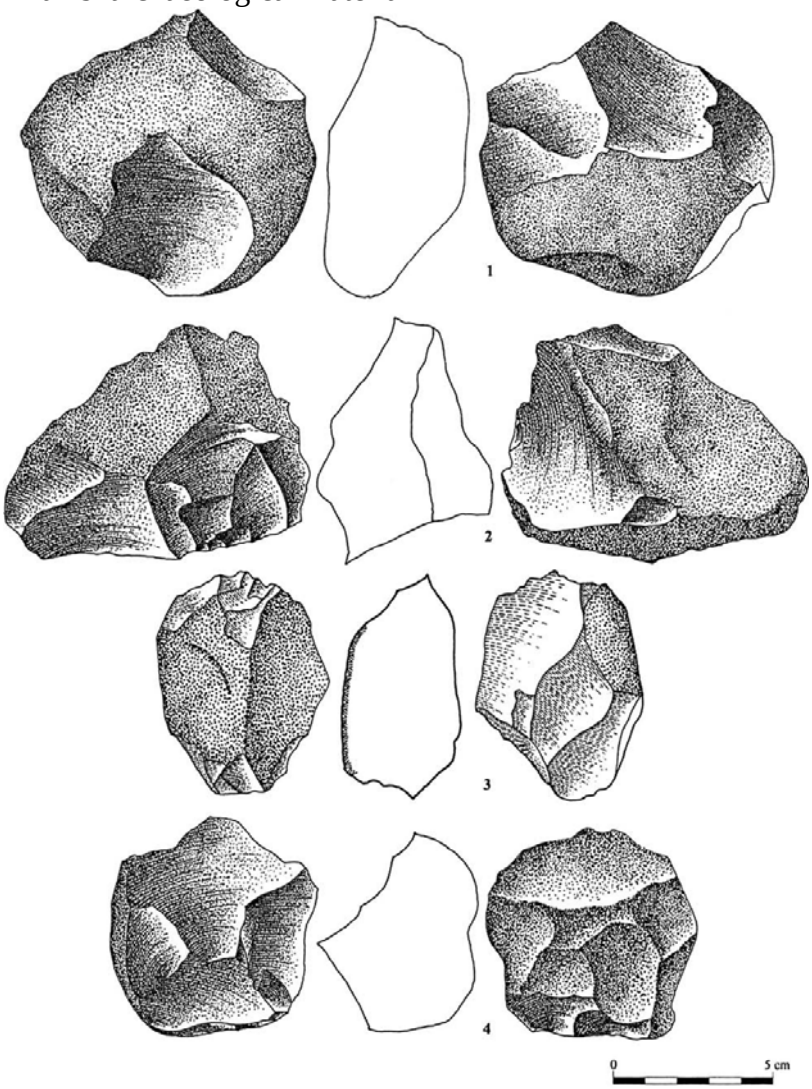


Figure 3.4 – Example of typical Dmanisi tool (from De Lumley 2005).

The majority of these remains are excellently preserved, several of them associated with each other on the basis of their spatial context, individual age, and anatomy. The combination of a large number of individuals including different associated elements, the excellent preservation, and the close spatial and temporal context make Dmanisi a unique site with regards to its potential to both ask and potentially answer questions regarding Plio-Pleistocene hominid evolution.

The Mandibular Sample:

At the time of publication, the Dmanisi mandibular sample consists of four, relatively complete mandibles; identified as D211, D2600, D2735, and D3900. Three of these mandibles, D211, D2735, and D3900 are associated with the cranial specimens D2282, D2700, and D3444, respectively. The following is a detailed anatomical description of each of the specimens and their stratigraphic context within the site. A complete set of images of the mandibles is located in Appendix A. Anatomical terminology, unless otherwise noted, is derived from Weidenreich's monograph on the Zhoukoudian mandibular sample (Weidenreich, 1936). In cases where the terminology is not found in Weidenreich's monograph, classification is based on White (2000).

D211

General Description:

D211 is a relatively complete, sub-adult mandibular corpus with a complete permanent dentition, broken just distal to the M_3 on both sides. In addition to the absence of both rami, the basal margin of the corpus is absent bilaterally, beginning at P_3 and continuing distally. On the right side, the fracture of the basal margin continues distal-superiorly, till by M_3, roughly half of the total corpus height (as observed at P_3) remains. On the left side, the fracture of the basal margin shears upward at M_2, removing nearly all the lateral corpus surface at M_2-M_3, although the medial surface remains largely intact. The M_3s of D211 are just coming into occlusion, suggesting a late adolescent age for the individual. Examination of the occlusal pattern of this specimen (damage to the left side of the palate of D2282 make simultaneous bilateral occlusion impossible), in addition to

its stratigraphic context, suggest D211 is associated with the cranium, D2282 (Wolpoff, 2002, Rightmire *et al*., 2005). As alluded to earlier, this mandibular specimen is most exceptional for its reduced molar size pattern (M_1>M_2>M_3), and particularly reduced M_3s.

Context:

D211 was the first hominid specimen recovered from Dmanisi, found following the conclusion of the 1991 field season by Gocha Kiladze. The specimen comes from Area I of the excavation, square 52/60 (during the 1991 field season, this was referred to as square 3). Its exact position was in quadrant 2, at x=90, y=75, z=1015.27. Owing to a different excavation layout during the early part of the excavation, the location of D211 at the time of its excavation is noted differently (at the time, it was considered quadrant 3, x=40, y=25, z=749). The position indicated above has been correlated with the current layout and orientation of the excavation and should be considered the correct position of the specimen. Based on the geological scheme developed during the early phases of the excavation, this mandible was believed to have come out of layer 5. As discussed above in the geological summary of the site, these layers have been reinterpreted and the validity of layer 5 is no longer accepted. However, because the reinterpretation of the site has been based largely on excavations within Area II, the exact stratigraphic setting of material recovered from Area I is based on inference, rather than observation. Most likely, the hominid material recovered from Area I (which also include the crania, D2280 and D2282) originate features within layer A2.

Pathology:

D211 displays no major pathology. As noted by Bräuer and Schultz (Bräuer and Schultz, 1996), evidence of periodontal disease are present throughout the alveolar margin, particularly distally. Such evidence of periodontal disease is common amongst fossil hominid material and great ape skeletal material (Ward *et al*., 1981; Wood, 1991; Dean *et al*., 1992; Czarnetzki *et al*., 2003). Evidence of moderate enamel hypoplasia are present on the canines, approximately 1/3 of the way between the cervicoenamel junction and occlusal surface.

Dentition:

The dentition of D11 is complete and excellently preserved. The M_3s are just coming into occlusion suggesting a late adolescent age for the specimen. The D211 dentition is exceptional for the relatively and absolutely small size of the posterior teeth, especially the third molars. This feature played a significant role in the initial debate regarding uncertainty in the temporal position of the Dmanisi fossils (Bräuer and Schultz, 1996; Rosas and Bermúdez de Castro, 1998).

The incisors of D211 are characterized by tall, narrow crowns, with a minimal amount of lingual development. The I_2s are slightly thicker along the labial-lingual axis of the cervicoenamel junction (bilateral average, 7.4[1]) than the central incisors (6.4), but display a similar crown profile in labial view (see table 4.2 for complete crown measurements). The crowns begins narrowly at the cervicoenamel junction (breadth, I_1, 4.3; I_2, 4.6), gradually widening towards the occlusal surface. The occlusal wear across

[1] All measurements listed in the text are expressed in millimeters unless otherwise stated and reflect, when available and appropriate, the bilateral average of the measure.

the incisors is generally flat, with a slight curvilinear, convex profile across the anterior margin of the occlusal surface, extending from the right lateral to left lateral incisor, where a small chip out of the labial-distal edge of its occlusal surface disrupts the pattern. Given the adolescent age of the mandible and the minimal to moderate wear elsewhere in the dentition, the wear across the incisors is quite pronounced.

Viewed labially, the canines of D211 have small, diamond, or 'mitten'-shaped crowns (labial-lingual breadth, 8.3; mesial-distal length, 7.3). Neither canine projects beyond the occlusal plane established by the other teeth. A small, vertical groove across the enamel surface distinguishes the 'thumb' of the mitten near the distal edge of the tooth. Moderate wear, mostly on the distal half of the apical occlusal surface has created a small dentin patch. The canines are both angled slightly labially relative to the adjacent teeth, causing the mesial edge of each canine to sit lingual to the distal edge of the lateral incisor. The lingual surfaces of the teeth have a weakly rounded central pillar, terminating in a small, rounded, distal tubercle.

The P_3s are asymmetrical and roughly triangular in profile when viewed in the occlusal plane. The broad, rounded buccal surface gradually narrows towards a smaller lingual edge. The crown is dominated by a large buccal cusp situated centrally along the buccal half of the tooth and occupying most of the occlusal surface. A much smaller, second cusp sits lingually along the major axis of the crown, separated from the primary cusp by a slight fissure. Mesial to this second cusp, along the obliquely-oriented mesial ridge of the tooth, sits an even smaller, minor cusp. The P_4s (buccal-lingual breadth, 8.8; mesial-distal length, 6.1) are considerably smaller than the P_3s (buccal-lingual breadth, 9.2; mesial-distal length, 6.9) and ovu-rectangular in shape, with the major labial-lingual

axis perpendicular to the tooth row. Again, these teeth are characterized by a large buccal cusp and a small lingual cusp. The buccal cusp occupies the entire buccal half of the P_4s, while the smaller lingual cusp is triangular and set off from the edge of the crown by a semi-circular fissure. None of the premolars display more than a polishing wear.

D211 has a decreasing molar size sequence (M_1>M_2>M_3). The M_1s are relatively large teeth (buccal-lingual breadth, 10.5; mesial-distal length, 10.9), ovu-rectangular in shape, and expanded mesially. The mesial expansion is characterized by a buccal swelling of the M_1 and the presence of a distinctive horizontal cingulum with a distal bifurcation, just below the occlusal surface. Occlusal wear on the M_1 is mild to moderate, focused mainly on the buccal cusps. These cusps are worn to low, rounded projections, with slight dentin exposure on the protoconid and hypoconid. A moderate amount of interproximal wear is present mesially, with a lesser amount along the distal edge. The M_2s are slightly smaller (buccal-lingual breadth, 10.4, mesial-distal length, 10.65), but also display an ovu-rectangular shape with a slight swelling of the buccal surface. Again, there is mild occlusal wear on the buccal cusps, while the lingual cusps are nearly unworn. The M_2s display standard Y-5 cusp pattern, but with a more complex pattern of micro-cusps interspersed between the cusps and fissures. The third molars are the most exceptional of the teeth. Instead of being ovu-rectangular, the M_3s are small, round and peg-like (buccal-lingual breadth, 9.4, mesial-distal length, 9.75). The M_3s are still in the process of occlusal eruption, with the occlusal surface of the crown oriented lingually relative to the occlusal plane established by the rest of the dentition. As a result, the only occlusal wear is a slight polishing of the buccal surface of the paraconid. The

occlusal surface itself is highly invaginated with grooves, obscuring any more standard cusp pattern.

Radiographs of the material allows for a partial description of the roots of D211. The anterior dentition, incisors and canines, are all characterized by shallow roots, particularly for the incisors. The premolars are both single-rooted, with straight, slightly anterior-oriented roots. The M_1 displays a typical bifurcated root with splayed anterior and posterior root segments. The M_2 and M_3 are noteworthy for having a convergent, or pyramidal root morphology (see figure 3.5).

Figure 3.5 – Radiograph of D211

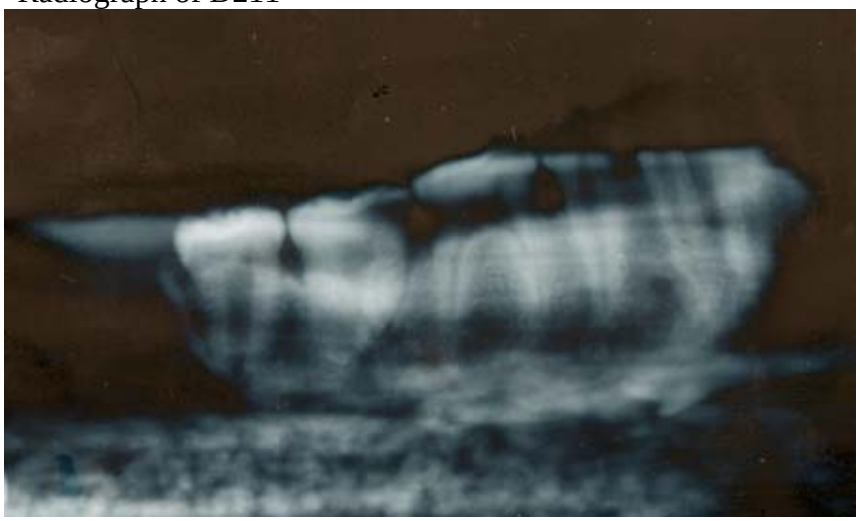


Figure 3.5 – Lateral radiograph of D211. Notice the convergent root morphology of M_2 and M_3 (modified from Macaluso, n.d.).

Lateral corpus:

The lateral corpus of D211, despite the absence of the basal margin across the molar row, preserves much of its morphology. In general, the corpus of this specimen is low and broad (corpus height at P_3: 27.0, corpus breadth at P_3: 17.95; see tables 4.6 and 4.7). On the right side, the root of the absent ramus and associated *prominentia lateralis* begins at approximately midcorpus height, inferior to the M_1-M_2 junction. The nature of

the basal fracture in this area partially obscures the morphology of this region, however, possibly obscuring the distinction between the root of the ramus and *torus lateralis superior*. The *prominentia lateralis* begins as a mild, horizontally oriented swelling at M_1, expanding to a breadth of approximately 6 mm at the beginning of the *sulcus extramolaris* at M_2, beyond which point it expands its maximum breadth (breadth at M_3, 7.5) and begins to curve slightly superiorly into the anterior margin of the ramus. Were it intact, the anterior margin would have crossed the alveolar margin at M_2-M_3. The presence and/or prominence of a *torus marginale* is lost on the right side by the absence of a distal, basal margin. The palpable presence of a *sulcus intertoralis* suggests that if preserved, a clearly identifiable, although weak, *torus marginale* would have been present. A pronounced *tuberculum marginale anterius* is present along the basal margin, between P_3-C. The superior margin of the tubercle projects strongly anterio-superiorly, almost giving the impression of the development of a crest. The presence of a distinct fossa mesial to this projection creates a clear separation between this feature and that of the *tuber symphyseos*, suggesting that it is indeed the *tuberculum marginale anterius* and not the *tuberculum laterale* of a fully developed *trigonum frontale*. The *foramen mentale* faces distal-laterally and is situated just below midcorpus at the mesial half of P_4 (14.1 from the alveolar margin, 12.0 from the center of the base). The superior margin of the *foramen mentale* is slightly damaged on this side. The alveolar margin along the right side of the mandible is largely intact, except for a semi-circular fracture along the mesial half of P_3.

The left side is similarly preserved and presents the same morphological pattern. The *prominentia lateralis* begins as a mild swelling at M_1, with the *sulcus extramolaris*

reaching its full breadth at M_2 (7.2). Slightly more of the basal half of the corpus is present, confirming the presence of a weak *torus marginale*. The *sulcus intertoralis* on this side is narrow and shallow. As on the right side, the *tuberculum marginale anterius* has a prominent, anterior-superiorly projecting prominence. The left side has two *foramina mentale*, the larger one situated at just below midcorpus (13.5 from the alveolar margin, 13.5 from the center of the base) in line with the distal half of P_3, facing laterally . A smaller foramen is situated immediately distal-inferiorly and is mesial-distally elongated. The alveolar margin is present along the length of the tooth row and has a slight swelling at the beginning of M_1. The fracture in the lateral surface of the corpus on this side exposes the internal structure of the corpus from mid-M_2 to distal to M_3. The cortical bone is thickened along the lateral margin, with thinner lingual development. Neither the roots of M_2 nor M_3 are exposed.

Symphysis, anterior:

Unlike the lateral *corpora*, the symphysis is completely intact and well preserved. Like the lateral *corpora*, the symphysis is relatively low (height, 31.0, see table 4.10) and broad (breadth, 17.2). The anterior symphyseal surface of D211 is quite flat, forming a pentagonal shaped surface between P_3-C along the alveolar margins and the *tuberculum marginale anteriori* along the basal margin. A *tuber symphyseos* is present along midline, elongated superiorly-inferiorly. Mild and gently rounded, the *tuber symphyseos* forms a clear prominence, projecting from the surrounding pentagonal, flat plane, but not exceeding the anterior projection of the alveolar margin at midline. The prominent *tuberculum marginale anteriori* accentuate a mild fossa just lateral to *tuber symphyseos*.

There are three mild, but separately identifiable fossae above *tuber symphyseos*; one situated inferior to *infradentale*, with slightly larger ones inferior to I_2 on each side (*incisura mandibulae anterior*). Slight ridges separate each of these fossae. In anterior view, the basal margin is weakly 'm'-like in profile, with mild, linear depressions associated with each *fossa digastrica* and an inferior projection at midline. A small foramen is present lateral to *tuber symphyseos* on the right side.

Medial corpus:

The medial aspect of the corpus is well preserved, particularly on the right side, and presents a great deal of surface topography. The distinction between an alveolar and subalveolar region begins posteriorly at M_2-M_3. This distinction is, in part, obscured by surface damage to the specimen which creates the impression of three separate areas divided by a superior and inferior groove. The superior groove, beginning 3-4 mm below the alveolar margin at M_2-M_3 and continuing anterior-inferiorly to M_1-P_4 appears to be the result of preservation damage. This false groove has the added effect of creating a sense of two distinct convexly projecting regions along the posterior, medial surface. The true distinction between the *prominentia alveolaris* and *fossa subalveolaris* also begins at M_2-M_3, but occurs more inferiorly and continues more directly anteriorly to M_1-P_4. The *fossa subalveolaris* is largely absent owing to the lack of a basal corpus, but appears to be expressed as a weak concavity. The *prominentia alveolaris* projects in a slightly rounded fashion, achieving its greatest breadth between half and two-thirds of the corpus height At P_4-M_1 the *prominentia alveolaris* extends medially forming a palpably and visually distinct *torus mandibularis*.

Symphysis, posterior:

The *planum alveolare* extends at an angle of ~45 degrees posterior-inferior from the *orale mandibulare*, projecting 17.3 mm posteriorly as far as P_3-P_4. Mild fossae are located bilaterally beneath I_1-I_2 separated by a slight central ridge. The *torus superioris transverse* extends towards midline, beginning as an inferior continuation of the medial swellings at P_4-M_1 and terminating near mid-corpus height at midline (21.2 from *infradentale*, 14.1 from the posterior point of the symphysis base at midline). The *torus superioris transverse* is only mildly robust. The *fossa genioglossi*, also weak, transects the lower portion of the *torus superioris transverse*. A raised vertical line extending inferiorly from the *fossa genioglossi* is the only expression of *spina mentalis* development. A distinctive *torus inferioris transverse* does not exist, although the continuation of the basal margin remains quite thick throughout the symphysis.

D2600

General Description:

D2600 is a nearly complete, adult mandible. This specimen is the most striking mandible within the Dmanisi sample because of its near completeness, excessive dental wear, and large size. The corpus preserves the anterior dentition from P_3 to I_1 on both the right and left sides. P_4 is absent bilaterally with signs of associated alveolar resorption. The right side preserves M_1-M_3, while the left side only has M_2 and M_3 remaining. The corpus itself is largely intact, although characterized by several anomalous features (see pathology section). The rami are preserved, although both lack substantial inferior portions around and including the gonial angle. On the right side, the coronoid tip is

present but the coronoid notch is damaged; on the left side, both features are damaged. Both condyles are preserved.

Context:

D2600 was recovered after the 2000 field season and was the first identified hominid specimen from Area II of the excavation. Unfortunately, like the D211 specimen, D2600 was initially discovered after the completion of the 2000 field season in the course of acquiring soil samples for geochronological purposes. Therefore, some uncertainty exists surrounding its exact stratigraphic context. However, notes taken at the time of excavation indicate that it came from square 64/59, quadrant 2, x=96, y=75, z=1014.56. At the time, this was identified as stratigraphic layer 5, current layer A2, although some debate existed as to whether it came out of A1, the basal black ash layer. Were it in layer A1, it would be the only hominid thus far recovered from this layer. The finding of other hominid fossil material associated with the D2600 specimen in the A2 layer during the course of the 2005 field season (unpublished at the time of writing) supports the former, less problematic stratigraphic position. If this association proves correct, all of the hominid material from Area II will have come out of the same stratigraphic feature within layer A2.

Pathology:

The pathological condition of the D2600 specimen is discussed briefly by Gabunia *et al* (2002). The specimen shows several pathologies associated with extreme dental attrition. Evidence of periodontal disease is associated with nearly all of the

surviving teeth. Where teeth have been lost, significant resorption of the alveolar margin has occurred. In addition, abscesses are present on the right side near the distal extension of the M_1 root and anteriorly at the distal edge of the right I_1 and I_2. The abscess associated with the right M_1 root appears to be the product of the exceptional vertical drift of the right M_1. In order to maintain occlusion, the tooth appears to not only have drifted superiorly, but also shifted lingually in order to accommodate the curvature of the occlusal surface. This shift resulted in a rotation of the distal root tips buccally, potentially compromising the corpus wall and resulting in the formation of the abscess. The anterior abscess seems to have resulted from a similar process with the right incisors. This abscess has been accentuated by a small degree of excavation damage. Aside from the dental anomalies, the left condyle displays a degree of degradation associated with osteoarthritis.

Dentition:

The dentition of D2600 is of particular interest owing to its large size relative to the other mandibles from Dmanisi, and most especially, for the dramatic wear of the teeth. All of the surviving teeth display exceptional wear, many beyond the crown itself and into the roots. The P_4s are bilaterally absent, as is the left M_1; the remainder of the dentition is present.

The enamel of the crowns of the incisors are completely worn away with the exception of a slight portion of the labial surface of the right I_2 (see table 4.2 for crown size data). What remains of these teeth are rounded, peg-like roots. The surviving central incisor roots are ovu-rectangular and oriented anteriorly. The lateral incisor roots

are also ovu-rectangular, but considerably elongated in the labial-lingual axis. The lateral incisor roots are also oriented obliquely relative to the central incisors, with a long-axis angled medial-posteriorly. One of the striking features of the wear across these teeth is the curvature of the wear, along both labial-lingual and mesial-distal axes. All of the teeth display a strong, convexly arched wear pattern along a labial-lingual axis. Additionally, two separate mesial-distal wear patterns are characterized across the teeth. In anterior view, the occlusal margin of the right I_1, left I_1, and left I_2 form a concave, arched surface. Likewise, the right I_2 and right canine appear to form a similar, although smaller arched wear surface.

The canines are also extremely worn, although the inferior-most portion of the cervicoenamel junction, especially on the left side, remains intact (left side labial-lingual breadth, 10.6, mesial-distal length, 9.0). The crown profile of the better preserved left canine, in the occlusal plane, is broad with a major axis parallel to the tooth row and a smoothly arched the labial surface. The occlusal surface contracts lingually and narrows to a wedge, producing a minor axis which, if extended, would intersect the posterior aspect of the *planum alveolare*. As mentioned above, the wear on the right canine is arched, with more heavily worn areas along the mesial edge. This appears to be part of a wear complex shared with the right I_2. The right canine is also heavily worn interproximally at this junction. The left canine is less worn and has a flat occlusal wear surface.

The P_3s are the only surviving premolars, as the P_4s have been lost, apparently *in vivo* (as evidenced by partial resorptive surfaces around the P_4 alveoli, see pathology section for more details), on both sides. The left P_3 is ovular in shape, with heavy wear

creating a broad, hollow exposure of dentin across the central portion of the crown. None of the occlusal cusp morphology is preserved. The distal edge of the enamel surface has been completely lost to strong interproximal wear. The exposed roots of the premolars, bilaterally, are double-rooted. The right P_3 appears to be shifted labially in its occlusal position, with its 'buccal' surface facing more anteriorly than its left counterpart. Also noteworthy is that, unlike the left P_3, the distal edge shows no interproximal wear and retains a thick enamel surface (buccal-lingual breadth, 8.3, mesial-distal length, 9.1). The absence of the interproximal wear on the right P_3 suggest the possibility of some developmental anomaly or agenesis of the right P_4. However, the exact condition, orientation, and positioning of the right P_4 in life is uncertain.

The molars continue, and even add to, the exceptional wear pattern. The left M_1, like the adjacent P_4, is absent and shows partial resorption of the surviving alveolus. The right M_1 is present, but is worn well below the cervicoenamel junction throughout most of the tooth, particularly mesially and buccally. The only surviving portion of the cervicoenamel junction is a small, distal-lingual segment. The wear of the right M_1 extends however onto the root itself, with clear polishing of the posterior root segment. The lingual half of the root is fractured and largely absent above the alveolar margin.

The M_2s and M_3s are present bilaterally, but also show heavy wear. Only the M_3s preserve crowns which remain largely intact, although worn flat and beneath the level of any occlusal features. Both the M_2s (buccal-lingual breadth, 12.4, mesial-distal length, 13.4) and the M_3s (buccal-lingual breadth, 13.1, mesial-distal length, 15.9) are large and rectangular in shape. Like the incisors, a wear complex extending across several teeth is present along the right molar row. The wear begins on the buccal-occlusal surface of the

right M_1 (extending onto the buccal surface of the exposed roots, as mentioned above) and continues in a spiral fashion forming an oblique surface across the M_2 and finally onto the M_3 occlusal surface where the wear is flat. This pattern is particularly noticeable when examining the buccal profile of the M_2 cervicoenamel junction, which is nearly absent mesially and expands distally, and at the contour of the occlusal surface of the M_2, which drops off in the mesial-buccal quadrant. The wear on M_1 is also notable in that it, like the incisors, appears to show an arching pattern of wear along a buccal-lingual axis, in addition to the spiraling mesial-distal wear it shares with the other molars.

Again, a radiographic examination of the roots provides some appraisal of the root morphology for D2600. The incisors, like those of D211, are shallow and contribute to prominent *incisura mandibulae anteriori*. As stated above, the canines, unlike those of D211, are very deeply rooted, extending between two-thirds and three-quarters of the height of the symphysis. Also different from D211, the surviving P_3s are double-rooted (see figure 3.6). The posterior molar roots show a typical, bifurcating and splayed morphology, rather than the convergent form seen in D211.

Lateral ramus/Condyle:

The overall impression of the rami of D2600 is of extremely tall structures, though with lightly constructed features. On the better preserved right side, the coronoid process sits 56.7 mm above the occlusal plane, while the superior aspect of the condyle sits 57.3 mm above the occlusal plane (see table 4.4). These large dimensions are coupled with thin and delicately developed features of the superior rami. The anterior

Figure 3.6 – Radiograph of D2600

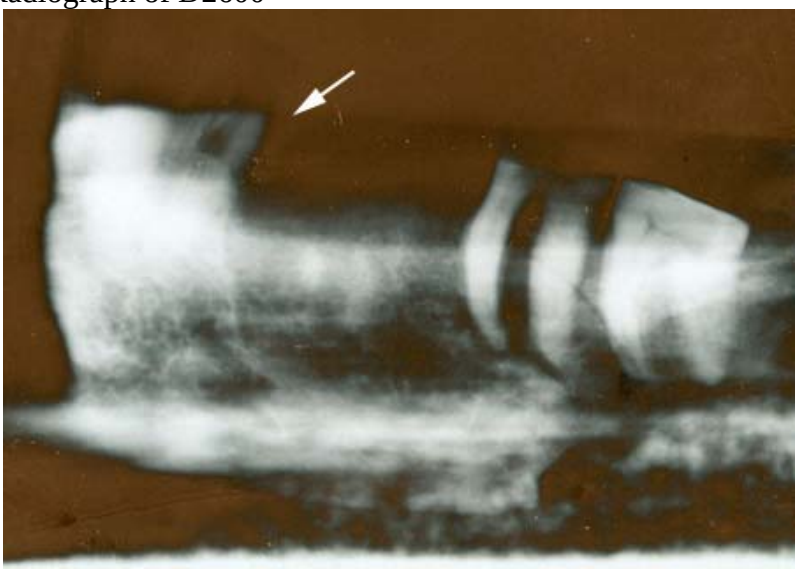


Figure 3.6 – Lateral radiograph of D2600. The arrow indicates the double-rooted P_3 (modified from Macaluso, n.d.).

margin of the ascending ramus begins emerging from the corpus and slopes distal-superiorly below the mesial half of M_3, crossing the alveolar plane in the distal half of M_3, at which point it proceeds more sharply vertically. The anterior margin of the ramus is thin, only thickening in the superior third of the structure, where the margin begins sloping anterior-superiorly, before returning to a posterior-superior direction as it approaches the tip of the coronoid process. The anterior margin of the rami therefore display an 'S'-shaped profile in lateral view. Viewed in the occlusal plane, the coronoid process extends vertically to a height approximately equal to the most superior aspect of the condyle and separated by a distance 34.5 mm. The coronoid notch is damaged on both sides, although the preserved portions of this region suggest it was low and relatively narrow, with an inferior point positioned between the midpoint and distal third of the structure.

Neither side preserves the entirety of the lateral ramus, particularly inferiorly, although the right side retains significantly more. On the right side, the posterior margin of the ramus is preserved for approximately 20 mm below the condyle, proceeding predominantly inferiorly with just a slight anterior orientation. There is evidence of a weak *crista ectondyloidea* beginning in line with the coronoid process, just slightly above the occlusal plane.

The right condyle is well preserved and retains its complete anatomy, with a breadth of 24.1 mm and a length of 11.2 mm. The left condyle is also preserved, but shows evidence of moderate to heavy *in vivo* osteoarthritic degradation, obscuring much of the normal anatomy. Based on the right side, the condyle is particularly medially-laterally elongated, with its long axis oriented approximately perpendicularly to the molar row of the right side. The broadest point, anterior-posteriorly, sits near the medial edge of the condyle, owing to posterior expansion of the condyle in this region. The most anterior point lies near the lateral edge, where the ridge of the notch rises superior-laterally to meet the condyle. Overall, the condyle displays three main surfaces; a large anterior-medial surface, small medial-anterior surface, and a posterior surface of intermediate size. The posterior facet is set off from the two anterior surfaces by a curved, concave ridge with concavity facing posteriorly. Viewed distally, the largest portion of the condyle is situated medially of the condylar midpoint, with the lateral aspect extending as a narrowing wedge. The articular surface of the left condyle retains the same basic shape, but is worn to a single flat, roughly surface plane, approximately 5 mm lower than the right condyle.

Lateral corpus:

The lateral corpus of D2600 reflects the extreme tallness of the mandible as observed in the rami (corpus height of 44.1 at P_3; 41.5 at P_4; 41.0 at M_1; and 36.5 at M_2; see table 4.6), but is dominated to a large degree by the effects of the pronounced dental wear and attrition. Although the corpus of D2600 is also quite broad in absolute terms (corpus breadth of 21.9 at P_3; 21.5 at P_4; 20.3 at M_1; and 21.4 at M_2; see table 4.7), relative to the height, the breadth is not nearly as pronounced. On the right side, loss of P_4 is associated with accompanying resorption of the alveolar margin, at this point down to just above the level of the *foramen mentale*. As mentioned above, a large abscess is located along the right lateral margin, associated with and exposing the root tips of the M_1. On the left side, features associated with the dental attrition of the mandible play an even more dominant role. Here, both P_4 and M_1 have been lost. The area inferior and distal to P_4 shows extensive resorption, similar to that seen on the right side. The loss of M_1 however, appears to have occurred very shortly before death, as some evidence of the bony separation between anterior and posterior roots is preserved. The resorption of the alveolar region in this area, coupled with preservation damage to the alveolar margin around M_2, make the identification of features on the upper part of the lateral corpus on this side impossible.

The *prominentia lateralis* is only weakly expressed on both sides in the area of the ramus-corpus junction, at the border of M_2-M_3. The ascending ramus emerges posterior-vertically at the M_2-M_3 junction, crossing the alveolar margin and turning more vertically at the distal half of M_3. The *sulcus extramolaris*, although somewhat broad (7.8 on the better preserved right side), is confined to the areas lateral to M_2 and M_3. The

torus lateralis superior is weak and discontinuous on the right side, owing to the loss of P_4, and not visible on the left side because of the more substantial loss of both P_4 and M_1. A moderately well developed *torus marginale* is present on both sides although its posterior end is lost. Separating the *torus marginale* from the superior aspect of the corpus is a broad, shallow, *sulcus intertoralis*, extending from M_1 to P_3, though more strongly expressed anteriorly than posteriorly. On the right side, a single, relatively small *foramen mentale* is present, oriented anterior-superiorly, situated well beneath mid-corpus at the junction of P_3 and P_4 (25.5 from the alveolar margin, 16.8 from the center of the base). On the left side two *foramina mentale* are present. The first, and larger one, very similar to that seen on the right side. The second is situated posteriorly to the first, below P_4-M_1, and is horizontally elongated (very diminished vertically) and oriented posteriorly. The *torus marginale* continues anteriorly, culminating in a large, broad, *tuberculum marginale anterius*. This structure, situated along the basal margin anterior to the *foramen mentale* on each side, reaches a maximum height below P_3-C. The roots of P_3 and C project from the surface of the corpus, forming prominent jugae and serving to distinguish the lateral *corpora* from the symphysis.

Symphysis, anterior:

The symphysis of D2600, particularly its great height (50.0; see table 4.10), is one of the mandible's most striking features. The canine roots, which are marked by prominent pillars extending from the plane of the corpus, reach 2/3 of the length down the symphysis (approximately 30 mm) and serve to bracket the region. The incisors have comparatively shallow roots, which, coupled with the extensive roots of the canines,

create elongated, shallow *incisura mandibulae* inferior to the lateral incisors. Immediately inferior to the right I_1 and I_2 is a round depression which apparently is an abscess whose outlines have been slightly extended in the process of excavation. The *tuber symphyseos* is a vertically elongated, low, rounded protuberance beginning just below midcorpus height and extending to the basal margin. As it approaches the basal margin the *tuber symphyseos* broadens laterally, eventually merging with the anterior projections of the *tuberculum marginale anteriori* on either side. The texture of the bone along the basal margin is slightly different than elsewhere on the specimen. Rather than a smooth surface, the basal margin features a light rugosity, extending from the inferior margin of the symphysis laterally towards the *torus marginalis* along each *corpora*.

Medial ramus:

The medial surfaces of the rami, as with the lateral surfaces, have been extensively damaged and are missing large portions of the potentially identifiable anatomy. Nevertheless, certain characters, particularly on the right side, remain visible. The *torus triangularis* is separated from the distal tooth row by a broad *sulcus extramolaris*. The torus is oriented approximately 45 degrees relative to the occlusal plane in a superior-posterior direction and bifurcates into the *crista endocoropterygoidei* and *crista endocondyloidea* just anterior to the *foramen mandibulare*. The *crista endocoropterygoidei* begins sharply from the bifurcation of the *torus triangularis*, arcs slowly anterior-superiorly, and finally fades into the anterior margin of the ramus. The *crista endocondyloidea* , in contrast, is broad, but only weakly distinguished. The *planum triangulare* is sharply demarcated and recessed at its inferior margin but fades

superiorly along with the *crista endocoropterygoidei*. There is a small, but projecting, *tuberculum pterygoideum superius* just inferior and anterior to the front of the condyle. The *foramen mandibulare* is oriented superiorly and opens in a broad, circular, horizontal foramen, with a distinct lingual associated with the sphenomandibular attachment site at its anterior margin. None of the gonial angle or its associated morphology is preserved.

Medial corpus:

The medial *corpora* are tall, but generally indistinct in their morphology. The *linea mylohyoidea* forms a distinct ridge which divides the corpus obliquely from the distal half of M_3 to the middle of M_2, where it fades away. As in the other Dmanisi specimens, there is a broad mesial swelling *torus mandibularis* along the alveolar portion of the medial corpus, just lingual to P_4. In the case of D2600, this feature is mild and diffuse, but still easily palpable. The *fossa subalveolaris* of the medial corpus is marked by only a slight concavity at the border with the alveolar portion, but generally remains quite thick throughout its length. An inferior torus appears to be present, but is largely indistinguishable from the superior edge of the basal margin. A distinct sulcus exists between the *prominentia alveolaris* and this basal torus. The dental arch broadens smoothly from an internal breadth of 32.3 mm at P_3 to 47.1 mm at M_3.

Symphysis, posterior:

The posterior symphysis is narrow, owing largely to the narrowing of the mid-corpus internal breadth in the area of P_4 and the general robustness of the specimen. The *planum alveolare* is a concave depression, gently rounded and culminates in the *torus*

superioris transverse with a length of 24.6 mm. Two small foramina are present near the alveolar margin of this concavity, just posterior and inferior to I_1. The *torus superioris transverse* itself is weakly expressed relative to the overall curvature of the symphysis and, when viewed in the occlusal plane, extends posteriorly to the distal side of P_3. Below the torus a shallow *fossa genioglossi* is present (depth, 1.3), inferior to which is a pronounced, fin-like *spina mentalis*. The *spina mentalis* lies on the posterior aspect of a transverse swelling which might be considered a weak, *torus inferioris transverse*. The *fossa digastrica*e are broad, indistinct, and angled posteriorly.

D2735

General Description:

D2735 is a nearly complete, sub-adult mandible. Aside from minor damage to the anterior alveolar region and the gonial angles, the only portion of the mandible that is absent are the condyles, both right and left. In addition to the dentition preserved within the corpus, which includes P_3-M_2 on both sides, several isolated teeth have been reassociated with the mandible. These include a left canine (D2723), left I_2 (D3698), right I_2 (D2854), and right canine (D2678). Based on radiograph images, the left M_3 is congenitally absent, while the right side preserves a portion of the M_3 alveolus, but the tooth appears to have been incompletely erupted and is not preserved. Like D211 and D2282, spatial and occlusal associations can be made with D2735 and the complete cranium, D2700. The maxillary M^3s, in the process of eruption, support the notion of D2735 as a late adolescent specimen, likely a year or two younger developmentally than D211/D2282.

Context:

The D2735 mandible was found during the course of the 2001 field season by Slava Ediberidze. Situated in square 66/60 of Area II of the excavation (x=52, y=78, z=1014.83), the D2735 mandible is spatially and morphologically associated with a cranium (D2700), numerous maxillary and mandibular isolated teeth (see General Description above), as well as post-cranial material. These were described at the time as belonging to stratigraphic layer IV, now identified as A2.

Pathology:

D2735 exhibits dental agenesis of the left M_3. It also displays pronounced enamel hypoplasia across the lower third of the P_3s and canines, bilaterally. These features are especially striking on the premolars.

Dentition:

D2735 has a complete set of dentition minus the absent central incisors and unerupted right M_3 (there is agenesis of the left M_3). The remaining teeth are well preserved and generally show only slight to moderate wear.

The lateral incisors are similar to those of D211 with tall, narrow crowns, broadening at roughly the midpoint of the labial surface. In terms of absolute size, the lateral incisors of D2735 are slightly larger than those of D211 (labial-lingual breadth, 7.4; mesial-distal length, 5.0; see table 4.2). The I_2s are only weakly worn and show a

slight inferior dip along the distal edge of the occlusal surface. Like the incisors of D211, there is no sign of any lateral pillars along the lingual surface.

The canines are moderate in size, with relatively large cervicoenamel junction dimensions (labial-lingual breadth, 9.3; mesial-distal length, 9.00) coupled with a moderate sized crown. The crown, again similar to D211, is diamond shaped, with a mitten-like profile in labial view. The groove which distinguishes the 'thumb' is quite pronounced in D2735, terminating near the swelling of the cervicoenamel junction. The occlusal surface is only lightly worn on the distal half of the apical surface and presents a more projecting profile than the canines of D211. The lingual side of the crown is dominated by a moderate tubercle-pillar complex.

The premolars are similar, but larger than those seen in D211. The P_3s are assymetrical, though generally triangular in occlusal profile, with a broad buccal surface and a narrow, wedge-shaped lingual edge (buccal-lingual breadth, 10.3; mesial-distal length, 7.0). In buccal view, the occlusal profile of the P_3s is semicircular with a distal extension towards the contact with P_4. The tooth is dominated by a large buccal cusp, with a much smaller lingual cusp. In addition, there is a mesial, moderately-sized swelling along the distal ridge of the tooth. A very weak interproximal wear between the premolars is present. The occlusal wear is weak across all of the premolars. The P_4s are buccal-lingually elongated rectangles in occlusal profile, roughly two-third the size of the P_3 and half the size of the M_1 (buccal-lingual breadth, 9.3; mesial-distal length, 6.4). The P_4 have a large buccal cusp and a slightly smaller, mesial-lingual oriented second cusp. While there is a minimal amount of interproximal wear with P_3, a moderate to large interproximal facet exists between P_4 and M_1.

The molars of D2735 are large and rectangular, with M_1 (buccal-lingual breadth, 11.0; mesial-distal length, 11.0) slightly greater in size than M_2 (buccal-lingual breadth, 10.4; mesial-distal length, 11.1). The M_1s, in occlusal profile, are rectangular with rounded edges. There is moderate occlusal wear, particularly focused on the hypoconid, entoconid, and hypoconulid. The M_2s are similar in shape, but slightly smaller in breadth than M_1s. The M_2s have mild occlusal wear, with a partial flattening of the protoconid, hypoconid, and hypoconulid, particularly on the right side.

Unfortunately, neither third molar is preserved. While the left M_3 was in the process of eruption at the time of death, leaving a partially excavated alveolus, the right M_3 appears to have been congenitally absent. No evidence of an alveolus or developing crown is preserved. The surviving alveolus of the left M_3 suggests it was a small tooth, closer in size to that of D211 than the large M_3 of D2600.

The root morphology of the surviving anterior dentition is similar to that of D211, with shallowly rooted incisors and canines. The M_1s and M_2s show typical, bifurcated and splayed root morphology, similar to that of D2600. The radiograph also shows evidence of a Tomes root in the P_3 on both sides (see figure 3.7), with a bifurcation of the root occurring beneath the alveolar margin.

Lateral ramus:

The rami of D2735 are low, broad (minimum breadth of 37.4), and marked by only weak surface development. The coronoid process is preserved on both sides, but displays slight damage on the tip and, on the left side, the anterior margin (coronoid

Figure 3.7 – Radiograph of D2735

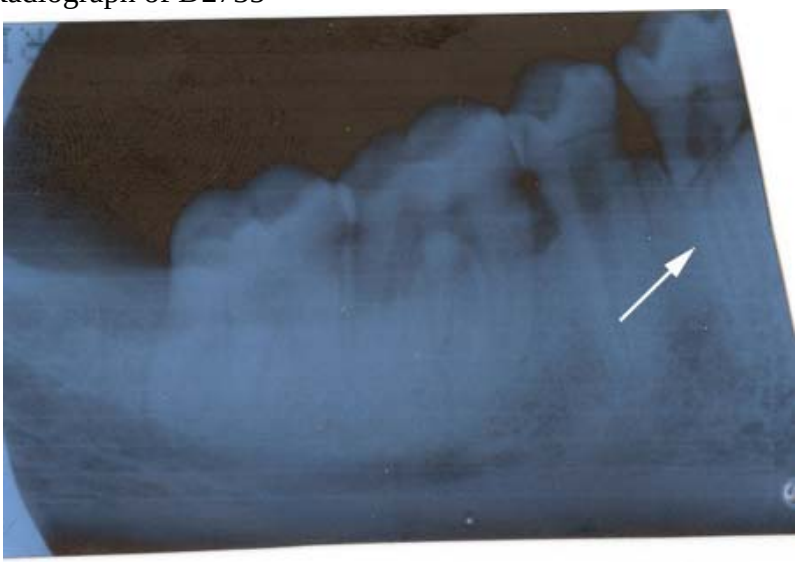


Figure 3.7 – Lateral radiograph of D2735. The arrow highlights the subalveolar point of bifurcation in the P_3 (modified from Macaluso, n.d.).

height from occlusal plane, 36.0; from basal plane, 59.3; see table 4.4). The process everts from the corporal and ramal planes, particularly in its most superior aspect above the level of the coronoid notch. On the right side, the area posterior to the coronoid process is absent, including both the notch and the condyle. The left side preserves more of the morphology, although the coronoid notch on this side, low and situated approximately midway between the coronoid process and condyle, is damaged and the condyle is absent superior to the beginning of the condylar neck. The anterior margin of the rami slope continuously superiorly and posteriorly, beginning below M_1, sloping first posteriorly to M_2, then angling superiorly, crossing the alveolar margin at the mid-point of M_2.

A shallow, weak *fossa masseterica*, expressed as a general concavity of the lower portion of the lateral rami, sits in the distal inferior corner separated from the corpus by a mild, broad tuberosity. A weak *crista ectondyloidea* is present on the left side (surface

abrasion on the right side prevents conclusive bilateral diagnosis), extending from roughly the height of the occlusal plane in the anterior half of the ramus distal-superiorly in a straight line towards the condylar neck, where it turns more vertically. There is a triangular shaped fossa above this crest which is accentuated by the crest and the mild eversion of the coronoid process. In general, the rami are angled in the same plane as the lateral *corpora*. The gonial region, damaged on the left side, shows mild, generalized eversion. The angle begins along the basal margin anterior to the coronoid process but does not begin arching significantly superiorly till the apex of coronoid process, where it proceeds at approximately a 30 degree angle for 10 mm, before angling much more sharply vertically, presumably in line with the posterior ramal margin, which is not preserved.

Lateral corpus:

The D2735 mandible displays a typical profile of a sub-adult specimen, with a low (corpus height of 26.9 at P_3; 24.7 at P_4; 22.3 at M_1; and 20.9 at M_2; see table 4.6), broad corpus (corpus breadth of 18.9 at P_3; 19.6 at P_4; 20.7 at M_1; and 22.3 at M_2; see table 4.7), marked by little surface development. The lateral surface of the corpus, particularly on the right side of the specimen, appears to be damaged by *in situ* root action prior to excavation, affecting the ability to recognize precise surface detail, but not limiting general anatomical assessment. The ascending ramus emerges out of a relatively well developed *prominentia lateralis* at the M_1-M_2 junction and begins arching significantly vertically, crossing the alveolar margin at the midpoint of M_2. The *prominentia lateralis* itself is anteriorly situated on the lateral corpus near the *foramen*

mentale and in line with the posterior half of P_3. By the M_1-M_2 junction the *prominentia lateralis* achieves its greatest breadth, creating a relatively broad extramolar sulcus (breadth, 7.7). The smoothly rounded swelling of the *prominentia lateralis* dominates the morphology of the lateral corpus. There are no distinguishable *torus lateralis* or *torus marginalis*, but rather, the entire *prominentia lateralis* fades into the corpus body gradually both at its basal and anterior limits. The presence of a *sulcus intertoralis* is confined immediately posterior to the *foramen mentale* and requires palpation to be noticeable on the left side. The *foramen mentale* lies below the far distal edge of P_3 near mid-corpus height and is oriented superiorly and slightly anteriorly on both sides (12.8 from the alveolar margin, 13.5 from the center of the base). Anterior and inferior to the *foramen mentale* (near the junction of the symphysis and lateral *corpora*) along the basal margin is a swollen, rounded, *tuberculum marginale*. The lateral *corpora* reduce in height between the canine (26.7) and M_2 (20.9).

Symphysis, anterior:

The symphysis of D2735 connects the lateral *corpora* in a smoothly and continuously rounded arch. Relative to the D2600 specimen, the D2735 symphysis is quite small, with a height of only 34.0 mm (see table 4.10). The *incisura mandibulae*, inferior to the incisors shows slight flattening relative to the more broadly defined curvature of the region. The anterior *incisura mandibulae anterior*, like those of D2600, result from three separate fossae, one underneath I_1-I_1, the other two underneath the right and left I_2. Unlike D2600, no evidence of significant alveolar development associated with prominent root development is visible. There is a distinctive, although weak *tuber*

symphyseos in the form of a smoothly rounded protuberance in the inferior half of the midline. A slight inferior midline projection exists on the basal margin disrupting an otherwise horizontal anterior profile. The orientation of the symphysis at midline is relatively straight, inferior-posteriorly oriented, with a smooth curve along its basal margin.

Medial ramus:

The medial aspect of the rami display the same surface damage as described with the lateral corpus. The right side retains the medial aspect of the coronoid process and the gonial angle, while the left side preserves a larger portion of the condyle. The medial projection of the *prominentia alveolaris* extends posteriorly well past the anterior margin of the ascending ramus, thus playing a large role in the morphology of this area. The M_3 alveolus on the right side sits entirely concealed, in lateral view, by the ascending ramus. Posterior to the M_3 alveolus, the medial edge of the *prominentia alveolaris* cuts laterally and superiorly towards the medial surface of the ramus. The *torus triangularis* is prominent, projecting as a solid bar continuing from the posterior *prominentia alveolaris* superiorly and distally towards just above the *foramen mandibulare*, where it splits into distinctive and well-defined *crista endocoronoidea* and *crista endocondyloidea*. On the left side, with the absence of an M_3 alveolus, the *torus triangularis* is oriented more distally and forms more of a natural triangle. The *crista endocoronoidea* is oriented nearly vertically from the mesial aspect of the *foramen mandibulare*, gradually fading as it approaches the coronoid process. The *crista endocondyloidea* is oriented more obliquely and is broader, but less sharply defined than the *crista endocoronoidea*. The

foramen mandibulare is oriented posterior-superiorly with an ovular, horizontal opening, slightly superior to the occlusal plane, with a distinct lingual associated with the sphenomandibular ligament, visible on the right side. The mylohyoid groove proceeds anterio-inferiorly from the base of the *foramen mandibulare*, demarcating the lower border of the *prominentia alveolaris*. Several weakly projecting medial pterygoid tuberosities are present, beginning at the initial curvature of the angle, approximately in vertical line with the coronoid process.

Medial corpus:

The medial aspect of the corpus is notable most for a pronounced medial swelling *torus mandibularis*, found bilaterally, at P_4. This medial projection of the *prominentia alveolaris* appears to be similar to that seen in D2600 and especially D211 and is not associated with an erupting dental crown or any obvious feature of the mandible or dentition. The inferior margin of the *prominentia alveolaris* runs largely parallel to the tooth row, dipping at P_4 where it encounters the *torus mandibularis*. The line between the medial projection of the *prominentia alveolaris* and the inferior margin of the corpus is significantly oblique. The internal breadth of this specimen as measured at root position increases from 31.1 mm at P_4 to 40.5 mm at M_2.

Symphysis, posterior:

The posterior aspect of the symphysis has partial damage along the alveolar margin and also just posterior to the central incisors, where a small, circular concavity has been opened in the incisive plane. The *planum alveolare* is short (length, 17.3) and

oriented more inferiorly than posteriorly. The twin swellings of the *torus mandibularis* at P_4 serve to separate the anterior portion of the mandible from the internal lateral *corpora*. The *torus superioris transverse* is weak and presents as an extension of the *torus alveolare* along either *corpora*. In superior view, the *torus superioris transverse* creates a tight semi-circular profile ending at the *torus mandibularis* on each side. There is a shallow *fossa genioglossi* (depth, 0.6) inferior to the torus which contains a weakly projecting *spina mentalis*. A slight protuberance near the basal margin marks the beginnings of each *fossae digastrica*, which are focused centrally, shallow, moderately broad, and separated by a midline projection.

D3900

General Description:

The D3900 specimen is another remarkable mandible within the Dmanisi sample because of its pronounced alveolar resorption. While the adult mandible preserves a significant portion of the right ramus, corpus, symphysis, and left corpus, the specimen has no surviving dentition and exhibits an extreme degree of resorption across every aspect of its anatomy. The degree of resorption in this specimen makes comparisons with other specimens nearly impossible given the almost total absence of complete homologous characters. Additionally, what bone does survive is extremely fragile and, on the left side, covered in a fine matrix. In general size terms, the mandible in life was likely much closer to the D211 and D2735 specimens than D2600. Comparing what remains of the basal margin, strong similarities in the size and shape of the basal arch can be seen between D3900 and D2735. Compared to the La Chapelle Neandertal mandible,

the best known hominid mandible with a high degree of alveolar resorption, the D3900 specimen shows dramatically greater resorption, particularly in the lateral *corpora* and gonial regions. While the general pattern of resorption in this specimen follows that seen in older adult human specimens (especially in pre-dentistry populations), the degree of wear seen in both the angle and lateral alveolar regions is extreme. As with D211 and D2735, D3900 is also associated with a near complete cranium, D3444. The maxillary alveolar margin also shows complete resorption, confirming a relatively, if not absolutely, old age for this specimen.

Context:

The D3900 mandible was unearthed during the 2003 excavation season by Dato Taqtaqishvili. The mandible was found, positioned on its side, directly adjacent to the D3444 hominid cranium, which, both its spatial position and anatomy suggest belong to a single individual. The material was found in square 64/61 of Area II, at an elevation of 1014.80 m, in layer A2 of the excavation.

Pathology:

The only evidence of pathology in D3900 is in the pronounced dental attrition and resorption of the specimen. Although the degree of dental and bone loss is exceptional, nothing about the pattern of resorption appears atypical from a normal pattern of mandibular decay.

Dentition:

The dentition of D3900 is completely absent, with almost complete resorption of the alveolar portion of the mandible. The left canine alveolus is the most complete remaining alveolus and may have been the only tooth present in the mandible at or near the time of death. The right canine alveolus is also partially preserved, but shows considerable resorption. A small, inferior portion of the left P_3 alveolus is also preserved.

Lateral ramus:

Only the right ramus remains intact and its degree of preservation leaves a great deal to be desired. The resorption across the specimen and a fracture of the superior aspect of the ramus make the identification of describable and comparable anatomical features difficult. The gonial angle appears to be almost completely resorbed, being replaced instead by a long, gradual curvature from midway through the lateral corpus towards the posterior margin of the ramus, just inferior to the condyle. This edge, although displaying a slight eversion along its anterior margin, is inverted relative to the general projection of the ramus and corpus. A sharp groove is present along the anterior-inferior border of the surviving 'angle', terminating in a hole which passes directly through the ramus. The edges of this hole show no sign of fresh fracture and therefore suggest the hole is either the result of an *in vivo* process of resorption or a diagenic feature associated with fossilization. The absence of such erosional taphonomic features in other Dmanisi fossils suggests the former is a more likely explanation. A small portion of the subcondylar region survives, showing a small but obvious *crista ectondyloidea*, angled from the inferior edge of the condylar neck towards the root of the ramus.

Lateral corpus:

Fine, adhering surface matrix on the left side of the mandible make the identification of surface features along that side impossible. On the right side, the natural basal margin of the mandible appears to survive, intact, from the lateral symphysis to the *foramen mentale*, likely in the area of P_3-P_4 contact. Resorption along the alveolar margin on the right side has exposed a large section of the inferior alveolar canal. Again, the edges of this exposure are smooth, rounded, and show no sign of fresh fracture, suggesting this was the product of an *in vivo* process. The ramus intersects the corpus at the posterior opening of this feature along what is the surviving superior margin of the mandible, indicating that approximately half of the total corpus height remains. A *foramen mentale* is present at what was probably the P_3-P_4 contact, now roughly 5 mm inferior to the superior margin of the surviving corpus. On the left side, a weak but palpable tubercle, presumably the *tuberculum marginale*, is present along the basal margin distal to the canine alveolus and separated from the symphysis by a palpable sulcus.

Symphysis, anterior:

The alveolar margin of the symphysis is largely, but not completely resorbed, preserving more than either lateral corpus. In this manner, the pattern of resorption is consistent with that seen in older human mandibles (see figure 3.8). The area around the central incisors is broken away but portions of the alveolar margin survive laterally. A

very prominent, rounded *tuber symphyseos*, accentuated by the general resorption across the symphysis, is present.

Figure 3.8 – Characteristic human resorption

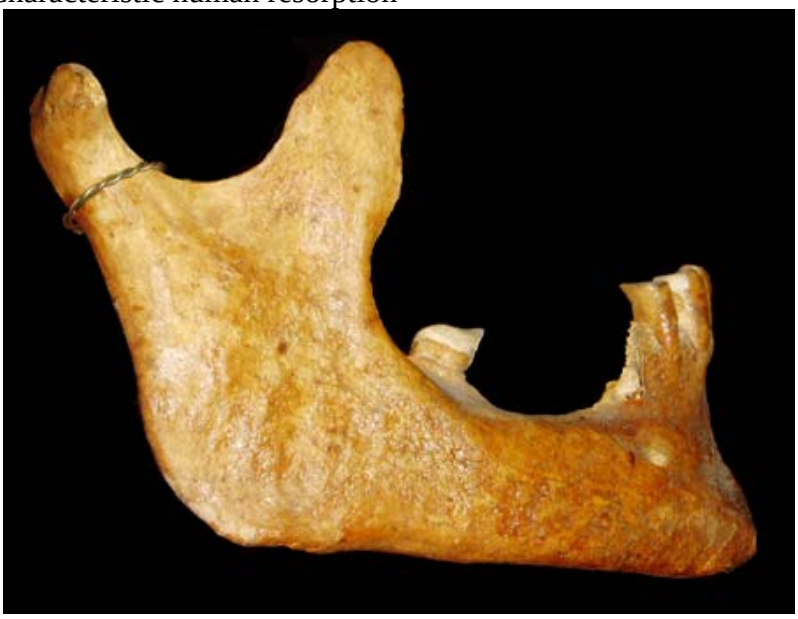


Figure 3.8 – Typical late adult mandible with characteristically strong resorption along the lateral alveolar margins and preservation of the symphysis region.

Ramus, medial:

As with the lateral aspect of the ramus, resorption makes the identification of specific features difficult. The fracture along the superior margin of the ramus occurs at the superior margin of the mandibular foramen. Although the gonial angle, as previously mentioned, is largely resorbed, irregular swellings and rugosity along the medial aspect of the surviving edge suggest continued medial pterygoid contact.

Corpus, medial:

Only the subalveolar portion of the medial corpus, smooth and evenly rounded, remains. Little distinctive morphology is present.

Symphysis, posterior:

The *planum alveolare* proceeds inferiorly-distally for approximately 10 mm, where it ends in a narrow, rounded, superior transverse torus which dissipates laterally into *corpora*. This torus forms the superior margin of a small, rounded, moderately deep *fossa genioglossi*. A bifurcated, narrow, superio-inferiorly elongated and very weakly projecting *spina mentalis* originates in the fossa. The *fossa digastrica*e are shallow and only expressed in a weak, anterior crest.

Summary:

The site of Dmanisi, Georgia, has provided abundant fossil and archaeological evidence of an early hominid presence outside of Africa. The current evidence suggests that all of the Dmanisi hominid material comes from the same stratigraphic layer within the Dmanisi deposits and likely dates to immediately after the Olduvai-Matuyama paleomagnetic reversal, currently dated to 1.77 MA. In addition to hominid fossils, a rich collection of faunal and archaeological material are also present at the site. Analyses of these materials and their significance for understanding the site are ongoing. The hominid material shows a remarkable degree of preservation and provides the unique circumstance of multiple associated skeletal elements from multiple individuals. Most of this material has only been recovered in the several years since 1999 and has only been partially described and analyzed.

Within the hominid sample are four moderate to excellently preserved mandibles. These mandibles are exceptional amongst the Dmanisi remains for the remarkable variation presented by them, with two smaller, sub-adult specimens (D211 and D2735),

one of the largest known Pleistocene hominid mandibles (D2600), and the earliest known edentulous hominid mandible (D3900).

The D211 mandible, the first hominid element recovered from the site, consists of a complete dentition and partially preserved corpus. The molars are noteworthy for showing a reducing pattern of size from M_1 to M_3, with particularly small M_3s. The M_3s are just entering into occlusion in this specimen, suggesting a late adolescent age. The corpus shows moderately developed features including a prominent *tuber symphyseos*, upwardly flaring *tuberculum marginale anterius*, and a particularly well expressed *torus mandibularis*.

The D2600 mandible is a well preserved and exceptionally large specimen, with a complete corpus and rami only lacking the gonial regions. The dentition, particularly the posterior teeth, are considerably larger than those of the D211 specimen. The teeth are also noteworthy for their exceptional wear, across both the anterior teeth and molars. The P_4s and left M_1 have been lost, presumably as a result of dental attrition. The differential wear seen between M_1 and M_3 displays one the greatest wear gradients of any fossil *Homo* individual. The corpus and rami of D2600 are extremely tall, although the great corpus height is not accompanied by an exceptional degree of corpus breadth. The *tuberculum marginale anterius* and *torus mandibularis* show similar expression as observed in the D211 mandible.

D2735, found in association with the D2700 complete cranium, is another sub-adult specimen. Although the left M_3 is congenitally absent and the right M_3 is not preserved, it appears they would have been in the process of alveolar eruption (the presence of erupting M^3s in the D2700 specimen confirm this). Excepting these teeth and

the central incisors, the dentition is well preserved and intermediate in size between that of D211 and D2600. The corpus does not show many of the surface features associated with a mature mandible, although a rounded *tuber symphyseos* similar to those observed in the other Dmanisi mandibles is present. The rami are low and broad and do not retain either condyle.

The D3900 is also found in association with a complete cranium (D3444). Unlike D2735, this individual is an older adult as determined by the presence of a completely edentulous mandible and maxilla. At or near the time of death, the only surviving tooth was likely the lower, right canine. Resorption in this specimen is extensive across the alveolar margin, particularly laterally, and the gonial region. The effects of this resorptive process are so extensive as to make homologous comparisons between this specimen and the remaining Dmanisi specimens difficult, if not impossible. With regards to overall size, this mandible appears to have much more similar in size to D211 and D2735 as opposed to the large D2600 specimen.

Chapter four will provide detailed comparisons both within the Dmanisi group and with other fossil hominid material.

CHAPTER 4

A comparative anatomical perspective on the Dmanisi mandibles

The following chapter will serve two purposes. The first goal is to synthesize the anatomical descriptions presented in the previous chapter, including relevant comparisons between the Dmanisi specimens and other hominid mandibles, in order to develop a more thorough understanding of the preserved anatomy. In the spirit of the Weidenreich quote presented at the beginning of this work, the comparisons with fossils from other localities are intended to clarify the anatomy of the Dmanisi specimens, place the variation within a broad comparative context, and point out potentially interesting points of similarity and difference with other hominid fossils. They are not intended as a formal statement of taxonomic affinity for the Dmanisi specimens.

The second goal of this chapter is to examine how the anatomy of the Dmanisi specimen serves to inform the development of an appropriate null hypothesis. Do particular details of the anatomy suggest important differences associated with either intraspecific or interspecific sources of variation? In particular, aspects of the age and sex classification of the Dmanisi specimens are considered in the context of fossil comparisons. These observations are summarized at the conclusion of the chapter. For clarity, these comparisons are organized as much as possible in the same manner as the preceding descriptions. Unless otherwise stated, the D3900 specimen is excluded from

these comparisons owing to the overwhelming level of resorption and its effect in obscuring or destroying homologous features.

Dentition:

The teeth of the Dmanisi specimens show a considerable amount of variation and serve as a convenient starting point for comparisons within the group. The following section will examine differences and similarities within the Dmanisi sample in occlusal morphology, tooth size, root structure, and dental wear. Comparisons will also be presented with other Plio-Pleistocene hominid mandibles.

D211 and D2735 both retain excellently preserved dentition with minimal to moderate wear. Unfortunately, the dentition of D2600, which would be of considerable comparative interest, is so extensively worn as to make detailed comparisons of the occlusal morphology impossible. Nevertheless, the most striking difference amongst the Dmanisi teeth is that observed between the M_3s of D2600, which are large and rectangular, and D211, which are small, rounded, and peg-like (see table 4.2 for a complete listing of Dmanisi dental measures). Even before the discovery of additional Dmanisi mandibles, the small M_3s of D211 (as well as the $M_1>M_2>M_3$ molar sequence) were highlighted by commentators as one of the most noteworthy features of the specimen (Dean and Delson, 1995; Gabunia and Vekua, 1995; Bräuer and Schultz, 1996; Rosas and Bermúdez de Castro, 1998). As Vekua and Gabunia (1995) point out, the reduction from M_1 to M_2, and even more between M_1 and M_3, are more similar to that generally observed in hominids much later in time, such as some representatives of the mid-Pleistocene Zhoukoudian sample (Weidenreich, 1936). This suggests that even

outside of the context of the much larger D2600 M_3s, the very small D211 M_3s are exceptional. Indeed, while still existing at the metrically large end of the scale, the D2600 M_3 crown area is more similar to the average value of the larger sample of Plio-Pleistocene hominids coming from East Africa, South Africa, and Southeast Asia (see tables 4.1 and 4.2).

Table 4.1 – M_3 crown area

Specimen	Crown Area (mm^2)	Specimen	Crown Area (mm^2)
Dmanisi 211	116.6	OH 13	177.4
Dmanisi 2600	193.0	Sangiran 4/5	200.2
ER 730	149.5	Sangiran 31	165.4
ER 806	178.9	Sangiran 34	157.0
ER 992	160.0	Ternifine 1	147.0
BK 67	149.5	Ternifine 2	165.4
BK 8518	170.8	Ternifine 3	126.5

Table 4.1 – M_3 crown area for selected Plio-Pleistocene early *Homo* mandibles (data taken from Wolpoff, personal communication).

An examination of the root structure of these teeth is revealing in this comparison. The M_3 root of the D211 is pyramidal in nature, appearing as a single, convergent peg. In contrast, that of D2600 shows two, divergent roots. To a lesser degree, this difference is present in the M_2 as well. Again, D211 has a convergent root structure in M_2 while that of D2600 has divergent root tips. D2735 can be added in the comparison of the M_2 however and, perhaps surprisingly, it is more similar to D2600 than D211 in size, shape, and root structure. This observation comes despite the recognition that the preserved right M_3 alveolus of D2735 appears far more similar in size and shape to that of D211 than D2600. Further complicating the evidence derived from the root morphology is the presence of double-rooted P_3s in both D2600 and D2735, to the exclusion of D211 (see figures 3.6 and 3.7).

Table 4.2 – Crown size, measured across the cervicoenamel junction (right side, unless otherwise indicated, * - left side)

	D2735	D2600	D211	WT 15K	ER 992	ER 3734	OH 7	Tern 3
I_1 breadth	-	7.1	6.2	6.8	6.9*	-	6.3	7.0
I_1 length	-	4.7	4.3	4.1	5.2*	-	6.3	4.1
I_2 breadth	7.3	9.0	7.2	8.1	-	-	7.4	8.2
I_2 length	5.1	5.5	4.6	5.2	-	-	7.4	4.9
C breadth	9.3	10.3	8.2	9.4	9.2	6.1*	10.2	10.5
C length	9.0	9.0	7.4	7.6	7.1	6.5*	9.0	6.6
P_3 breadth	10.3	7.4	9.0	10.2	10.6	7.7*	10.6	10.2
P_3 length	7.2	8.9	7.3	7.0	7.7	6.4*	8.8	7.8
P_4 breadth	9.4	-	8.7	10.9	10.8	7.8*	10.8	9.8
P_4 length	6.7	-	6.3	7.8	6.9	6.4*	10.1	7.2
M_1 breadth	11.0	11.4	10.3	11.2	10.3	9.4*	12.3	10.9
M_1 length	11.2	13.7	11.0	10.4	10.7	11.3*	14.1	11.7
M_2 breadth	10.4	12.3	10.3	11.7	11.7	11.4*	13.4	11.5
M_2 length	10.9	13.1	10.7	11.7	12.6	12.0*	15.6	11.7
M_3 breadth	-	13.2	9.5	10.6	11.7	-	-	10.5
M_3 length	-	16.7	9.7	11.8	12.0	-	-	11.7

Table 4.2 – Dimensions of tooth crown breadth and length for the Dmanisi mandibular sample and other terminal Pliocene and Pleistocene members of *Homo*.

Differences in root structure and root number occur within and between human populations (Tomes, 1923; Abbott, 1984; Scott and Turner, 1997; Shields, 2005), suggesting that the Dmanisi pattern, while perhaps unlikely and surprising given the diversity in a sample of just three specimens, is the possible outcome of a similar pattern of polymorphism (Wood *et al*., 1988). This interpretation is supported by the intermediate position of D2735 relative to D211 and D2600. Although absolutely small and preserving a reduced M_3 alveolus like D211, D2735 presents an M_2 much more similar in size, shape and root structure as that seen in D2600. Thus, no clear division can be made among the three specimens. Additionally, while the relative difference in the cervical size dimensions of the M_3 in D211 and D2600 is extremely large,

comparable differences exist in such fossil specimens as KNM-ER 403 and KNM-ER 1468, both assigned to *A. boisei* (Wood, 1991).

Comparisons of the molar occlusal morphology are difficult given the lack of any preserved morphology in D2600. The molars of D2735, while broadly similar to those of D211, are distinguished by having a slightly more developed protoconid and hypoconid, resulting in a more square occlusal profile. The molars of D211, in contrast, are more ovular and rounded. These individuals also show strong similarities with Lower Pleistocene specimens such as KNM-ER 992 and KNM-WT 15000 from the Turkana Basin. The increased mesial-distal elongation of the D2600 molars relative to D211 and D2735, in spite of the increased interproximal wear, is similar to the elongation of the molars in OH 7 relative to OH 13.

The premolars of D211 and D2735 are also quite similar, with small, square P_4s with a reduced talonid, and larger, triangular P_3s, with a reduced lingual cusp. Again, the surviving P_3s of D2600 are too worn to compare occlusal morphology, but appear to be absolutely larger, while retaining a similar, somewhat irregular, triangular shape. Also complicating the comparison between D2600 and the remaining specimens is the alveolar rotation of the right P_3 and the pronounced distal interproximal wear of the left P_3. The distal wear of the left P_3 cuts completely through the enamel and into the central tooth basin. This, coupled with the rotation of the tooth on the right side, make an exact assessment of the shape of the D2600 P_3s difficult. These features also make it difficult to estimate what space the P_4 would have occupied *in vivo* in D2600.

Comparisons with Plio-Pleistocene East African fossils are also informative. The Dmanisi specimens are clearly distinguished from any of the penecontemporaneous

hominids assigned to either *Australopithecus* (*Paranthropus*) *boisei* or *Australopithecus robustus* by the complete lack of any expansion or molarization of either premolar . In this regard, the Dmanisi specimens fit nicely within the early *Homo* specimens from Olduvai and the Turkana Basin such as OH-22, KNM-WT 15000, KNM-ER 992, and KNM-ER 3734, with the Dmanisi P_4 slightly more reduced than the Kenyan specimens (Leakey and Wood, 1973; Leakey *et al*., 1978; Tobias, 1991; Walker and Leakey, 1993) (see table 4.3).

Table 4.3 – P_4 crown area

Specimen	Crown area (mm^2)
D211	78.7
D2735	69.8
OH-22	82.3
KNM-WT 15000	88.2
KNM-ER 992	95.2
KNM-ER 3734	69.7
KNM-ER 729	201.5
KNM-ER 3229	164.9

Table 4.3 - P_4 crown area for Dmanisi hominids, early *Homo*, and several *A. boisei* specimens, ER 729 and ER 3229.

As mentioned earlier with regards to the molars, a difference in root structure is present between D2600 and the remaining two mandibles with preserved premolars. The P_3s of D2600 are double-rooted, those of D2735 have a Tomes root, and those of D211 are single-rooted. The distinction of D2600 in this character was part of the argument for the assignment of the D2600 mandible into the new species, *Homo georgicus* (Gabunia *et al*., 2002). Again, root structure differences in premolars occur within human populations, so, by itself this does not constitute grounds for a taxonomic separation. Even more relevant, however, is the relatively high frequency with which double-rooted premolars occur within other Plio-Pleistocene hominids, including representatives of both *Homo* and *Australopithecus* (Wood, 1991). The frequency of root structure anomalies,

including double-rooted premolars, may also be associated with normative size factors (Shields, 2005), and thus reflect the larger size of the D2600 specimen.

The size of the canine crowns as measured around the cervicoenamel junction suggests that the canines of D2735 and D2600 do not differ to the extent that might expected by cursory visual inspection of the size difference between the mandibles (see table 4.2). The difference in root length is substantial however, with the D2600 mandible showing massively developed canine roots. The D211 canines are the smallest and also have the least developed root structure. Relative to other mandibles with tall symphyses such as the *A. boisei* specimens, KNM-ER 3230 and KNM-ER 729, the roots of D2600 appear to occupy a greater portion of the symphysis height and area. This is true for tall mandibles within the genus *Homo* such as Ternifine 3 or later specimens like the Neanderthal specimens from Kebarra or Wadi Amud. Although the large canine roots of D2600 appear exceptional relative to comparable Plio-Pleistocene hominids, the differences amongst the preserved crowns are not extraordinary (see table 4.2). The occlusal morphology of the canines is nearly identical between D211 and D2735, the latter being distinguished principally by its larger size.

The Nariokotome specimen again serves as a good comparison for the Dmanisi individuals. The canines of KNM-WT 15000 are nearly identical to those of D211, distinguished mainly by the lack of the distal phalange, or 'thumb,' and associated labial surface groove described for the Dmanisi specimens in the previous chapter. D2735 is distinguished also by canines which project above the occlusal plane slightly more than those of KNM-WT 15000 (more similar to the condition seen in KNM-ER 3734).

The incisors of D2600 are too heavily worn to be of comparative value, while the preserved lateral incisors of D2735 and D211 are similar. All of the mandibles have shallowly rooted incisors, helping to create a consistent expression of the *incisura mandibulae* across the specimens. However, comparisons of the incisal wear pattern are of interest. The preserved wear pattern across the anterior dentition of D2600 show clear evidence of incisor wear inconsistent with standard, incisal biting. The heavy, although predominantly flat wear on the incisors of D211 relative to the molars raise the possibility of some consistency between the two specimens. Added to this is the obvious dental attrition observed in D3900. Were it found in isolation, the D3900 specimen might be considered extraordinary to the point of invoking a pathological component to its explanation. However, given its context and the presence of the exceptionally worn dentition of D2600, an emerging picture of consistently severe dental attrition seems plausible amongst the Dmanisi mandibular specimens. These extraordinary wear patterns may serve as an interesting are of future exploration regarding their relationship to the diet and general dental use of the Dmanisi hominids.

Comparisons of the posterior dental wear across the Dmanisi sample add to this picture. As discussed in Chapter three, the dental wear of D2600, and particularly the wear gradient seen between M_1 and M_3 is exceptional among Pliocene and Pleistocene hominids. Even such specimens such as MLD 18 and SK 12, or the erectine specimen BK 8518 from Baringo (see figures 4.1 and 4.2) that display large wear gradients do not equal the gradient seen in the large Dmanisi mandible. Furthermore, these specimens do not contain the specific pattern of wear across the posterior dentition. The D2600 specimen shows clear evidence of a downward directed wear force across the cheek teeth,

expressed most noticeably by the wear along the buccal root surface of the right M_1, absent in other specimens with such wear.

Figure 4.1 – D2600 dentition

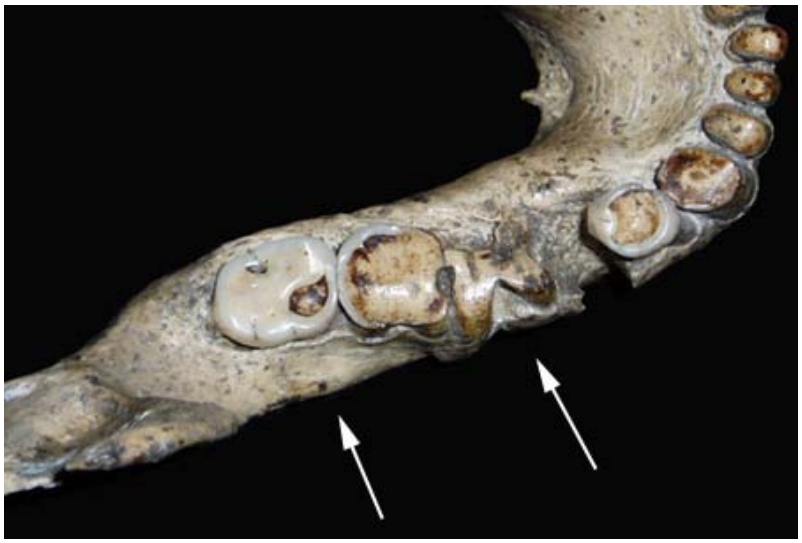


Figure 4.1 – D2600, highlighting the exceptional wear gradient between M_1 and M_3.

Figure 4.2 – BK 8518 dentition

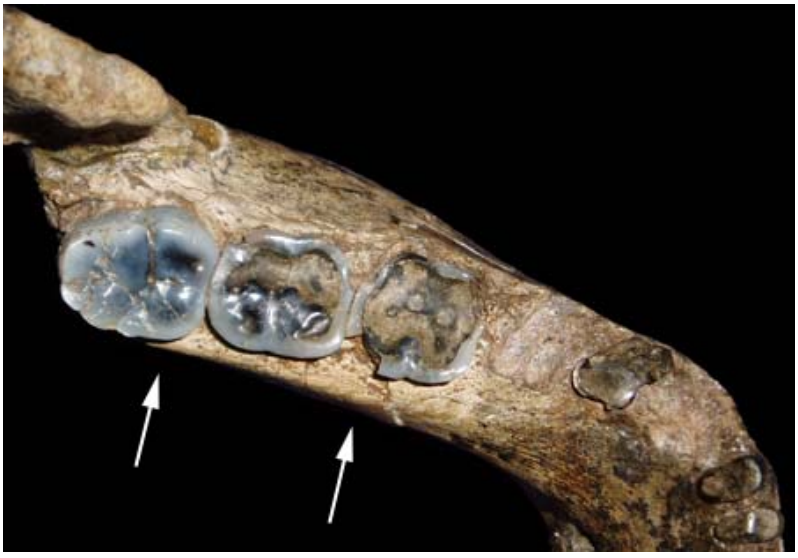


Figure 4.2 – BK 8518, and middle Pleistocene erectine specimen from the Lake Baringo region, Kenya.

These observations suggest that D2600 wore its teeth at an extreme rate compared with other hominids. The question then is whether evidence of such an extreme wear rate can be seen in the remaining Dmanisi specimens. The answer from D211, although not

completely clear given the wear on the incisors, would seem to be no. The M_3s of D211 are just coming into occlusion, with only slight wear on the left M_3 and only minor buccal polishing on the right M_3. At this point of dental eruption, the wear of the other molars is only moderate at most. Cusp patterning remains visible on both the M_1 and M_2, with little or no dentin exposure. It would take a highly non-linear acceleration of wear in the M_1 and to a lesser degree the M_2 in order to achieve the wear observed in D2600 by the time the D211 M_3s reached the stage observed in D2600. Comparisons with D2735 are more difficult given the lack of a preserved and erupted M_3. However, it can be observed that the wear of M_1 is stronger than that seen in D211, even though it is at an earlier stage in its eruption sequence.

The edentulous D3900 mandible is worthy of mention here, even if only in a speculative manner. Obviously, no teeth remain for comparison, but this absence of teeth may itself be of note. In humans prior to modern dental care, the most likely cause of extensive tooth loss along the molar row is extreme wear of the dentition and subsequent alveolar-gingival pathology. In this regard, the dental losses in D2600 are not inconsistent with a general pattern of tooth wear and loss. The dental loss and resorption seen in D3900, although extreme, is also consistent with this pattern, with greater alveolar loss along the lateral *corpora* and greater preservation anteriorly in the symphysis. Therefore, it is possible the edentulous nature of D3900 is the product of rapid dental attrition similar to that observed in D2600, progressing to an even further extent.

Regarding the second point, that of general wear patterns, more clear observations can be made. The observations outlined earlier during the description of D2600 of

possible 'wear complexes,' both in the anterior and posterior dentition, are relevant to this point. Here, the differences between D2600 and D211 appear not nearly as great. Unlike its posterior dentition, the incisors of D211 are relatively much more heavily worn, with a flat, slightly sinusoidal wear pattern extending from the right I_2, downward to the midpoint of the left central incisor, and up onto the left I_2. The absence of preserved central incisors on D2735 and D3900 prevent further comparisons within the group. The pattern of anterior wear in D211 and D2600 suggests the possibility of anterior tooth use for activities other than regular masticatory incising.

Ramus:

The largest and most striking difference in the two specimens with preserved rami (D2600 and D2735) is simply the size of the ramus structure. While the ramus of D2735 is low and relatively broad, that of D2600 is extremely tall (see tables 4.4 and 4.5). The available measurable components of the D2600 rami place them as one of the largest amongst Pleistocene hominids. The height of the D2600 coronoid process and condyle, relative to both the basal plane and occlusal plane, is slightly greater than that observed in Ternifine 3 (Arambourg, 1963), the largest available Middle Pleistocene hominid (see table 4.4). In order to find a larger hominid ramus, one must consider the robust australopithecines, such as SK 34, which exceeds D2600 in overall ramus size. D2735, in contrast, is far more comparable to the Nariokotome specimen, KNM-WT 15000, another sub-adult, Lower Pleistocene hominid.

Table 4.4 – Ramus size (right side, unless indicated*)

	D2735	D2600	WT 15K	ER 992	SK 34	Tern 3	ZKD G1	Mauer
Coronoid height above basal plane	59.3	94.1	64.1	78.2*	100.9	92.0	76.4	67.2
Coronoid height above occlusal plane	36.0	56.7	35.1	37.2*	61.1	50.0	-	32.1
Condylar height above basal plane	-	82.6	53.0	-	85.7*	80.2	73.0	65.3
Condylar height above occlusal plane	-	57.3	27.2	-	41.0*	41.4	-	34.7
Minimum ramus breadth	37.4*	-	41.1	-	54.0	47.1	40.7	51.2

Table 4.4 – Measures of ramus size for the available Dmanisi mandibles and several other Plio-Pleistocene hominids.

Lack of preservation limits the number of comparisons which can be made on the morphology of the medial ramus. The D2600 and D2735 mandibles show similar development of their observable medial rami structures, however, particularly the *crista endocoronoidea*. These features are more marked on D2600, but the difference between them appears to be one of degree and not nature. Richards *et al* (Richards *et al*., 2003) provide an excellent review of the complicated nature of human and great ape variation in this region. Their argument is specifically directed at the morphology of the *tuberculum pterygoideum* as it pertains to arguments surrounding modern human origins (Rak *et al*., 1994; Rak *et al*., 2002), but their discussion regarding the necessity of considering the interaction between the hard and soft tissues associated with the mandible throughout the course of ontogeny is applicable for any anatomical feature of the mandible and highlights the difficulty in establishing character states in complex morphological systems.

The shape and orientation of the *foramina mandibularis* are also similar (round, with a posterior-superior orientation), although D2735 differs in that the foramen is 'hooded' by a thin, overhanging section of bone which creates the impression of a posterior-facing slit-shaped opening. Interestingly, this configuration is a distinctive feature of later European hominids, such as the large Neandertal sample from the Krapina rock shelter in Croatia (Radovcic *et al*., 1988).

Considerable attention has been paid towards in recent years towards the potential utility of flexure of the posterior ramal margin for sexing of mandibles (Koski, 1996; Loth and Henneberg, 1996; Donnelly *et al*., 1998; Couqueugniot *et al*., 2000; Haun, 2000; Hill, 2000; Balci *et al*., 2005). Loth and Henneberg (1996) initially suggested that human, adult, male mandibles show a distinguishable flexure along the posterior margin of the ramus near the height of the occlusal plane. This observation has since been examined in larger populations of recent humans and fossil hominids with mixed results. Unfortunately, this area is poorly preserved in the Dmanisi specimens, offering little comparative value.

The lateral surface does not provide a great deal to compare, as what is present in D2735 is largely absent in D2600. However, both specimens exhibit fairly minimal signs of ectocondylar or ectocoronoidal development. Both rami feature thin margins of the ascending ramus that thicken only towards their superior ends. The superior portion of the ascending ramus differs in D2600 in that it forms an anteriorly projecting portion, creating an 's' profile viewed laterally, whereas 2735 continuously slopes superiorly and posteriorly. Such differences in ramus profile show high degrees of variation in modern and fossil samples, as outlined by Weidenreich regarding the Zhoukoudian fossils

(Weidenreich, 1936). Given the large size of the D2600 mandible, it is perhaps surprising that it does not show more prominent attachment features associated with any of the masticatory muscles.

Examining measures of the span of the rami (see table 4.5), the similarity in absolute size between D2600 and later middle Pleistocene specimens is apparent. D2600 is particularly similar to larger specimens such as those from Ternifine and the Mauer specimen. However, the superior features of D2600, the span between the coronoid processes and coronoid notch, are relatively more narrow than their Middle Pleistocene counterparts. This may in part be a reflection of the reconstruction of this region in the Dmanisi specimen. The D2735 specimen again shows a close metrical similarity with the Nariokotome specimen. Unfortunately, there is a dearth of adult early *Homo* specimens from Africa which preserve the rami bilaterally, making desired comparisons with D2600 impossible.

Table 4.5 – Biramus breadth

	D2735	D2600	D211	WT 15K	BK 67	Tern 3	Mauer
Biramus breadth at alveolar margin	81.8	94.1	80.0	82.1	83.5	92.9	95.7
Bicoronoid breadth	95.0	103.8	-	93.2	-	118.9	115.7
Binotch breadth	89.4	107.5	-	97.1	-	127.7	113.9
Maximum bicondylar breadth	-	133.3	-	116.7	118.0	155.9	131.1

Table 4.5 – Measures of biramus span for the Dmanisi mandibular sample and several other Pleistocene *Homo* specimens.

Corpus:

The intersection between the ramus and corpus in all of the Dmanisi specimens is only weakly developed, featuring at most a moderately developed *prominentia lateralis*, with D211 and D2735 displaying the larger variants. Also in D211 and D2735 this intersection takes place more mesially in the tooth row, near M_1-M_2 rather than M_2-M_3 as in D2600. Many of the features surrounding this junction, such as the position of the *prominentia lateralis*, are dependent to a large degree on the age of the specimen and subsequent bone resorption and deposition associated with the anterior margin of the ramus and the *prominentia lateralis* of the corpus (Atkinson and Woodhead, 1968; Atkinson and Woodhead, 1972; Andresen *et al*., 2000).

The most striking difference in the lateral *corpora* of these specimens, and in the overall morphology, is the large height difference between D2600 and the other two specimens (see table 4.6). The height of D211 is somewhat obscured because of fractures along the basal margin, but it is clearly significantly less than that observed in D2600. D2735 is even shorter, although shows clearer signs of future age-related growth as seen in the pronounced corpus height reduction extending posteriorly along the tooth row and the lack of any significant development of lateral surface features, such as the marginal and superior lateral tori.

The height of the D2600 corpus is comparable to that of the hyper-robust Sangiran 6 specimen, from Java (von Koenigswald, 1954; Jacob, 1973). However, unlike the Sangiran 6 specimen, which has an extremely robust, rounded corpus, that of D2600 is relatively much less robust and thinner (see table 4.7). The relative difference in corpus height between that of D2600 and D2735 remains exceptional compared to later

Pleistocene hominid samples, even such large and variable samples as those from Zhoukoudian, Atapuerca, and Klasies River Mouth (Weidenreich, 1936; Rosas, 1987; Rosas, 1995; Lam *et al*., 1996; Rosas *et al*., 2002). However, the relative difference in corpus height of large (KNM-ER 729, KNM-ER 1806, KNM-ER 3230) and small (KNM-ER 725, KNM-ER 3729, KNM-ER 3731) specimens assigned to *A. boisei* from East Africa are comparable (Wood, 1991). This latter observation will be discussed in more detail in chapter six.

Table 4.6 – Corpus Height

	D2735	D2600	D211	ER 992	WT 15K	Tern 3	ZKD H1	Mauer
Symphysis height	34.0	50.0	31.0	37.4	33.8	37.2	33.0	36.5
Corpus ht at P_3	26.7	44.0	26.5	33.8	29.1	35.1	30.7	32.5
Corpus ht at P_4	24.4	41.5	-	32.1	26.0	37.6	29.8	34.1
Corpus ht at M_1	22.4	41.0	-	33.0	25.0	35.8	26.7	34.9
Corpus ht at M_2	21.2	37.1	-	33.0	23.4	35.6	26.7	32.7
Corpus ht at *foramen mentale*	26.6	42.5	26.4	32.9	26.9	36.7	29.0	34.7

Table 4.6 – Measures of corpus height for the Dmanisi mandibular sample and several other Pleistocene *Homo* specimens.

The *foramina mentale* are in similar positions across all three specimens, located between P_3-P_4 and slightly inferior to mid-corpus height. Both D211 and D2600 have a second *foramen mentale* on the left side, slightly inferior and distal to the main foramen. D2600 is distinguished by much greater development of the basal margin in the form of an increased *torus marginale*. However, all three of the specimens, and in particular D211 and D2600 show well developed *tuberculum marginale anteriori*. This is a feature

common in specimens typically identified as later *Homo erectus* (Weidenreich, 1936; Aguirre *et al*., 1980), but is expressed in an exaggerated form within the Dmanisi group. Rosas (Rosas, 1995), based on the extensive remains from Sima de los Huesos, Atapuerca, suggests a possible size effect related to the expression of the *tuberculum marginale anteriori*, whereby larger specimens display this feature and smaller specimens do not. This is clearly not observed at Dmanisi, where both D2600 and D211 show well developed tubercles.

Table 4.7 – Corpus breadth (right side, unless indicated*)

	D2735	D2600	D211	WT 15K	ER 992	ER 1802	ER 1805	Tern 3
Symphysis breadth	16.1	22.7	17.2	15.9	-	23.7	23.5	19.4
Corpus breadth at P_3	18.5	22.1	18.0	18.3	21.3	20.9	22.9*	18.0
Corpus breadth at P_4	19.4	21.9	17.5	19.0	20.2	19.5	21.9*	18.3
Corpus breadth at M_1	21.0	21.3	17.8	20.3	19.5	23.3	21.6*	18.8
Corpus breadth at M_2	22.7	21.8	20.7	21.7	21.3	27.3	24.2*	20.5
Corpus breadth at *formane mentale*	19.7	21.8	17.9	18.4	20.5	20.0	24.0	18.0

Table 4.7 – Measures of corpus breadth for the Dmanisi mandibular sample and several other Plio-Pleistocene hominid specimens.

Medially, all three Dmanisi mandibles show some degree of a medial swelling at P_4 along the inferior portion of the *prominentia alveolaris*, marking the presence of a *torus mandibularis*. This feature was described by Weidenreich in regards to the Zhoukoudian mandibles (Weidenreich, 1936) but does not appear commonly in the collection of Plio-Pleistocene hominids from Africa. Amongst these specimens, only Sts 52 clearly shows a *torus mandibularis*, although more pronounced and slightly more

anteriorly positioned than that of D2735, the most strongly expressed torus amongst the Dmanisi specimens. D2600 differs along its medial corporal border in showing the least amount of distinction between the alveolar in subalveolar portions. Again, this seems to be the result of added growth in this specimen and an increase in the verticality of this specimen through increased height and breadth of the posterior corpus. A cross section of the mandible anywhere along the molar row would show D2735 to have a predominantly diagonal orientation, stretching superiorly from the medial extension of the posterior *prominentia alveolaris* inferiorly to the basal margin of the mandible. D211 would appear to be slightly less diagonal and more vertical, although along a similar axis, whereas D2600 would present the most vertical profile of the three mandibles.

Table 4.8 displays size differences in several dental arcade dimensions within the Dmanisi group. As in other areas, the D2600 specimen displays the largest dimensions across all observable measures, especially across the posterior dental arcade. While D2600 is large, its size is not as striking in these proportions as in those for corpus height. In terms of corpus height, D2600 is one of the largest known Pleistocene specimens placed in *Homo*. In terms of dental arcade dimensions, D2600 fits within the range of erectine specimens such as the Baringo specimen, BK 8518, and the large sample from Ternifine, including Ternifine 3. D2735 shows strong similarities once again with the Nariokotome juvenile specimen. The smallest of the Dmanisi specimens for dental arcade size, D211, is slightly larger than OH-13, the smallest of the well preserved habiline specimens from Olduvai Gorge.

Table 4.8 – Corpus external breadth

	D2735	D2600	D211	WT 15K	OH 13	ER 1805	Tern 3	BK 8518
External breadth at canine	34.0	36.8	30.6	35.6	29.5	-	37.8	34.4
External breadth at P_3	49.8	48.8	42.5	49.0	39.6	43.8	50.5	42.6
External breadth at P_4	53.5	-	48.7	54.3	46.2	52.1	55.8	49.7
External breadth at M_1	59.2	-	56.7	59.9	51.7	59.2	64.9	56.3
External breadth at M_2	61.3	69.0	60.9	64.9	55.8	65.8	72.4	62.2
External breadth at M_3	-	71.6	60.9	-	61.1	67.7	76.6	69.0
Bi-*foramen mentale* breadth	50.2	45.2	45.3	48.1	37.3	46.1	54.6	39.5

Table 4.8 – Measures of external corpus breadth for the Dmanisi mandibular sample and several other Plio-Pleistocene hominid specimens.

While there are large differences in absolute size, the shape of the dental arcade amongst the Dmanisi specimens is quite similar. Two indices of dental arcade shape are presented in table 4.9 below. The first of these, labeled here as an anterior dental arcade index (ADAI=[*infradentale* to P_4/external breadth at P_3] x 100), allows for comparisons across all three specimens. Ideally, this index would consider the external breadth at P_4, rather than P_3, but this measure is not available for the D2600 specimen. The three show very little difference with index values of 79, 81, and 79 across D211, D2600 and D2735, respectively. The latter index, called here total dental arcade index (TDAI=[*infradentale* to M_3/external breadth at M_3] x 100), only allows for comparisons between D211 and D2600, but produces identical index values of 109. These values are consistent with other Lower Pleistocene representatives of *Homo,* including the enigmatic and possible *Homo* specimen of KNM-ER 1805.

Table 4.9 – Indices of dental arcade shape

	ADAI		TDAI
D211	79	D211	109
D2600	81	D2600	109
D2735	79	D2735	-
WT 15K	81	WT 15K	-
OH 13	80	OH 13	114
ER 1805	80	ER 1805	107

Table 4.9 – Indices of dental arcade shape for the Dmanisi specimens. API is anterior dental arcade index, defined as [(*infradentale* to P_4/external breadth at P_3) x 100]. TPI is total dental arcade index, defined as [(*infradentale* to M_3/external breadth at M_3) x 100].

Symphysis:

The symphyses of D2600, D211, and D2735 show considerable variation. In regards to general shape, D2735 is a low, rounded, evenly sloping symphysis. D211, instead, is much flatter, with a more squared off or pentagonal shape to the anterior symphysis. D2600, different from both, is dominated by its marked height and the pronounced jugae associated with the long canine root complex. D2600 also appears to decrease in lateral-medial width from the alveolar to basal margins, the opposite pattern expressed in D211. The appearance of D2735 seems to be characteristic of a mandible which still has growth remaining. The *tuber symphyseos* is only slightly developed (although it is low and evenly rounded like D211), and only the slightest hints of *incisura mandibulae anterior*, as seen on the other two mandibles, are present. The pronounced *tuberculum marginale anterius* seen on D211 and D2600 are present, but much more weakly expressed than in either of the other two specimens. D2600 is the only specimen to show pronounced jugae associated with both the canines and P_3.

Posteriorly, the three specimens show marked differences, particularly D211. D2735 and D2600 have a slightly concave *planum alveolare* leading into a smooth,

rounded superior transverse torus that makes only a small distinction between the incisive plane and genioglossal region. D211 has a relatively longer and straighter *planum alveolare*, featuring a midline crest, leading to a weak, but less rounded superior transverse tori, which then cuts away into the genioglossal (see table 4.9).

Table 4.10 – Symphysis measures

	D2735	D2600	D211	WT 15K	ER 1482	Tern 3	ZKD H1	Mauer
Symphysis height	34.0	50.0	31.0	33.8	36.4	37.2	33.0	36.5
Mandibular orale to gnathion	33.1	46.1	33.9	33.8	37.2	37.4	32.7	33.0
Infradentale to *torus superioris transverse*	23.5	28.5	21.2	18.8	25.9	25.0	17.5	-
Infradentale to *torus inferioris transverse*	33.6	44.8	-	30.3	36.1	35.3	29.9	-
Planum alveolare length	17.3	24.6	17.3	16.9	21.3	18.9	12.3	18.1
Mandibular orale to *fossa genioglossi*	24.2	34.2	21.8	24.4	26.6	26.1	23.8	22.5

Table 4.10 – Measures of the symphysis in the Dmanisi sample and several other Plio-Pleistocene hominid specimens.

As demonstrated by Bräuer and Schultz (1996) in their initial analysis of the D211 mandible, the cross-sectional morphology of Pleistocene hominid symphyses is quite variable (see figure 4.3). In this regard, the variation within the Dmanisi sample does not show an exceptional pattern when compared with that observed elsewhere in the Pleistocene hominid record.

Figure 4.3 – Pleistocene symphyseal cross-sections

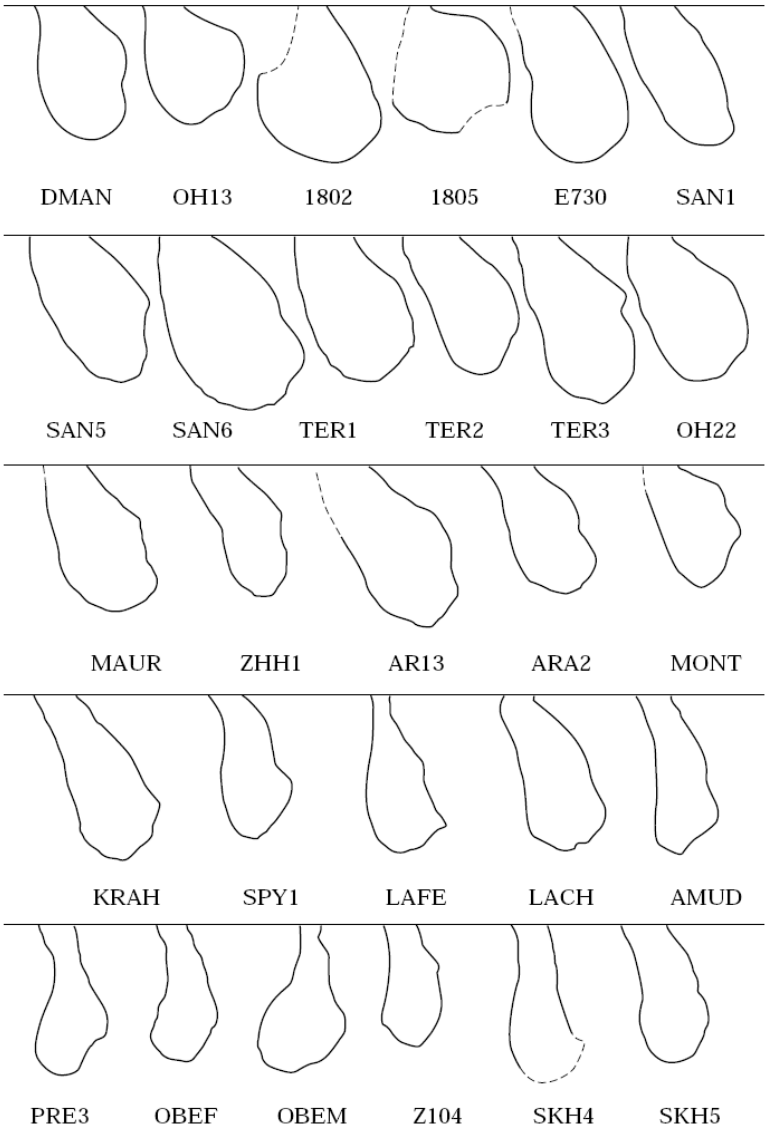


Figure 4.3 – Symphyseal cross sections, from Bräuer and Schultz (1996), of D211 (DMAN) and other Pleistocene hominid remains.

Relative Age of the Dmanisi Mandibles:

An important issue to consider based on the anatomy of the Dmanisi specimens is their relative age. As will be discussed in greater detail in chapter five, age is an important factor because the mandible undergoes significant anatomical changes throughout the life history of an individual, even extending late into life (Moss, 1960;

Israel, 1969; Moss and Salentij.L, 1970; Walker and Kowalski, 1972; Enlow, 1975; McNamara, 1975; Björk and Skieller, 1983; Kiliaridis, 1995; Enlow and Hans, 1996). Here, relative age on the basis of dental eruption and wear patterns is stressed instead of absolute age. Relative age is advantageous in that it only requires an assumption of general similarity of eruption patterns, rather than the rate with which they occur (Mann, 1975; Smith, 1986; Mann *et al*., 1987). Rates of dental wear are notoriously variable, but used within a limited context and conservatively, they can help distinguish the relative age of individual specimens.

Regarding the Dmanisi mandibles, the D2735 individual is clearly the youngest of the group. Not only is it the least developed on the basis of dental eruption, with the M^3s (of the accompanying D2700 cranium) just beginning alveolar eruption, but the corpus of the mandible supports this assertion. Unlike the other Dmanisi mandibles, D2735 has very little development of superficial structures on either the lateral *corpora* or the symphysis. In humans, these features develop during adolescence. Interestingly, this lack of corpus development is in contrast to that seen in D211, despite the observation that D211 is likely only a year or two more developed on the basis of dental eruption. While the M_3s of D2735 are just beginning the process of alveolar eruption, those of D211 are just completing this stage. D2735 has little in the way of superficial corporal development, but D211 has well developed features, including pronounced *tuberculum marginale anteriori*, and distinguishable *tori lateralis superior* and *tori marginale*. Part of this can be explained by the relatively older age of this specimen. However, the pronounced corporal differences also raise the possibility that D2735 was a slightly 'slow developer,' D211 was a 'fast developer,' or some combination of the two. Another

possibility is that these two individuals are on opposite sides of a period of accelerated developmental, or growth spurt. These hypotheses are difficult to distinguish or support on the basis of the mandibular anatomy alone and are not the focus of the work here. The primary point of interest is that both D211 and D2735 are sub-adult, likely middle to late adolescent in age on relative basis.

D2600 is assuredly an older, adult individual. Not only are all of the permanent teeth fully erupted, but all of the surviving teeth show extremely pronounced wear (with several teeth presumably lost owing to extreme dental attrition). What is not entirely clear is how old an adult D2600 is. The initial reaction of considering an old adult must be dealt with cautiously when the possibility of an extreme dental wear gradient is considered. Conservatively considering a typical rate of molar dental eruption, the rate at which the teeth of D2600 were worn down is exceptionally rapid. Given this, the mandible may not be the 'old adult' it appears to be. Again, however, the important point for consideration here is that it is clearly an adult, and quite a bit older (and more developed) than D2735 and D211.

The D3900 mandible is worth considering in this same framework, even though it is edentulous. Although this specimen will not appear in the quantitative analyses which follow (owing to the lack of existing homologous measures), its relative age is worth considering. If this specimen were found within a modern human osteological sample, it would appropriately be considered a very old adult as a result of the extreme dental loss and resorption. The understanding that it is a 1.77 million year old hominid gives pause to this assessment however, owing to notions of hominid behavior, development, and social care at this early age. Were it the only mandible present at Dmanisi, it might be

viewed as the product of some sort of dental pathology resulting in premature dental loss. Given that it is found in close association with the D2600 mandible, another specimen that shows extreme levels of dental wear, this assertion is not necessary. Indeed, if the same kind of rapid dental wear observed in D2600 is assumed for D3900, it too might appear 'older' than it actually is. These questions of the relative age are worthy of further pursuit as the entire sample of hominid material, including cranial remains, is considered in greater detail.

As with many other fossil comparisons, the KNM-WT 15000, Nariokotome specimen, serves as an excellent starting point. The D2735 and KNM-WT 15000 mandibles are strikingly similar in many of their corporal dimensions and corporal development (or lack thereof). Based on the dentition, KNM-WT 15000 is likely a year or two younger than the D2735 individual, as no strong evidence of the M_3 eruption process is yet visible. D2600 and D3900 appear to be the oldest known fossil hominid mandibles for the Plio-Pleistocene time period, although as mentioned above on the basis of dental wear gradients, their age estimation might be somewhat exaggerated. Nevertheless, a clear relative age gradient can be observed between D2735 (as the youngest), followed closely by D211, then the adult specimens of D2600 and D3900.

Sex Classification of the Mandibles:

The sex classification of the Dmanisi specimens is more difficult than that of age. Sex classification amongst hominids, particularly later hominids, is complicated by the assumed, and sometimes demonstrated (McHenry and Coffing, 2000), lack of dimorphism, and particularly the lack of a bimodal distribution of canine size (Wolpoff,

1976a; Wolpoff, 1978; Plavcan, 2001). Given the abundance of mandibular material in the fossil record and the potential significance of the effects of sexual dimorphism for shaping the variation of these specimens, numerous efforts have been made to examine mandibular dimorphism (Giles, 1964; van Wowern and Stoltze, 1978; Leutenegger and Shell, 1987; Wood *et al*., 1991; Kelley, 1995; Loth, 1996; Loth and Henneberg, 1996; Couqueugniot *et al*., 2000; Lockwood *et al*., 2000; Loth and Henneberg, 2000; Loth and Henneberg, 2001; Plavcan, 2002; Rosas *et al*., 2002; Taylor and Groves, 2003). Yet, despite the great effort put into it, no clear means of differentiating male and female mandibles on the basis of discrete anatomical characters has been presented.

Despite the difficulties of assigning sex to fossil mandibles, the issue is worth pursuing for the Dmanisi sample. The Dmanisi remains are advantageous in that all of the specimens presumably come from the same stratigraphic layer, with minimal dispersion across time and space. While it would be unsupportable conjecture at this point to suggest they represent a single population, they are more confined in these dimensions than are most comparable fossil samples. Dmanisi is also advantageous in that much of the material has other associated skeletal elements, adding to the evidence brought to bear on the question of sexual classification.

Focusing strictly on the mandibular material here, it is tempting to suggest the obvious divide between the large (D2600) and small (D211, D2735, and D3900) specimens represent male and female groupings, but, unlike the observation of the relative age differences, the assessment of sex is one of hypothetical conjecture rather than anatomical observation. The hypothesis of sexual dimorphism will be specifically tested in chapter five. For now, it is worth considering some points regarding the sexual

classification of these specimens. D2600 is absolutely much larger across nearly all measures than the remaining Dmanisi specimens. In the dentition, the difference is most notable in posterior dentition size and the development of the canine roots. In contrast, the D211 mandible preserves the smallest recorded values for these features, supporting the notion of a female classification. The identity of D2735 is more complicated, in part due to its status as the youngest, or least developed of the individuals. In general, like D211, this specimen is considerably smaller than D2600. However, for many of these features, especially aspects of the dentition, D2735 is intermediate between D211 and D2600. Also, the close similarity with KNM-ER 15000, a specimen identified as male by examination of a preserved innominate (Walker and Leakey, 1993), is noteworthy. Nevertheless, the absolute size differences within the Dmanisi sample support a grouping of D2735 with the other, smaller specimens of D211 and D3900. D3900, while preserving little specific anatomy, can be identified as similar in size to D211 and D2735 on the basis of the preserved basal margin, and therefore can possibly considered a female individual as well.

Hypothesis Formation:

As discussed in chapter two, a detailed consideration of the anatomy is critical to the development of an appropriate hypothesis testing structure. The primary question of this work is how can the variation within the Dmanisi mandibular sample best be explained and understood. The first step towards answering this question is considering what sources of variation are present. As outlined above, age differences within the Dmanisi sample are clearly present. This is a matter of pure observation rather than

hypothesis. However, for the question of interest, the important aspect of age-related variation is not that it is present, but what its likely effects on the variation are. Age related variation, and specifically the question of what are the expected effects of the observed age differences therefore form part of the null hypothesis for explaining the Dmanisi variation. This hypothesis will be considered in detail in Chapter five.

Differences in sex classification may also play a role in explaining the observed Dmanisi variation. Thus, an additional part of the null hypothesis for the Dmanisi variation is that sexual dimorphism have a role. The appropriateness of this as a null hypothesis can be questioned, however. Where one researcher might see the effects of sexual dimorphism, another might see the difference between one species and another (Zihlman, 1985). Here, both the site background and anatomy discussed in this and the previous chapter is important. The stratigraphic position of the material provides no independent cause for considering the Dmanisi hominid material as taxonomically different. It does not rule the possibility out, but nothing about it specifically supports the notion of any internal differences within the sample. The anatomy presents a combination of shared and unique features. Of particular interest however, despite the numerous and sometimes dramatic differences, is the presence of a shared and unique set of mandibular features within the Dmanisi group. These features include the presence of a pronounced *torus mandibularis*, exaggerated *tuberculum mandibulare anterius*, and horizontal *foramen mandibulare*. Other aspects of the anatomy could also be brought to support this argument, including the premolar anatomy, exceptional dental wear pattern, shape of the dental arcade, and *foramina mentale* pattern. Given both the anatomical and stratigraphic observations, the argument for beginning with a hypothesis of sexual

dimorphism is more than reasonable. Furthermore, as discussed in chapter two, beginning with hypotheses regarding intraspecific variation can allow for a systematic examination of these sources in addition to potential interspecific sources of variation, without making *post hoc* assumptions regarding either.

Therefore, quantitative assessment of the Dmanisi mandibular variation presented here begins with the null hypothesis that the variation observed within this group is the result of resampling individuals of different age and different sex within a single evolutionary group. This hypothesis will be tested in the following chapter.

H_0: the variation within the Dmanisi mandibular remains is the result of sampling individuals of different age and sex within a single evolutionary group.

Summary:

Paleoanthropology is inherently a discipline of comparative anatomy. The beginning of any process of questioning begins with an examination of the anatomy of those specimens involved and related and relevant material. Regarding the Dmanisi mandibular sample, this includes both comparisons within the Dmanisi group and with other Plio-Pleistocene hominid mandibles. The previous two chapters have presented both detailed descriptions of the anatomy of the Dmanisi specimens and systematic comparisons of the material.

Of the Dmanisi hominid material known at present, the mandibular sample is by far the most variable element of the sample, and raises important questions regarding the nature of the Dmanisi hominids. The mandibular sample shows a large degree of variation in overall size, dental size, as well as particular anatomical features associated

with the posterior symphysis and lateral *corpora*. The variation in some of these traits, although large, shows a mixture of relationships between the specimens. For example, while some aspects of the dentition, such as M_3 and premolar crown morphology would appear to group D211 and D2735 more closely, others, such as the size of the canine crown and M_2 appear to group D2735 and D2600 more closely. Additionally, several features, such as the expression of the *torus mandibularis* and *tuberculum marginale anteriori* show continuity across the mandibles. The dental wear displayed in sample provides more evidence, in addition to specific anatomical features, of a mixture of unique and shared traits. The dental wear story also suggests potential lines of questioning and continuity regarding the diet and behavior of the Dmanisi hominids demanding of further investigation.

In comparison with other Plio-Pleistocene hominids, the Dmanisi material clearly groups with other members of early *Homo* to the exclusion of the robust australopithecines on the basis of reduced premolars and development of the lateral *corpora*. Within the large sample of *Homo,* and even within the sub-grouping of material placed into early *Homo*, the relationships are less clear. In many regards, specimens such as D2600 and D3900 are exceptional in the Pleistocene *Homo* record. D2600 is matched in size only by a few later specimens from Ternifine and Sangiran, and nowhere with regards to the apparent rate of dental wear. No obvious comparable mandibles exist for D2600 within the Lower Pleistocene record of *Homo* from East Africa in terms of size. Likewise, D3900 shows a degree of dental attrition and alveolar resorption found only in the Neanderthal specimen from La Chapelle aux-Saints. D211 is also exceptional in early *Homo* for its tremendously reduced M_3. In other respects, however, D2735 and

D211 show strong similarities with early *Homo* specimens such as KNM-WT 15000 and OH 22.

Within the Dmanisi sample, features can be divided into ones which are shared and those which distinguish the specimens. The most significant difference within the group is the overall size of the D2600 specimen relative to the remainder of the sample. This difference in absolute size is most acutely expressed in aspects of corpus and ramal height. A large difference also exists in the size of the posterior dentition, with D2600 showing somewhat expanded posterior teeth and D211 showing greatly reduced posterior teeth. The root structure, both of the premolars and molars, differs within the sample as well. The exceptional long canine roots of D2600 also distinguish this specimen from the others in the sample.

Alongside these differences, however, are a number of similarities. Several unique features are shared within the Dmanisi, including a pronounced *torus mandibularis*, upwardly flaring *tuberculum marginale anterius*, and projecting *tuber symphyseos*. The mandibles also share a similar pattern of expression in both the *foramina mentale* and *foramina mandibulare*. Structures of the medial ramus and lateral corpus are also similarly expressed within the group. Despite the pronounced difference in the posterior teeth, the anterior teeth are quite similar in size and observable shape. Finally, the shape of the dental arcade is very similar within the group.

Given the context of the site and the combination of differences and shared, unique features, it is worthwhile to consider the possible effects of intraspecific factors on the Dmanisi variation. The details of the Dmanisi site and the anatomy of the mandibular sample support, as a starting point, the hypothesis that the Dmanisi variation is the result

of resampling individuals of different age and different sex. Specifically, the null hypothesis states that D2600 represents an adult male, D3900 an adult female, and D211 and D2735 sub-adult females. This hypothesis will be quantitatively examined in the next chapter.

CHAPTER 5

Dmanisi: Intraspecific Variation

The purpose of this chapter is to present a quantitative test of the null hypothesis put forth in Chapter four. This hypothesis states that a significant part of the variation within the Dmanisi mandibular remains is the result of resampling individuals of different age and sex within a single evolutionary group. For purposes of analysis, this hypothesis is further broken down into three components. These three components reflect the possible explanatory models for the observed Dmanisi variation and are reflected as follows:

1. The observed Dmanisi variation is explained by the resampling of male (D2600) and female (D211, D2735) individuals and the associated effects of sexual dimorphism.
2. The observed Dmanisi variation is explained by the resampling of adult (D2600) and late adolescent (D211, D2735) individuals and the associated effects of continued mandibular growth and development between these two age groups.
3. The observed Dmanisi variation is explained by the combined effects of resampling an adult, male individual (D2600) and late adolescent, female individuals (D211, D2735)

The prediction of these hypotheses is that the variation observed within the Dmanisi group can be drawn from a comparative sample for which age and sex are known within an expected range of frequency. In other words, the observed Dmanisi variation does not lie beyond the expected range of variation for a given comparative group. A failure to reject any one of these statements means the null hypothesis cannot be rejected. If however, all three of these statements are rejected, alternative hypotheses must be considered. Three comparative samples are employed in this analysis; *Homo sapiens, Pan troglodytes troglodytes*, and *Gorilla gorilla gorilla*. Each of these comparative groups provides a different model of expected intraspecific variation based on different morphology, size, and dimorphism patterns (see chapter two). How the Dmanisi variation fits within the comparative samples provides potentially significant information about both the morphological pattern of the Dmanisi hominids in particular, and early *Homo* in general, and also addresses the possible presence of multiple hominid taxa at the site. These issues will be explored in greater detail in the following chapters.

Intraspecific variation:

As outlined in chapter two, numerous sources of variation can be recognizably and systematically characterized within a species. In the case of primates, these include, but are not necessarily limited to, variation associated with age (i.e. growth and development), sexual dimorphism, geographic or population affinity, and temporal position (changes through evolutionary time). Intraspecific variation can also be associated with the presence of pathology, or atypical anatomy, although on a far less systematic basis. Owing to the stratigraphic position of the Dmanisi mandibular material,

variation associated with geographic or population affinity and temporal position will be excluded here. Possible effects of pathology on the Dmanisi variation have been discussed in chapters three and four and are not viewed as major explanations for the observed anatomical differences. This chapter will instead focus on variation associated with sexual dimorphism and age, and the possible combined effects of both of these processes.

Before quantitative analyses are undertaken, a brief review of specific issues relevant to these two categories of variation will be presented. Sexual dimorphism and growth are both widely discussed and researched topics for primates and are each associated with extensive bodies of literature. This review focuses on those specific aspects of this literature with particular relevance for understanding variation in the Dmanisi hominid sample. In the case of sexual dimorphism this includes literature associated with how sexual dimorphism is best quantified and analyzed as well as particular ideas regarding the degree and pattern of sexual dimorphism in members of early *Homo*. Regarding variation associated with age, the relevant literature includes a brief discussion of the basic processes of hominid mandibular growth and development, specifically from late adolescence into adulthood, as well as different ideas regarding the pattern of mandibular development in fossil hominids related to that of the living great apes and humans. Also discussed briefly is the differing patterns of development and sexual dimorphism within the *Homo*, *Pan*, and *Gorilla* groups used as comparative samples.

Sexual Dimorphism:

The most striking outlier in the Dmanisi sample is the D2600 mandible, with its sizable corpus and large canine roots relative to the remaining sample. Considering the anatomy and context of the site, the difference between this mandible and the remainder of the sample presents the possibility that this individual is a male and the remaining specimens are female. This hypothesis has been presented previously by at least one group of researchers and will be examined in greater detail below (Gabunia *et al*., 2002; Rightmire *et al*., 2005). The hypothesis of at least a portion of the variation being explained in terms of sexual dimorphism is also consistent with the larger effort within this work to systematically address the Dmanisi variation, beginning with sources of intraspecific variation.

Sexual dimorphism amongst hominids is a widely discussed topic within physical anthropology, touching on numerous significant issues (Plavcan, 2001). With regards to approaching the question of sexual dimorphism within the Dmanisi sample three issues are of importance. The first of these is how sexual dimorphism is quantified and especially how it is best assessed in small and fragmentary fossil samples (Richmond and Jungers, 1995). The second issue is what prevailing thoughts exist regarding sexual dimorphism during the course of hominid evolution and in particular during the Plio-Pleistocene emergence of early *Homo*. Finally is the potential significance of different levels of sexual dimorphism with regards to understanding the hominid remains from Dmanisi. These issues will be discussed briefly followed by an analysis of sexual dimorphism within the Dmanisi sample.

Quantifying sexual dimorphism:

Sexual dimorphism generally refers to quantifiable and systematic differences between the male and female of a species that are not attributed to primary sex characteristics. These differences can encompass aspects of behavior, morphology, or both (Wolpoff, 1976b; Wood *et al*., 1991; McHenry, 1994; Plavcan and van Schaik, 1997). In morphological studies, sexual dimorphism is most often discussed as it pertains to differences in body size (Clutton-Brock *et al*., 1977; Frayer and Wolpoff, 1985; Leigh, 1992; McHenry, 1992; Andersson, 1994). The focus on body size relates to the overall importance of body size as a general biological variable associated with a host of life history traits and energetic constraints. In primates and some other groups, differences in canine size represent a special case of dimorphism with particular significance for interpretations of mating strategies (Leigh, 1992; Plavcan and van Schaik, 1992; Plavcan and van Schaik, 1997; Leigh *et al*., 2003; Leigh *et al*., 2005). Both body size dimorphism and canine dimorphism can result in dimorphism of individual skeletal elements. This has important implication for fossil studies, where the preservation of complete specimens is extremely rare and body size is most often estimated on the basis of whatever elements are preserved. Therefore, estimates of dimorphism in fossil samples either refer to dimorphism of the specific element in question or an estimate of body size dimorphism based on a proposed relationship between a particular element and body size.

Mathematically, sexual dimorphism is a relationship between the male and female distributions of a given character. Generally, the important concepts to be considered in any index of dimorphism are the expected difference between an average male and average female and the degree of overlap between male and female distributions.

Numerous indices exist to quantify the level of dimorphism within a group for a given metrical character. Smith (1999) provides a comprehensive review of a number of these indices, including their relative mathematical utility. Smith covers a series of ratio values used to assess dimorphism, from simple male/female ratios (e.g. M_i/F_i) to more complicated ratio based indices (e.g. "Storer's index", $(M_i-F_i)/[(M_i+F_i)/2]$, Storer, 1966). Smith comes to the conclusion that in most situations, a simple male-female log ratio is as mathematically and functionally appealing an index as exists. It typically avoids problems of non-symmetry, non-linearity, and if used correctly, difficulties associated with the use of ratios in traditional parametric statistics. Smith also presents a critique of residual-based statistics to assess dimorphism.

The index used here will be both the natural logarithm ratio of male to female values and the ratio of male to female values. The former of these indices is advantageous in that it creates a symmetric distribution with respect to the neutral value of sexual dimorphism (male = female). One drawback of the unlogged ratio is that for cases where females are larger than males, the value of the index scales from one to zero. In contrast, when males are larger than females, the value scales instead from one to infinity. This can potentially be a problem depending on the specific nature of the data involved and the statistical analyses used. In the case of the analyses here, no meaningful difference existed between tests conducted using the unlogged index of sexual dimorphism and the natural log ratio index. This is likely owing to the relative uniformity in the propensity of larger male values relative to females and the simple nature of the statistical tests. The values of the unlogged tests will be presented here, owing to increased intuitive value of the numbers involved.

Estimating magnitudes of sexual dimorphism within fossil samples poses special difficulties (Richmond and Jungers, 1995; Lee, 2001). Fossil samples generally represent a small number of fragmentary individuals, consisting of several different skeletal elements. An additional problem posed by fossil samples is the potential for the inaccurate sexual identification of individual specimens. Even when the sex of individual specimen is known, the number of individual specimens required to provide an accurate estimate of the level of sexual dimorphism may be large, depending on the difference and overlap of male and female characters for that distribution. Examining linear craniometric traits in a sample of modern humans, Van Arsdale and Meyer found that as many as 12-15 pairs of known sex specimens are required to get an estimate within five percent of the observed, or "actual", level of dimorphism within that group (Van Arsdale and Meyer, 2004; Van Arsdale and Meyer, 2005). This has obvious implications for studies of fossil hominids where such large samples are almost never present, and will be discussed in greater detail below.

Numerous strategies have been presented to best deal with the statistical difficulties posed by such problems. These will be discussed in the context of the resampling strategy presented later in this chapter.

Sexual dimorphism in hominid evolution:

Numerous opinions exist as to the amount of dimorphism at various points in hominid evolution. It is generally thought that sexual dimorphism has decreased over the course of human evolution, from the time of the divergence with the last common ancestor of humans and chimpanzees some five to seven million years ago up until the

emergence of humans today (Wolpoff, 1975; Wolpoff, 1976b; Wolpoff, 1976a; Kay, 1982; Frayer and Wolpoff, 1985; Kimbel and White, 1988; McHenry, 1991; Leigh, 1995; McHenry and Coffing, 2000; Plavcan, 2001; Collard, 2003).

It is also generally believed that canine dimorphism is not a significant factor in hominid evolution. Reduction in canine size is often cited as one of the defining features of hominids (Simons and Pilbeam, 1965). This has come under increased scrutiny with recent fossil discoveries of possible hominids in the terminal Miocene from Chad, Ethiopia, and Kenya (White *et al*., 1994; White *et al*., 1996; Haile-Selassie, 2001; Senut *et al*., 2001; Brunet *et al*., 2002). Not enough material is known at the present to produce estimates of the level of dimorphism at the beginning of the hominid lineage, but reduction in canines relative to preceding Miocene ape fossils is apparent early in the hominid lineage.

A lively debate regarding the level of sexual dimorphism amongst the australopithecines has also occurred in recent literature (Lockwood, 1999; Reno *et al*, 2003; Plavcan *et al*., 2005; Reno *et al*., 2005). This debate highlights the difficulties of estimating levels of dimorphism in fossil samples and interpreting these results. Also, as it pertains to Dmanisi, this debate has implications for the ancestral condition in early *Homo*. Lockwood (1999) and Plavcan and van Schaik (Plavcan and van Schaik, 1997) argue that the australopithecines display a unique pattern of dimorphism, with high levels of body mass dimorphism and low levels of canine dimorphism. Among the conclusions drawn by the authors is that this unique pattern of dimorphism makes interpretations of australopithecine behavior difficulty. Reno *et al* (2003), using a novel method to "optimize" the australopithecine post-cranial data, suggest that when their technique is

applied to the known Hadar australopithecine sample and recent humans and great apes, the fossil specimens appear to most closely resemble humans in their levels of dimorphism. The authors thus conclude, contrary to Plavcan and van Schaik (1997), that the low levels of dimorphism suggest a pattern of reproductive monogamy among the australopithecines (Lovejoy, 1981).

The difference in understanding between the two groups of researchers stems from several important, but problematic areas. First, the issue of sample size and sample integrity in fossils is, and likely will always be, an ongoing problem. Some of the trepidations of Plavcan *et al* (2005) are reflections of concern over the data optimization strategy employed by Reno *et al* (2003) which allows well preserved fossil specimens, such as A.L. 288-1 ("Lucy"), to serve as templates upon which less well preserved elements can be reconstructed. This method increases the number of available comparisons and thus the precision of the estimate of dimorphism, but at the possible expense of its accuracy.

A second problem is the relationship between dimorphism in various skeletal elements and dimorphism in body mass. Most ecological discussions of dimorphism focus on body mass. Estimates of body mass dimorphism for fossil samples require a hypothesis of relationship between whatever skeletal element is used as the estimator of dimorphism and body mass. Sometimes this relationship is clear and is independently testable, but sometimes is left unaddressed or impossible to assess. Finally, these competing arguments also display the difficulties in predicting behavior on the basis of limited or imprecise estimates of dimorphism (Frayer and Wolpoff, 1985).

Regarding early *Homo*, views are also mixed. Some authors believe by the time the genus *Homo* emerges (but not during the preceding time period), a level of sexual dimorphism on a scale with modern humans is achieved (McHenry and Coffing, 2000). Others believe it possible that a greater level of dimorphism existed during this time period (Thackeray *et al*., 1997; Thackeray *et al*., 2000). Disagreement as to the levels of sexual dimorphism within *Homo*, particularly those fossils found in terminal Pliocene and Lower Pleistocene deposits is often intertwined with arguments of taxonomy. Uncertainties regarding the taxonomy of the various fossils assigned to early *Homo* and have been present since their initial discovery (Leakey *et al*., 1964; Montagu, 1965; Tobias, 1965; Tobias, 1966; Simons *et al*., 1969). Tobias initially viewed *Homo habilis* as a transitional species between *Australopithecus africanus* and *Homo erectus* (Tobias, 1965; Tobias, 1966). Furthermore, he felt the collection of fossils from Olduvai Gorge, although showing a large range of variation (including mandibles such as OH 7, OH 13, and OH 22), were contained within this taxon. Others argued either that the variation was too large within this group or that the transitional position, both temporally and anatomically, of the habiline material was ill-defined (Robinson, 1965). To a large degree, this argument continues today and continues to complicate discussions of sexual dimorphism and taxonomy as it pertains to early *Homo* (Chamberlain, 1987; Lieberman *et al*., 1988; Miller, 1991; Rightmire, 1993; Wood, 1993; Grine *et al*., 1996; Lieberman *et al*., 1996a; Albrecht and Miller, 1997; Miller *et al*., 1998; Wood and Collard, 1999b; McHenry and Coffing, 2000; Miller, 2000; Curnoe, 2001)

Behavioral implications:

Understanding the magnitude of sexual dimorphism within the Dmanisi sample is important not only for correctly interpreting the taxonomic status of the individual specimens, but also for inferring potential behavioral implications of differing levels of dimorphism. Sexual dimorphism in both body size and canine size has been shown to correlate with a variety of ecological variables and reproductive behavior (Kelley, 1989; McHenry, 1994; Plavcan and van Schaik, 1997). Particularly, models of sexual dimorphism based on sexual selection argue that increased mate competition produces greater levels of sexual dimorphism (Andersson, 1994; Mitani *et al*., 1996). Under this model, a reduction of sexual dimorphism in hominids towards the modern human range is thought to reflect a transition to a general strategy of reproductive monogamy.

Dimorphism in the Dmanisi sample:

Previous researchers have suggested the Dmanisi sample represents a hominid group with a high level of sexual dimorphism (Gabunia *et al*., 2002, Rightmire, 2005). This, too, is intertwined with discussions of the taxonomy of the Dmanisi specimens. Schwartz (2000) has suggested that to the contrary the large variation within the Dmanisi sample is caused by the presence of multiple hominid taxa. In Gabunia *et al* (2002), the Dmanisi variation is interpreted as representing a uniquely high degree of dimorphism within the genus *Homo*, and is a major observation used to justify the creation of a new taxon, *Homo georgicus*, for the sample. In a later paper by Rightmire (2005), this taxon is reduced to a sub-specific variant, *Homo erectus georgicus*, with little discussion of the estimated level of dimorphism. Nearly all of the dimorphism argument within the

Dmanisi sample rests on interpretations of the mandibular material, and the D2600 specimen in particular. Only D2600 stands out because of its seemingly huge proportions. Regardless of their taxonomic assignment, hypotheses of dimorphism within the Dmanisi sample are of considerable interest.

Age, Growth, and Development:

The mandible is an interesting skeletal element in that, unlike many other bones, it continues to undergo considerable morphological change throughout life. Therefore, even when comparing dentally adult specimens, continued growth of the mandible may play an important role in understanding the observed variation.

Part of the goal of this chapter is to examine to what extent the observed age differences within the Dmanisi group may account for the variation present within the group. Before this is done, a brief review of mandibular growth and studies of mandibular development, both in fossil hominids and living great apes and humans, is presented.

In this analysis age is treated as a relative, rather than an absolute, variable. In particular, age is classified on the basis of dental eruption and, to a lesser degree, dental wear. Age groups within the comparative samples are defined based on categories established within the Dmanisi sample. Amongst the Dmanisi specimens, both D211 and D2735 are in the process of M_3 eruption. In D2735, the M_3s are absent on both sides (molar agenesis on the left side), but a preserved alveolus on the right side and preserved maxillary M_3s suggest that in life, the right M_3 was likely just beginning to break the alveolar margin (see figure 5.1). D211, a slightly more developed individual, was just

reaching the point of full M_3 occlusion at its time of death (see figure 5.2). In contrast, D2600 and presumably D3900 are older adult individuals on the basis of the extreme dental wear and attrition observed (figure 5.3).

Given the observed differences in relative dental age within the Dmanisi specimens, the question of interest regarding the effects of age on the overall level of variability is how much growth can be expected between the age of the younger two specimens, and that of the older D2600 specimen (D3900 was excluded from these analyses as it cannot be compared with the other mandibles owing to the overwhelming effect of alveolar and corpus resorption on this specimen).

In order to answer this question, all of the comparative materials were classified into different relative age groups using the Dmanisi specimens to define group boundaries. Particular emphasis was placed on a "late adolescent" group and a "fully adult" group. The late adolescent group, meant to represent the developmental period encompassing the D211 and D2735 specimens, was composed of any individual in the process of M_3 eruption. The D2735 individual marked the lower boundary of this group, while the D211 individual marked the upper boundary. Any individual showing signs of the M_3 breaking the alveolar margin, but without yet attaining appreciable occlusal wear on the M_3, was placed into late adolescent group. In order to be included in this group all other permanent teeth had to be fully erupted.

Figure 5.1 – D211 molar sequence

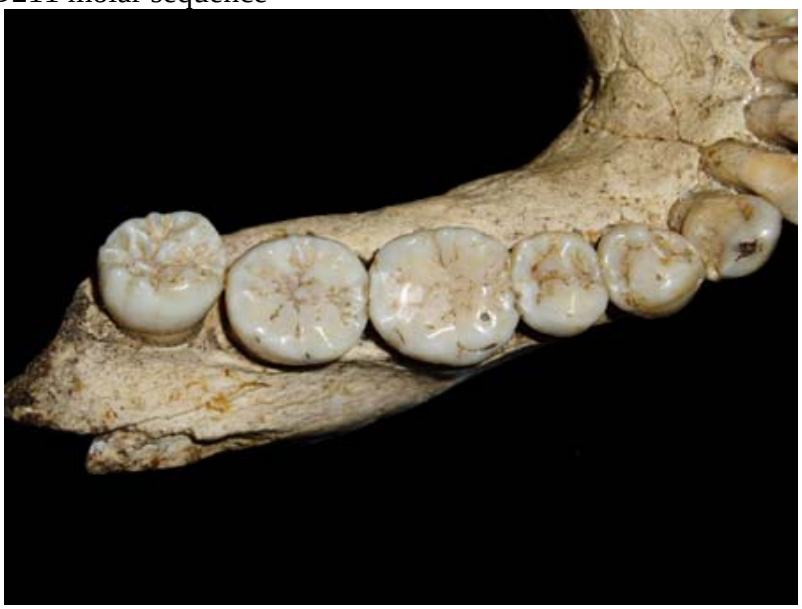


Figure 5.1 – D211, focusing on the dental eruption and wear of the molars. Note especially the near occlusal position of the third molar.

Figure 5.2 – D2735 Molar Sequence

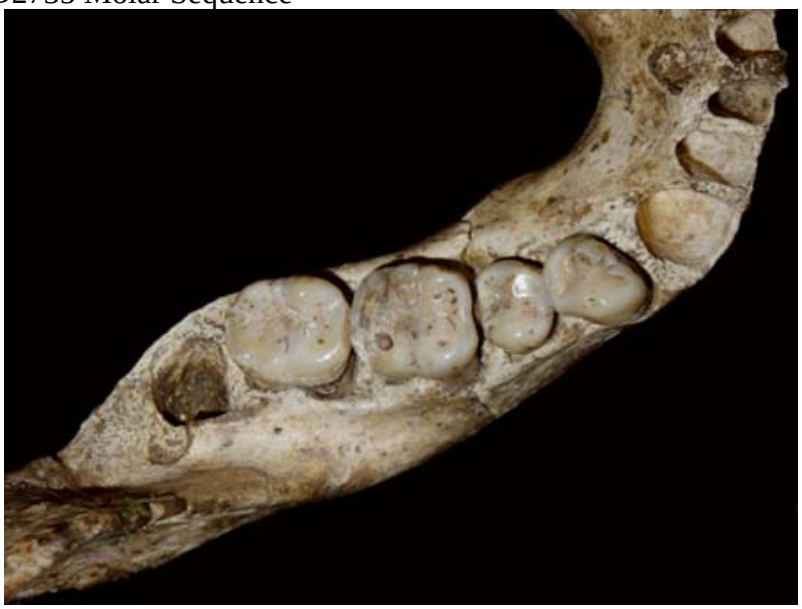


Figure 5.2 – D2735, focusing on the dental wear of the molars and status of the preserved right M_3 alveolus.

Figure 5.3 – D2600 Molar Sequence

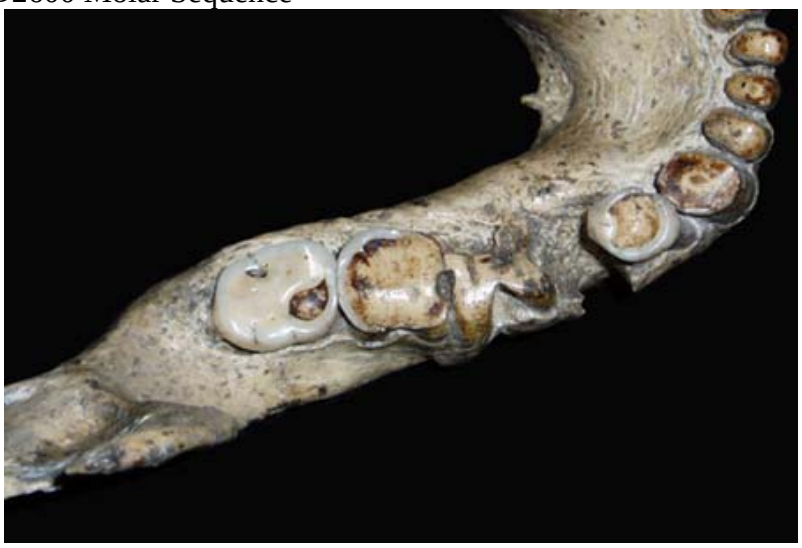


Figure 5.3 – D2600, focusing on the dental wear of the dentition, particularly the molars.

The fully adult group was meant to characterize the developmental/relative age status of the D2600 individual. Initially, an effort was made to classify members of the comparative samples into a category consisting only of older adults, based on the presence of pronounced dental wear. This attempt ran into difficulties and the older adult group was ultimately abandoned and broadened into a category consisting of all fully adult specimens. The problems in identifying older adult individuals were two-fold. First, the comparative samples of great apes examined preserved only a few specimens with dental wear comparable to D2600, creating a potential sample size problem. This problem was compounded in the human sample, not by the lack of individuals with pronounced dental wear, but by the poor dental preservation in these individuals. In the human comparative sample, while many specimens showed heavy to extreme dental wear, most of these individuals also showed moderate to extensive dental loss with associated alveolar resorption of the corpus.

In light of these difficulties, the adult category was expanded to include all individuals who displayed a fully erupted dentition and showed appreciable wear on the final erupting element. In the case of third molar agenesis, not uncommon in the human comparative sample, relative dental wear of the M_2 equivalent to that observed in the Dmanisi specimens was used as the criteria for classification. This broadening of the adult category had the advantage of both increasing the sample size of this group and making the analysis of age associated variation more conservative. Regarding the question of the expected change between the late adolescent and adult groups, D2600 sits near the extreme far edge of the adult group. It is thus likely the fully adult group is underestimating the expected change, making the identification of significant changes more difficult but the validity of such observations stronger. To the extent that these are anatomical and metric changes in adulthood, this makes the comparative sample conservative in that they do not demonstrate as much difference as they might.

Mandibular development:

From a developmental perspective, the mandible is interesting in that it is the product of the combined effect of different, integrated developmental systems (Cheverud, 1982; Maynard Smith *et al*., 1985; Alberch, 1990; Atchley, 1993; Ehrich *et al*., 2003; Cheverud *et al*., 2004). Embryologically, the mandible derives from the first pharyngeal arch. The cartilage of the first pharyngeal arch, known as Meckel's cartilage also plays a role, serving as a substrate upon which much of the corpus develops (Enlow and Hans, 1996). The maturation of the mandible requires the coming together of different, partially autonomous, skeletal growth centers in order to form a functioning unit. Growth

within the mandible is achieved through a complex interaction of the different skeletal regions of the mandible and the various skeletal, soft tissue and related connective tissues in head and neck (Moss, 1960; Moss, 1968; Moss and Rankow, 1968; Moss and Simon, 1968).

The mandible can be subdivided along several different anatomical lines. One division within the mandible is the distinction between the corpus and ramus (Enlow and Hans, 1996). This division reflects a fundamental functional divide between the ramus, which serves as the attachment point for most of the masticatory muscles and connects the mandible to the skull, and the corpus, which primarily serves as a housing and support structure for the dentition. Within the corpus a further division exists between the alveolar portion (that portion above the canal of the inferior alveolar nerve) and basal portion (below the inferior alveolar nerve) of the mandible (Enlow and Hans, 1996; Rosas and Bastir, 2004). This division is both functional and developmental in nature (Enlow and Hans, 1996; Rosas and Bastir, 2004). The bone above the inferior alveolar artery serves primarily as housing for the structures of the dentition. The bone below this divide acts as a support arch through which the forces of the primary muscles of mastication, the temporalis, masseter, and medial and lateral pterygoids, are transferred (Hylander, 1985; Daegling, 1988; Daegling, 1989a; Chen, 1995; Daegling and Hylander, 1998; Daegling and Hotzman, 2003).

As far as the Dmanisi mandibular sample is concerned, the primary point of interest is in how the mandible changes as it enters adulthood and what factors are responsible for these changes. This includes aspects of change both in the ramus/corpus division and the alveolar/basal division of the corpus. A quick glance at the anatomical

distinctions between D2735 and D2600 highlights the significance of these two areas. In contrast to D2600, the older specimen, in D2735 there is no development of any surface features along the corpus, no distinction between the alveolar and basal regions of the lateral *corpora*, and a broad and undeveloped area of connection between the ramus and corpus. All of these areas would have been subject to change as the specimen aged.

During growth the ramus acts as a critical link between the mandible and the changing aspects of the face, cranial base, and dentition. As such, the ramus and the structures associated with it undergo considerable change during the course of an individual's life. Generally, this process involves a series of growth rotations, resulting in posterior displacement, horizontal expansion, and vertical elongation of the ramus (Björk, 1963; Enlow and Harris, 1964; Björk, 1969; Enlow, 1975; Enlow, 1990; Björk, 1991; Enlow and Hans, 1996). These changes are accomplished by a continual process of differential growth, skeletal displacement, and bone remodeling designed to maintain a functional relationship between the mandible and the various aspects of the cranial base, maxillary dentition, cranial face, and soft anatomy of the palate and throat.

One of the primary growth processes in the mandible is the lengthening of the palate in order to maintain functional contact with the nasomaxillary structures and accommodate erupting posterior dentition. This is achieved by a gradual remodeling conversion of the anterior aspects of the ramus into the new posterior aspect of the mandibular arch and corpus (Enlow and Hans, 1996). Simultaneously, the posterior aspects of the ramus act as a site of bone deposition. Regarding the Dmanisi specimens, the last stage of this process is of interest in comparing the older and younger individuals. In D2735, especially, additional elongation of the mandibular arch and remodeling of the

anterior aspect of the ramus in order to accommodate proper dental occlusion can be expected. In addition, while the space for the third molar has already been established in D2735, additional changes along the posterior corpus can be expected in order to accommodate some degree of 'vertical drift' of the dentition. Enlow (Enlow and Hans, 1996) highlights the important distinction between the process of tooth eruption, in which the structures of the tooth develop and gradually drift towards the alveolar margin, and vertical drift, in which the entire structure of the functional tooth, including the associated periodontal ligament, drift vertically in order to maintain a balanced occlusal relationship between the dentition.

Changes in the ramus/corpus division also occur as a result of expansion in the middle cranial fossa and lengthening of the nasomaxillary region. This process occurs alongside that of dental maturation and the changes within the mandible occur almost simultaneously (Enlow, 1975; Enlow and Hans, 1996). Again, the ramus plays a critical role during this time period, as it undergoes both a horizontal and vertical expansion. These differences are visible between the older and younger Dmanisi specimens. The D2735 ramus is metrically shorter and narrower than that of D2600, while also positioned relative to the corpus at a more open angle. Another tendency for the ramus as it matures is the development of a resorptive field along the inferior margin of the anterior ramus and a depositional field along the superior margin of the anterior ramus. The difference in profile of the D2600 and D2735 anterior rami is likely reflective of this process.

Also occurring at this time and onto this changing anatomical landscape is the maturation of the masticatory apparatus. As the permanent dentition develops and erupts, the functional importance of the various masticatory muscle groups evolves in concert.

This has importance for the pattern of strain which occurs throughout the mandible during food manipulation and processing (Hylander and Crompton, 1980; Hylander, 1983; Hylander and Johnson, 1985; Dechow and Carlson, 1990; Daegling *et al*., 1992; Hylander *et al*., 1992; Daegling and Hylander, 1994; Kiliaridis, 1995; Herring *et al*., 2001). Analyses of strain profiles in mandibles during mastication suggest a high degree of local variability associated with aspects of cortical thickness and orientation (Daegling, 1989a; Daegling, 1989b; Chen, 1995; Daegling and Hylander, 1998; Breul *et al*., 1999; Daegling and Hotzman, 2002; Daegling and Hotzman, 2003). It is during this phase of masticatory maturation that many of the topographical surface features of the mandible (e.g. *tori superius lateralis, torus marginalis*) first develop. As the masticatory structures change through life through normal dental attrition or dental pathology, changes within these structures may also occur. The presence of a depositional field along the basal margin of the anterior corpus is also commonly associated with this stage of development.

Finally, changes in the condylar region throughout this time are also critical in the maintenance of the relationship of the temporo-mandibular joint. Given the lack of comparable condylar remains within the Dmanisi group, this region, although the subject of much critical research and anatomical significance (Angel, 1948; Lindblom, 1960; Moffett *et al*., 1964; Gingerich, 1971; Carlson *et al*., 1980; Mack, 1984; Nickel *et al*., 1988; Wall, 1999; Beek *et al*., 2001), will be discussed only briefly here. Historically, the condylar region was often viewed as the master control center for growth in the mandible (Todd, 1930; Enlow and Hans, 1996). Unlike much of the rest of the mandible, development of the condylar neck region involves an endochondral growth process

adapted for a compressive strain environment. Traditional views of mandibular growth as a process in which developing bone "pushes" existing bone anteriorly and inferiorly have relied on the unique structure of this region for support of such models. Another aspect of condylar development worth noting is the tremendous potential for directional and shape variability. Unlike a normal epiphyseal region, the condylar neck does not contain a series of stacked, linearly organized prechondral cells. Rather, these cells are more diffusely patterned and allow for multidirectional growth. As such, the condylar region of humans, and presumably that of fossil hominids, shows a tremendous amount of shape variability.

An important point to keep in mind for all aspects of mandibular growth, not just that of the condylar region, is the multi-dimensionality of mandibular development. Traditional views of mandibular growth often display it in a two-dimensional, linear fashion. This is almost uniformly inaccurate or misleading. Figure 5.4 shows the complexity of the generic pattern of growth in the human mandible.

If a normal pattern of mandibular development is assumed, many of the anatomical differences between D2600 and D2735 can be viewed as a product of this process. This is because, at least in terms of pattern, the differences between the two, as outlined above, reflect developmental changes known to occur in humans. Thus, the question of interest here is whether the degree of variation can be accommodated within this model or whether the magnitude of the differences within the Dmanisi is simply too great to support a null model of normal human development.

Figure 5.4 – Human mandibular growth

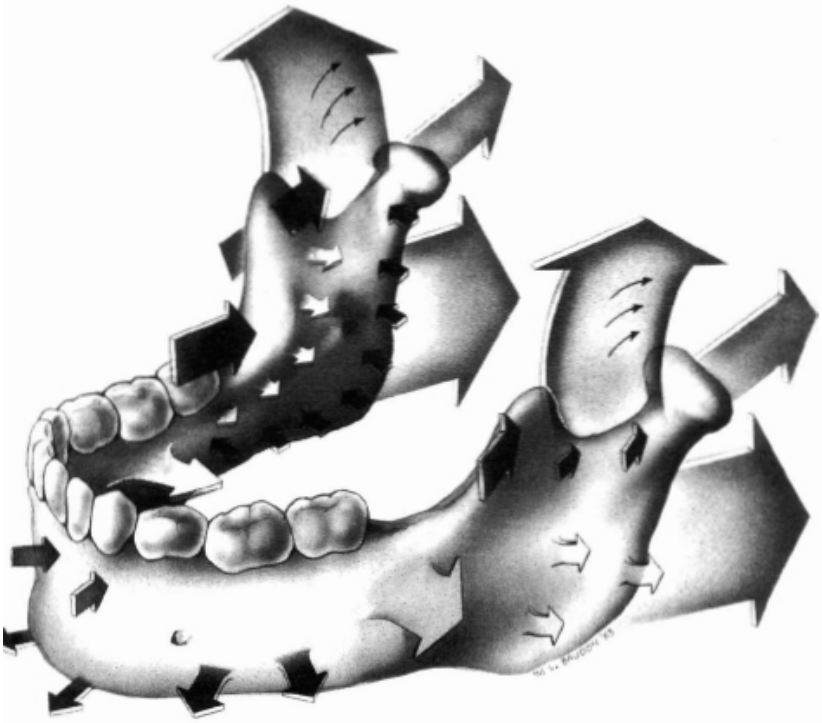


Figure 5.4 – Generic pattern of human mandibular growth pattern (from Enlow and Hans, 1996).

In contrast to a human developmental model, it is worthwhile to briefly consider those of chimpanzees and gorillas, the other comparative taxa used here. It has long been known that many aspects of craniodental form in *Pan* and *Gorilla* appear to reflect ontogenetic scaling of a similar, shared allometric pattern between the two (Giles, 1956; Shea, 1983a; Shea, 1985a). While much of the developmental pattern is conserved when comparing human and ape developmental model, the great apes go through an earlier and more rapid maturation process. This difference remains apparent, although is mitigated somewhat, when age is considered on a relative as opposed to absolute scale. The mandibles of great apes also support a larger masticatory apparatus and different characteristic masticatory behavior (Chivers and Wood, 1984; Ravosa, 2000; Daegling and Hotzman, 2003).

Controversy exists as to when in the course of human evolution the transition was made from a rapid, pongid developmental rate to a slower, more human-like rate (Mann, 1975; Smith, 1986; Smith, 1992; Bermúdez De Castro *et al*., 1999; Clegg and Aiello, 1999; Dean *et al*., 2001). Much of the research in this area that specifically pertains to early *Homo* has focused on the well preserved partial skeleton of the Nariokotome specimen, KNM-ER 15000. The Dmanisi material, with multiple individuals represented both craniodentally and post-cranially, potentially offers tremendous insight into this ongoing question.

Combined effects of sex and age:

The aim of these analyses is not only to test the extent to which sexual dimorphism (statement #1 derived from the null hypothesis) and age (statement #2) might explain the variation in the Dmanisi hominids, but also the combined effect of both age and sex (statement #3). Both factors are plausibly contributing significantly to the observed pattern of variation. Indeed, the presence of sexual dimorphism within humans (and other primates) is the result of the combined effects of the aging process on different sexual substrates (Shea, 1985b; Shea, 1986; Leigh, 2001; Leigh *et al*., 2005). In humans, sexual dimorphism is achieved through a slightly accelerated and slightly elongated (although initiating later) growth process in males (Leigh, 1992; Leigh, 2001; Leigh *et al*., 2005). Any complete rejection of the intraspecific null hypothesis must include not only individual rejections of both factors, but a rejection of the combined effect as well.

The results presented in this section will therefore be three-fold. In an attempt to provide an explanation for the observed Dmanisi variation, results will present whether or

not the observed variation meets the expectations of sexual dimorphism alone, age alone, and the combined effects of sexual dimorphism and age. The first set of results relate to the hypothesis that the Dmanisi variation is the product of resampling male (D2600) and female (D211, D2735) individuals. The second set of results addresses the hypothesis that the Dmanisi variation is the product of resampling old (D2600) and younger (D211, D2735) individuals. Finally, the third set of results addresses the hypothesis that the Dmanisi variation is the product of resampling an old, male individual (D2600), and two younger, female individuals (D211, D2735). D3900 is considered an old, female individual in this work, but is excluded in these analyses for the reasons outlined previously.

Measurements:

As described in chapter two, an extensive set of linear measurements were recorded for the comparative skeletal and fossil material examined (see Appendix B). From this complete set, a subset of measurements was chosen to use in the following analyses. This subset was chosen first because of their preservational status within the Dmanisi fossils and their potential for making comparisons between the Dmanisi specimens. However, the desire to provide as broad a coverage as possible of the mandibular morphology of these specimens, while including only a moderate level of morphological redundancy, was also an important factor in choosing the subset of data used in these analyses.

The final subset of measurements includes 31 different linear measures covering aspects of corpus height, breadth, tooth size, dental arcade size and shape, symphysis size

and shape, and ramus breadth. Unfortunately, the lack of comparable preserved ramal elements within the Dmanisi group limited the ability to in*corpora*te such measures in this analysis. The complete set of measures can be viewed in Figure 5.4-5.7.

Intraspecific Analyses:

The quantitative test of the sexual dimorphism hypothesis presented here is based on a random resampling strategy. One of the challenges in quantitatively assessing the variation within the Dmanisi sample is it is essentially limited to only three specimens given the lack of homology in the D3900 specimen. Furthermore, the anatomy of the specimens suggests (and the null hypothesis presented predicts) that the remaining three individuals fall into two distinct categories, an adult male (D2600) and two sub-adult females (D211 and D2735).

Figure 5.5 – Measurements, I

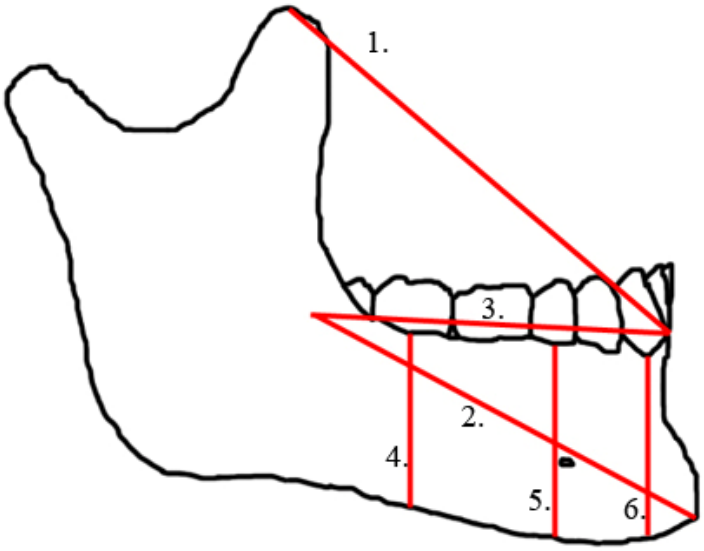


Figure 5.5 – Mandibular measurements: 1. Infradentale to coronoid tip, 2. Posterior M_3 to gnathion, 3. Posterior M_3 to infradentale, 4. Corpus height at M_2, 5. Corpus height at P_4, 6. Corpus height at canine.

Figure 5.6 – Measurements, II

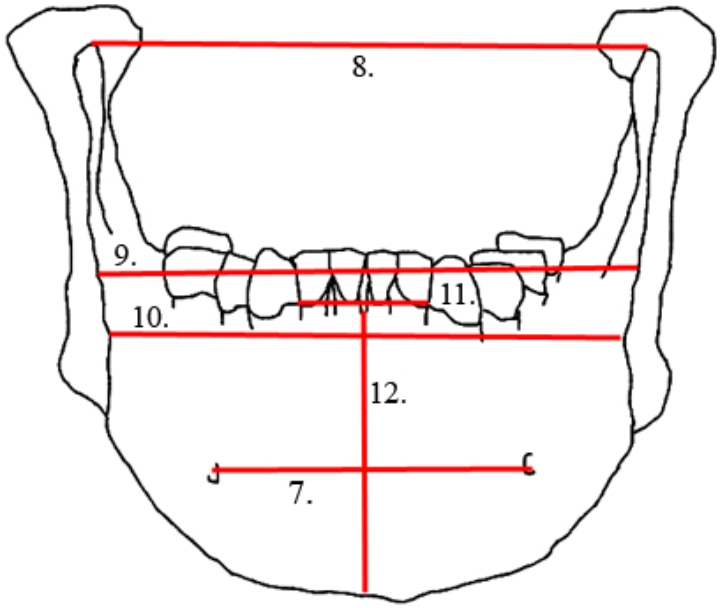


Figure 5.6 – Mandibular measurements: 7. Bimental breadth, 8. Bicoronoid breadth, 9. Biramus breadth at alveolar margin, 10. Biramus breadth at ramus root, 11. External breadth at I_2/canine, 12. Symphysis height.

Figure 5.7 – Measurements, III

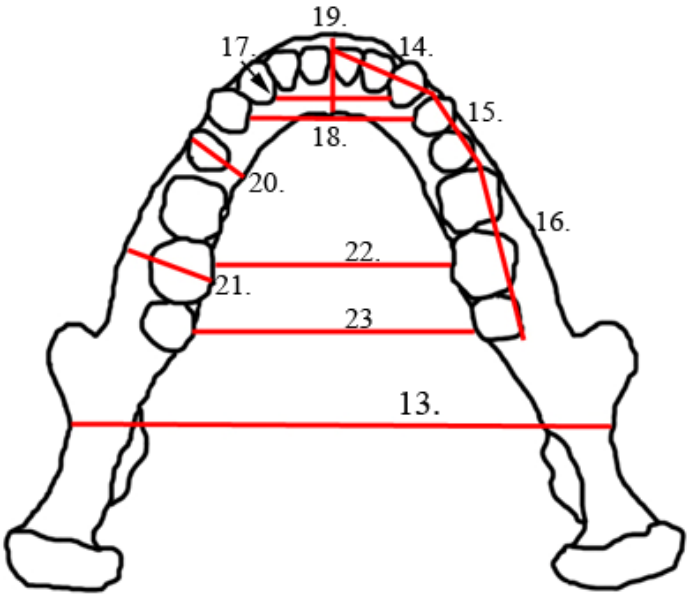


Figure 5.7 – Mandibular measurements: 13. Binotch breadth, 14. Mandibular length, I_1-canine, 15. Mandibular length, P_3-P_4, 16. Mandibular length, M_1-M_3, 17. Internal breadth at mid-canine, 18. Internal breadth at P_3, 19. Symphysis breadth, 20. Corpus breadth at P_4, 21. Corpus breadth at M_2, 22. Internal breadth at M_2, 23. Internal breadth at M_3.

Figure 5.8 – Measurements, IV

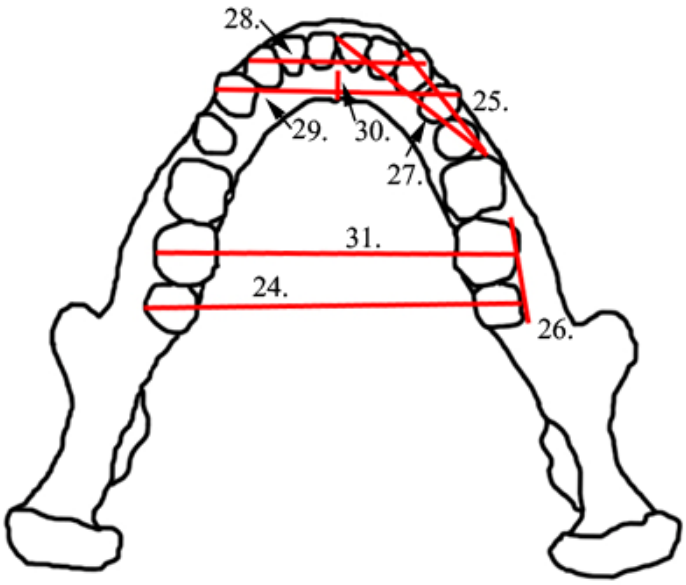


Figure 5.8 – Mandibular measurements: 24. External breadth at M3, 25. Mandibular length, canine-P_4, 26. Mandibular length, M_2-M_3, 27. Infradentale to P_4/M_1, 28. External breadth at mid-canine, 29. External breadth at P_3, 30. Alveolar plane length, 31. External breadth at M_2.

Given the small sample size and binary nature of the categorization, the random resampling strategy employed was pairwise in nature. For all of the predictions examined (age, sex, and sex+age) the test statistic employed is an index of relative variation. In the case of the sexual dimorphism test, this was the male to female ratio for each of the examined measures (M_i/F_j). Similar indices were calculated to examine the effects of age, from fully adult to late adolescent (FA_i/LA_j), and fully adult male to late adolescent female (MFA_i/FLA_j). Individual specimens for each of these categories were randomly drawn with replacement from the comparative sample 10,000 times in order to create a distribution of expected values for each of the indices. The observed values for the Dmanisi sample were then compared with this randomly generated distribution to calculate a functional p-value, with an alpha level of 0.05. These tests were treated as

one-tailed tests on the basis that only a result of significantly greater variation can be considered a rejection of the null hypothesis. Significantly less variable measures, while perhaps of interest, are not considered rejections of the null hypothesis. When all of the specimens preserved the necessary morphology, two ratios were calculated for the Dmanisi sample (D2600/D211 and D2600/D2735). In some cases, only one such comparison was possible. An individual measure was considered a significant difference if either of the observed values in the Dmanisi sample was significantly more variable than a given comparative sample. Therefore, while the individual Dmanisi pairings were tested separately, their results were considered jointly as they pertain to the sample as a whole. All analyses were conducted using code written for the Matlab software package (see Appendix C for specific program code).

This approach essentially asks the question; what is the likelihood of drawing a male-female (or adult-adolescent, etc.) pair with an index of sexual dimorphism equivalent to that observed in the Dmanisi sample from a sample of the respective comparative group? Recall that the prediction of the null hypothesis is that the observed Dmanisi index for sexual dimorphism (and age and age+sex) will lie within the expected range of variation for each of the comparative groups. Thus, this approach provides a direct assessment of these predictions. Also note that in this context, rather than assessing the variation, broadly defined, within the Dmanisi sample, the methodology aims to determine the association between the observed pairwise differences within the Dmanisi group with the variation observed within the comparative samples. The remainder of this chapter presents results from these analyses.

Results

The following section presents the results from the quantitative test of the null hypothesis first presented at the conclusion of chapter four.

> H_0: the variation within the Dmanisi mandibular remains is the result of sampling individuals of different age and sex within a single evolutionary group.

These results are subdivided into three sets in accord with the division of the null hypothesis into the three statements outlined at the beginning of this chapter.

1. The observed Dmanisi variation is explained by the resampling of male (D2600) and female (D211, D2735) individuals and the associated effects of sexual dimorphism.
2. The observed Dmanisi variation is explained by the resampling of adult (D2600) and late adolescent (D211, D2735) individuals and the associated effects of continued mandibular growth and development between these two age groups.
3. The observed Dmanisi variation is explained by the combined effects of resampling an adult, male individual (D2600) and late adolescent, female individuals (D211, D2735)

For continued clarity, the results are presented following the pattern of anatomical descriptions presented in chapters three and four. Following this initial presentation, the results will be collectively summarized and discussed in greater details.

Tooth size:

Measures of individual tooth size are not employed in the first analysis. This is in order to use a consistent set of measures between the analyses of age, sex, and age and sex. Given that it is unlikely one would expect an erupted tooth to change with age (excepting the obvious effect of interproximal dental wear, Wolpoff, 1971). Various measures of tooth row length were examined with the intent to encompass different aspects of the dentition. This includes examinations of the incisors, anterior dentition (incisors and canines), premolars, middle dentition (canines and premolars), molars, and posterior dentition (M_2 and M_3). In a complementary analysis, individual tooth measures are considered (see figures 5.9 and 5.10)

The difference in the posterior dentition within the Dmanisi group are particularly striking and have been noted as some of the most significant characters with regards to the identity of the Dmanisi remains (Gabunia and Vekua, 1995; Bräuer and Schultz, 1996; Rosas and Bermúdez de Castro, 1998; Gabunia *et al*., 2002). As such, an examination of the dentition provides a good starting point from which to test the hypotheses of age and sex. Tables 5.1-5.6 present the results for the analyses of these dental measures.

The format of these tables (and those that will follow in this chapter) is as follows. Each row in the table presents the results from one of the three divisions of the null hypothesis (sexual dimorphism, age, sexual dimorphism and age). Each of the three column headings presents the results based on each of the three comparative models examined, *Homo*, *Pan*, and *Gorilla*. These columns are then subdivided for each of the possible comparisons within the Dmanisi group, D2600/D211 and D2600/D2735. The

first subdivision represents the former of these comparisons, the second subdivision the latter. If a dash is present in the box, that measure was not available for that particular Dmanisi comparison. Otherwise, the information presented represents the degree of significance of the result in the form of a functional p-value or a non-significant result (ns). If any of the columns show significant results in all three assertions of the null hypothesis, they support a rejection of the null hypothesis.

Table 5.1: External breadth at I_2/C

Dimorphism model	Human		Chimpanzee		Gorilla	
Sex	ns	ns	ns	ns	ns	ns
Age	$p<0.05$	ns	$p<0.05$	ns	ns	ns
Sex+Age	ns	ns	ns	ns	ns	ns

Table 5.2: Mandibular length, I_1 to C

Dimorphism model	Human		Chimpanzee		Gorilla	
Sex	ns	ns	ns	ns	ns	ns
Age	$p<0.05$	ns	ns	ns	ns	ns
Sex+Age	ns	ns	ns	ns	ns	ns

Table 5.3: Mandibular length, C to P_4

Dimorphism model	Human		Chimpanzee		Gorilla	
Sex	ns	ns	ns	ns	ns	ns
Age	$p<0.05$	ns	ns	ns	ns	ns
Sex+Age	ns	ns	ns	ns	ns	ns

Table 5.4: Mandibular length, P_3 to P_4

Dimorphism model	Human		Chimpanzee		Gorilla	
Sex	ns	ns	ns	ns	ns	ns
Age	ns	ns	ns	ns	ns	ns
Sex+Age	ns	ns	ns	ns	ns	ns

Table 5.5: Mandibular length, M_1 to M_3

Dimorphism model	Human		Chimpanzee		Gorilla	
Sex	ns	-	$p<0.01$	-	ns	-
Age	$p<0.01$	-	$p<0.0001$	-	$p<0.05$	-
Sex+Age	$p<0.05$	-	$p<0.0001$	-	ns	-

Table 5.6: Mandibular length, M_2 to M_3

Dimorphism model	Human		Chimpanzee		Gorilla	
Sex	p<0.05	-	p<0.0001	-	p<0.05	-
Age	p<0.0001	-	p<0.0001	-	p<0.05	-
Sex+Age	p<0.0001	-	p<0.0001	-	p<0.05	-

Tables 5.1-5.6 – Tables 5.1-5.6 show the random resampling results for a hypothesis of intraspecific variation across various measures of dental size. The three columns show the results for each of the comparative models, subdivided into comparisons between D2600 and D211 (left) and D2600 and D2735 (right). The rows indicate the results for each of the three predictions subsumed within the overall hypothesis of intraspecific variation.

The observed size variation in the incisors (table 5.1), incisors and canines (table 5.2), canines and premolars (table 5.3), and premolars (table 5.4) fit within the expectations of all of the available intraspecific comparative models. In comparisons between D211 and D2600, several of these measures show significant levels of variation on the basis of age resampling. However, these significant results disappear when resampling related to sex is considered, either individually or in concert with age. This is also likely in part explained by the inconsistent relationship between tooth size and age as an explanatory factor, as discussed above.

In contrast to the anterior dentition, the posterior dentition show consistently high levels of variation, almost entirely outside the expected range of variation. As expected on the basis of the anatomy and previous analyses of the Dmanisi material, the variation in the posterior dentition is striking and, relative to the human and great ape comparative models, exceptional. This is true for most comparisons of the complete molar dentition (table 5.5) and all of the available comparisons when attention is focused solely on M_2 and M_3 (table 5.6). Across all of the predictions based on resampling of age, sex, and age+sex, the null hypothesis of intraspecific variation is rejected for all of the comparative models. The difference in length between the M_3s of D211 and D2600 is the

driving factor in this result. To put this into perspective, figures 5.9 and 5.10 show where the observed Dmanisi sexual dimorphism index for M_2 and M_3 length lies relative to an exact resampling distribution of this index in the human comparative sample.

Figure 5.9 – Exact resampling distribution of human M_2 length

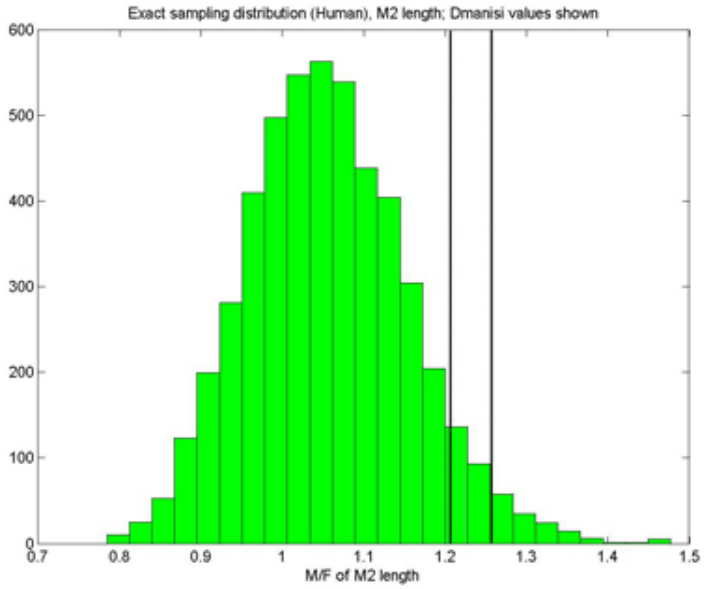


Figure 5.10 – Exact resampling distribution of human M_3 length

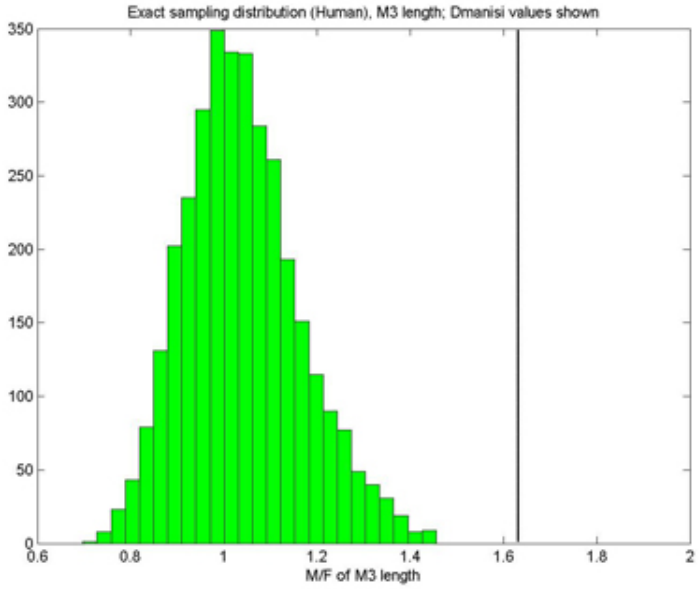


Figure 5.9-5.10 – Exact resampling distribution of M_i/F_i index of M_2 (5.9) and M_3 (5.10) length for human sample. The available observed Dmanisi indices are represented by the solid black line.

The distribution in figure 5.9 represents every possible M_i/F_i index for the human sample based on M_2 length. The two solid black lines show the values for the observable Dmanisi indices. While both values lie to the far right end of the distribution, they also both lie within the extreme range of the distribution. In contrast, the observed index value for M_3 length lies well outside the observed range for this value within the human sample (figure 5.10). These results quantitatively confirm the appearance of exceptional variation within the posterior dentition, particularly focused on the third molar.

Although the primary focus of these analyses is based on a random resampling method and the set of thirty-one measures listed above, measures of the dentition can be considered separately in order to examine each individual tooth. In a second analysis using the method presented above in the discussion of the posterior dentition, an exact resampling distribution of all possible male-female pairings for every buccal-lingual and mesial-distal tooth dimension was generated. These exact resampling distributions were based on an expanded data set, gathered from the same comparative collections and using the same measures, collected by M. Wolpoff. Theoretically, the exact resampling distribution and random resampling distributions should converge and give equivalent results. Again, the observed index for each measure within the Dmanisi sample was compared with the exact resampling distribution to calculate a p-value using a one-sided test of significance. The results are presented below in table 5.7.

An analysis of the individual dentition show the most striking variation lies in molars. In particular, the Dmanisi molars appear more disparate in their mesial-distal length measures than in the breadth of the teeth.

Table 5.7 – Individual dental breadth and length measures

	Human		Chimpanzee		Gorilla	
I_1 breadth	ns	-	ns	-	ns	-
I_1 length	ns	-	ns	-	ns	-
I_2 breadth	ns	ns	ns	ns	ns	ns
I_2 length	ns	ns	ns	ns	ns	ns
C breadth	ns	ns	ns	ns	ns	ns
C length	ns	ns	ns	ns	ns	ns
P_3 breadth	ns	ns	ns	ns	ns	ns
P_3 length	ns	ns	ns	ns	ns	ns
M_1 breadth	ns	ns	ns	ns	ns	ns
M_1 length	$p<0.01$	$p<0.05$	ns	ns	$p<0.05$	$p<0.05$
M_2 breadth	$p<0.05$	ns	ns	ns	ns	ns
M_2 length	$p<0.05$	ns	$p<0.01$	$p<0.05$	$p<0.05$	ns
M_3 breadth	$p<0.01$	-	$p<0.01$	-	ns	-
M_3 length	$p<0.01$	-	$p<0.01$	-	$p<0.01$	-

Table 5.7 – Results of exact resampling tests of the individual dental measures of breadth and length along the cervico-enamel junction. P_4 was excluded as it is not preserved in D2600.

The dramatic differences between the posterior molars of D2600 and D211 harkens back to the previously mentioned differences in root morphology. At M_2 (and at M_3 in D2600), both D2735 and D2600 display a typical, split and splayed root pattern. D211 is anomalous in both instances, in having a convergent root pattern at M_2 and a pyramidal, reduced root at M_3. It is also interesting to note that the canine dimensions, even given the exceptional difference in the size of the canine root, do not differ significantly more than the expected distribution of humans, chimpanzees, or gorillas. Indeed, when compared against either of the African apes, the indices of canine size place the Dmanisi values lie on the less variable side of the distribution.

Corpus height:

When examining the Dmanisi sample, one of the most striking differences is the difference in corpus height between D2600 and the remainder of the sample. This

contrast is present throughout the corpus, from midline through the posterior dentition. For this analysis, measures of corpus height were examined at symphysis, the midpoint of the canine, the midpoint of P_4, and the midpoint of M_2. These measurements are generally well preserved amongst the specimens (only corpus at height at M_2 D211 is absent, owing to the fractured basal margin) and provide a view of corpus height across the length of the mandible. Tables 5.8-5.11 present the resampling results for sex, age, and sex+age.

Table 5.8: Symphysis Height

Dimorphism model	Human		Chimpanzee		Gorilla	
Sex	p<0.0001	p<0.01	p<0.01	p<0.05	ns	ns
Age	p<0.01	p<0.05	p<0.0001	p<0.0001	p<0.05	ns
Sex+Age	p<0.0001	p<0.05	p<0.0001	p<0.0001	ns	ns

Table 5.9: Corpus height at Canine

Dimorphism model	Human		Chimpanzee		Gorilla	
Sex	p<0.01	p<0.001	p<0.01	p<0.01	p<0.05	p<0.05
Age	p<0.05	p<0.001	p<0.0001	p<0.0001	p<0.05	p<0.05
Sex+Age	p<0.05	p<0.01	p<0.0001	p<0.0001	ns	ns

Table 5.10: Corpus height at P_4

Dimorphism model	Human		Chimpanzee		Gorilla	
Sex	-	p<0.001	-	p<0.01	-	p<0.05
Age	-	p<0.01	-	p<0.0001	-	p<0.05
Sex+Age	-	p<0.0001	-	p<0.0001	-	ns

Table 5.11: Corpus height at M_2

Dimorphism model	Human		Chimpanzee		Gorilla	
Sex	-	p<0.01	-	p<0.0001	-	p<0.001
Age	-	p<0.01	-	p<0.0001	-	p<0.0001
Sex+Age	-	p<0.0001	-	p<0.0001	-	p<0.0001

Tables 5.8-5.11 – Random resampling results for indices of corpus height at symphysis (Table 5.8), mid-canine (Table 5.9), mid-P_4 (Table 5.10), and mid-M_2 (Table 5.11).

These results indicate that universally, the indices of variation for corpus height observed in the Dmanisi sample exceed what is expected in either a human or chimpanzee comparative model. The results for the gorilla model are less extraordinary, with only the index for corpus height at M_2 exceeding the expected range in all three of the possible tests.

In both the human and chimpanzee models, expectations of sexual dimorphism, continued growth with age, and the combined effects of age and sex all fail to explain the observed Dmanisi variation. For the human model, this result is particularly interesting in that the human sample shows measurable differences between both adults and late adolescents and males and females in all dimensions of corpus height (see figures 5.11-5.16).

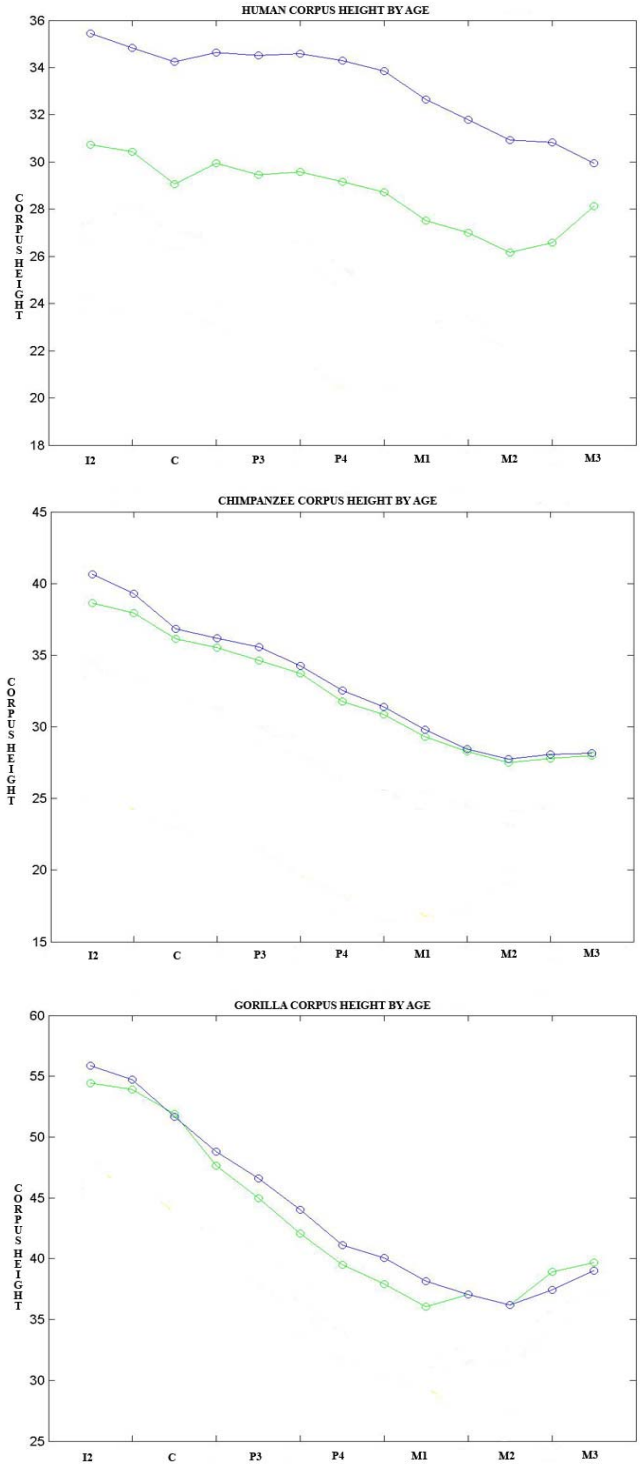
The chimpanzee and gorilla models also show an interesting pattern in that, based on the age categories defined for this analysis, very little continued growth past late adolescence occurs (see figures 5.11-5.16). This observation is reflected in the corpus height results, in which the observed Dmanisi variation is consistently less likely to be observed in a model based solely on differences associated with age than with either of the other two models. In contrast to the differences in age, the expression of dimorphism amongst these groups is fairly consistent throughout the corpus, with gorillas showing slightly expanded dimorphism in the symphysis, and humans showing an expansion in degree of dimorphism in the area of M_3. In humans, the level of dimorphism is relatively low, with an average difference between males and females of only about 2.5 mm, or 8% of average female corpus height. In chimpanzees this value is similarly low, with an average difference of only about 2 mm, or 6% of female corpus height. Gorillas show the

largest differences, with an average male-female difference of about 12 mm at canine, reducing to about 5 mm by M_3. Overall, this represents an average of about 10 mm difference, or just over 20% of female size.

In contrast to the human and chimpanzee models, the Dmanisi variation generally fits within the range expected on the basis of a gorilla model. Only at M_2 does the Dmanisi variation exceed the expectations of a gorilla model for sex and age (table 5.11). Of interest, however, is the observation that for several of the measures, the observed Dmanisi variation is greater than expected based on either age or sex alone, and can only be accommodated within the expected range when the two factors are sampled jointly. Given the large amount of sexual dimorphism in gorillas (for both body size and canine length), it is perhaps unexpected that the Dmanisi indices for these measures are significantly greater than observed in resampling male and females gorillas.

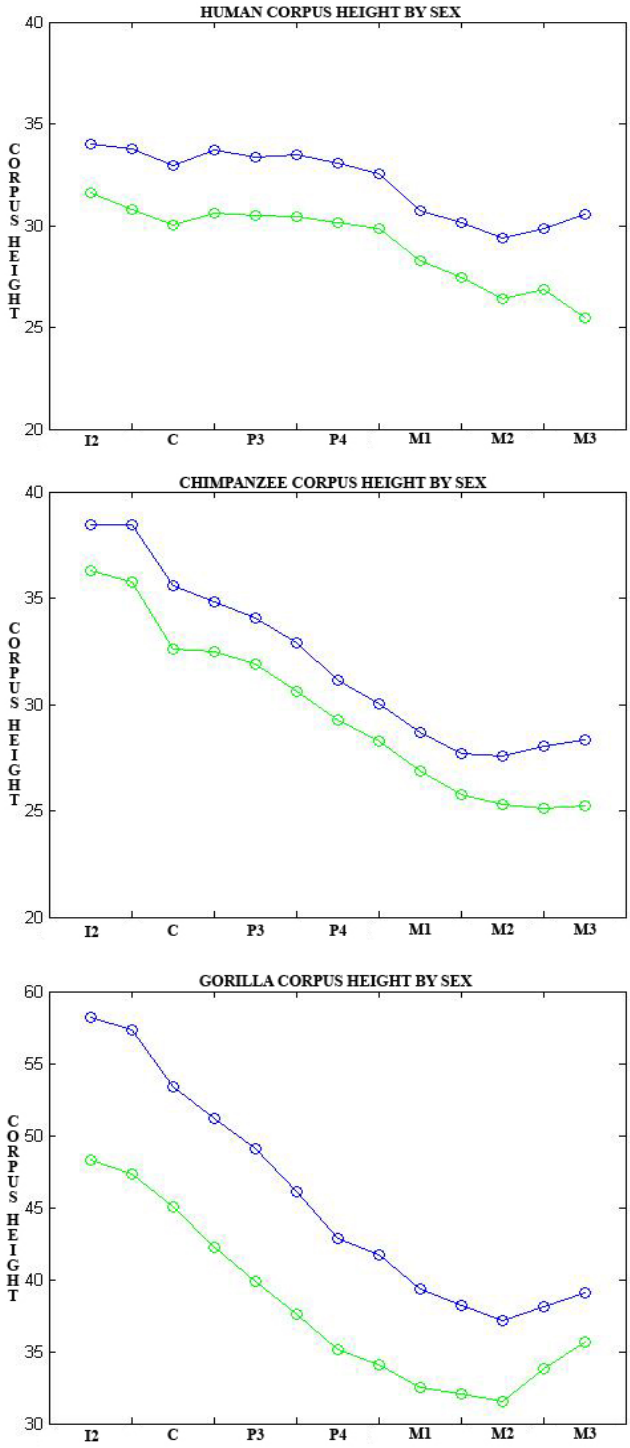
In sum, the apparent differences in corpus height are real and highly significant when compared to relatively low-dimorphism models as observed in humans and chimpanzees. Only when compared to gorillas, presumably a high-dimorphism model, can the variation seen in Dmanisi be largely accommodated by a model of intraspecific variation.

Figures 5.11-5.13



Figures 5.11-5.13: Average human, chimpanzee, and gorilla corpus height divided into adult and late adolescent samples. The Y-axis shows mean corpus height values for positions along the mandible, shown on the X-axis.

Figures 5.14-5.16



Figures 5.14-5.16: Average human, chimpanzee, and gorilla corpus height by sex. The Y-axis shows mean corpus height values for positions along the mandible, shown on the X-axis.

Corpus Breadth:

Despite the pronounced variability in corpus height and posterior dentition, the same differences do not carry through to many other aspects of the mandible. Included in this are measures of corpus breadth. The results for measures of corpus breadth are listed below in tables 5.12-5.14. Corpus breadth at canine is excluded owing to the difficulty of accurately gauging this measure in chimpanzee and gorilla mandibles.

Table 5.12: Corpus breadth at Symphysis

Dimorphism model	Human		Chimpanzee		Gorilla	
Sex	ns	$p<0.05$	ns	ns	ns	ns
Age	ns	$p<0.05$	ns	ns	ns	ns
Sex+Age	ns	ns	ns	ns	ns	ns

Table 5.13: Corpus breadth at P_4

Dimorphism model	Human		Chimpanzee		Gorilla	
Sex	ns	ns	ns	ns	ns	ns
Age	ns	ns	ns	ns	ns	ns
Sex+Age	ns	ns	ns	ns	ns	ns

Table 5.14: Corpus breadth at M_2

Dimorphism model	Human		Chimpanzee		Gorilla	
Sex	ns	ns	ns	ns	ns	ns
Age	ns	ns	ns	ns	ns	ns
Sex+Age	ns	ns	ns	ns	ns	ns

Table 5.12-5.14 – Random resampling results for indices of corpus breadth at symphysis (Table 5.12), mid-P_4 (Table 5.13), and mid-M_2 (Table 5.14).

The variability which characterizes the corpus height of the Dmanisi specimens is not expressed in measures of corpus breadth. Only in the symphysis and only for a human comparative model does the variability exceed some of the expectations (table 5.12). And even this result, the index of D2600/D2735 for both age and sex fails to achieve significance when both factors are considered together. In other words, the

difference in corpus breadth between these two specimens can be explained by the hypothesis that D2735 is both young and female. In none of the other measures or comparative models are any significant results observed.

These results can also be considered in light of the conclusions for dentition size and corpus height. The significant levels of variation in corpus height and length of the dentition, particularly characterized by excessive variation in the length of the posterior dentition, do not carry through into aspects of corpus breadth. Generally speaking, the neither the breadth of the dentition nor the breadth of the corpus display exceptional levels of variation. Most of this variation is the result of a vertically expanded corpus in D2600 and a combination of reduced posterior dentition in D211 and expanded posterior dentition in D2600. Interestingly, with regards to classical notions of 'robusticity' (the ratio of corpus height to corpus breadth), the D2600 mandible is in absolute terms the largest specimen, but also the most gracile. This relationship recalls the observation that the bone forming the well-developed basal margin of the D2600 specimen displays a somewhat different surface texture, possibly suggestive of substantial bone remodeling and deposition in this area.

Another relationship which is important in examining the corpus breadth results is the position and development of the *prominentia lateralis*. As stated in the discussion of general patterns of mandibular growth, the connection between the corpus and ramus is the point of considerable importance. Early in the development of the mandible this area is often quite robust, with a *prominentia lateralis* anterior positioned relative to the erupted dentition. As the dentition and corpus mature, this feature, at least among members of the genus *Homo*, generally reduces in prominence and shifts posteriorly

towards the area of M_2. Examining the Dmanisi corpus breadth dimensions it becomes apparent that the anteriorly positioned lateral prominence in D211 and D2735, particularly the latter of these, is a reflection of this process. Indeed, at M_1 and M_2 there is almost no difference in this measure amongst the specimens, with D2600 actually registering smaller measures at several point. This effect of age and growth contributes to the reduced levels of variation observed in the Dmanisi sample.

Dental Arcade Dimensions:

Numerous comparisons of the size of the dental arcade can be made within the Dmanisi group. These dimensions can be divided into several different regions. Tables 5.15-5.18 display the results for measures of external breadth across the dental arcade at the canine, P_3, M_2, and M_3.

Table 5.15: External breadth at mid-canine

Dimorphism model	Human		Chimpanzee		Gorilla	
Sex	ns	ns	ns	ns	ns	ns
Age	$p<0.05$	ns	ns	ns	ns	ns
Sex+Age	ns	ns	ns	ns	ns	ns

Table 5.16: External breadth at P_3

Dimorphism model	Human		Chimpanzee		Gorilla	
Sex	ns	ns	ns	ns	ns	ns
Age	$p<0.01$	ns	ns	ns	ns	ns
Sex+Age	$p<0.05$	ns	ns	ns	ns	ns

Table 5.17: External breadth at M_2

Dimorphism model	Human		Chimpanzee		Gorilla	
Sex	$p<0.05$	$p<0.05$	ns	ns	ns	ns
Age	$p<0.05$	$p<0.05$	ns	ns	ns	ns
Sex+Age	ns	ns	ns	ns	ns	ns

Table 5.18: External breadth at M_3

Dimorphism model	Human		Chimpanzee		Gorilla	
Sex	p<0.0001	-	p<0.05	-	ns	-
Age	p<0.0001	-	p<0.01	-	p<0.05	-
Sex+Age	p<0.0001	-	p<0.05	-	ns	-

Tables 5.15-5.18 – Random resampling results for indices of external dental arcade breadth at mid-canine (Table 5.15), P_3 (Table 5.16), M_2 (Table 5.17), and M_3 (Table 5.18).

A similar pattern is observed amongst these measures with an excess of variation in the Dmanisi sample associated particularly with aspects of the posterior corpus relative to expectations of either human or chimpanzee models. In comparisons with the human model, the available Dmanisi comparisons show some degree of significance throughout all of these measures, but only reject all three models in external corpus breadth measures at M_2 and M_3. Only the latter of these shows significance in the chimpanzee model and none of the measures show significance in comparisons with a gorilla model.

The excessive variation in these posterior measures appears to be a reflection of the absolute large size of the D2600 rather than marked differences in dental arcade shape. Indeed, an index of alveolar arcade shape shows D211 and D2600 as having nearly identical values (see table 5.19) in line with African specimens assigned to early *Homo*.

Table 5.19 – Index of alveolar arcade

	Index of alveolar arcade
D211	109.4
D2600	109.5
OH 13*	115.5
KNM-ER 1805*	108.5
KNM-ER 992*	109.4

Table 5.19 – Index of alveolar arcade, calculated as total alveolar arch length (*infradentale* to post-M_3) divided by external corpus breadth at M_3, multiplied by 100. Values for non-Dmanisi specimens (*) come from Rosas *et al* (1997).

Comparisons of the dental arcade dimensions can also be made along the interior surface of the corpus. These results are listed in tables 5.20-5.23.

Table 5.20: Internal breadth at canine

Dimorphism model	Human		Chimpanzee		Gorilla	
Sex	ns	ns	ns	ns	ns	ns
Age	ns	ns	ns	ns	ns	ns
Sex+Age	ns	ns	ns	ns	ns	ns

Table 5.21: Internal breadth at P_3

Dimorphism model	Human		Chimpanzee		Gorilla	
Sex	$p<0.05$	ns	ns	ns	ns	ns
Age	$p<0.0001$	ns	$p<0.01$	ns	ns	ns
Sex+Age	$p<0.0001$	ns	$p<0.05$	ns	ns	ns

Table 5.22: Internal breadth at M_2

Dimorphism model	Human		Chimpanzee		Gorilla	
Sex	ns	ns	ns	ns	ns	ns
Age	ns	ns	ns	ns	ns	ns
Sex+Age	ns	ns	ns	ns	ns	ns

Table 5.23: Internal breadth at M_3

Dimorphism model	Human		Chimpanzee		Gorilla	
Sex	ns	-	ns	-	ns	-
Age	ns	-	ns	-	ns	-
Sex+Age	ns	-	ns	-	ns	-

Tables 5.20-5.23 – Random resampling results for indices of internal dental arcade breadth at mid-canine (Table 5.20), P_3 (Table 5.21), M_2 (Table 5.22), and M_3 (Table 5.23).

The only measure in this set which shows any deviations from the expectations of intraspecific variation is in the internal breadth at P_3 between D2600 and D211. This difference is driven principally by the narrow dimensions of the D211 specimen. D2735 and D2600 have very similar values for this dimension.

Finally, two measures of dental arcade length are presented in tables 5.24-5.25. These include total alveolar arch length (*infradentale* to the distal-buccal corner of M_3) and anterior alveolar arch length (*infradentale* to the distal-buccal corner of P_4).

Table 5.24: Infradentale to P_4/M_1

Dimorphism model	Human		Chimpanzee		Gorilla	
Sex	p<0.05	ns	ns	ns	ns	ns
Age	p<0.01	ns	p<0.05	ns	ns	ns
Sex+Age	p<0.05	ns	ns	ns	ns	ns

Table 5.25: Alveolar arch length

Dimorphism model	Human		Chimpanzee		Gorilla	
Sex	p<0.05	-	p<0.05	-	p<0.05	-
Age	p<0.01	-	p<0.05	-	ns	-
Sex+Age	p<0.05	-	ns	-	ns	-

Table 5.24-5.25 – Random resampling results for indices of anterior alveolar arch length (Table 5.24) and total alveolar arch length (Table 5.25).

The combination of a wide anterior dental arcade and reduced posterior dentition in D211 and expanded dentition in D2600 yield significant levels of variation at both of these indices in comparison with a human model of variation. When compared with expectations from either a chimpanzee or gorilla model the combined effects of resampling age and sex accommodate the observed Dmanisi variation.

Ramus span measures:

The difference in corpus height might be expected to be accompanied by an equally large difference for a variety of dimensions associated with ramus height. Indeed, comparing D2600 with other well preserved hominid specimens, it is notable as having nearly the tallest ramus in the hominid record. Unfortunately, the lack of a preserved ramus for the D211 specimen and a dearth of comparable measures between the partially preserved rami for D2600 and D2735 minimizes the number of potential points of comparison.

What can be compared between D2600 and D2735 are several measures of the span between the rami, including; bi-ramus breadth at alveolar margin, bi-ramus breadth at ramus origin, bi-coronoid notch breadth, and bi-coronoid tip breadth. Again, we find that the variation observed within the Dmanisi sample fails to exceed the expected level of intraspecific variation for most of the comparative models. Tables 5.26-5.29 display the results for these measures.

Table 5.26: Bi-ramus breadth at origin

Dimorphism model	Human		Chimpanzee		Gorilla	
Sex	ns	ns	ns	ns	ns	ns
Age	ns	ns	ns	ns	ns	ns
Sex+Age	ns	ns	ns	ns	ns	ns

Table 5.27: Bi-ramus breadth at alveolar margin

Dimorphism model	Human		Chimpanzee		Gorilla	
Sex	ns	ns	ns	ns	ns	ns
Age	ns	ns	$p<0.05$	ns	ns	ns
Sex+Age	ns	ns	ns	ns	ns	ns

Table 5.28: Bi-notch breadth

Dimorphism model	Human		Chimpanzee		Gorilla	
Sex	-	ns	-	$p<0.05$	-	ns
Age	-	$p<0.05$	-	$p<0.05$	-	ns
Sex+Age	-	ns	-	$p<0.05$	-	ns

Table 5.29: Bi-coronoid breadth

Dimorphism model	Human		Chimpanzee		Gorilla	
Sex	-	ns	-	ns	-	ns
Age	-	ns	-	ns	-	ns
Sex+Age	-	ns	-	ns	-	ns

Tables 5.26-5.29 – Random resampling results for indices of ramal span at the ramus origin (Table 5.26), alveolar margin (Table 5.27), coronoid notch (Table 5.28), and coronoid process (Table 5.29).

Bi-ramus measures at the ramus origin (table 5.26) and where the ramus crosses the alveolar margin (table 5.27) reflect aspects of posterior corpus shape, the *prominentia lateralis*, and to a certain degree the development of the entire ramus-corpus junction. In neither of these measures are the Dmanisi excessively variable. Only the latter of these measures, and only based on a chimpanzee model of development, shows any degree of significance.

Measures of bi-notch breadth (table 5.28) and bi-coronoid process breadth (table 5.29) reflect size and developmental differences associated with the relationship between the mandible and development of the middle cranial fossa and associated soft tissue structures. The latter of these shows no significant deviations from the expected intraspecific models. The bi-notch breadth shows significant deviations from the chimpanzee model but is well explained by aspects of the other two models.

Other measures:

Finally, several other measures of interest can be compared within the Dmanisi sample. The results for these indices are given below in tables 5.30-5.33 and reflect bi-*foramen mentale* breadth (table 5.30), length of the *planum alveolare* (table 5.31), oblique corpus length (table 5.32) and *infradentale* to the tip of the coronoid process.

Table 5.30: Bi-mental breadth

Dimorphism model	Human		Chimpanzee		Gorilla	
Sex	ns	ns	ns	ns	ns	ns
Age	ns	ns	ns	ns	ns	ns
Sex+Age	ns	ns	ns	ns	ns	ns

Table 5.31: Alveolar plane length

Dimorphism model	Human		Chimpanzee		Gorilla	
Sex	ns	ns	ns	ns	ns	ns
Age	ns	ns	ns	ns	ns	ns
Sex+Age	ns	ns	ns	ns	ns	ns

Table 5.32: Post M_3 to gnathion

Dimorphism model	Human		Chimpanzee		Gorilla	
Sex	$p<0.01$	-	$p<0.01$	-	$p<0.0001$	-
Age	$p<0.0001$	-	$p<0.0001$	-	$p<0.0001$	-
Sex+Age	$p<0.0001$	-	$p<0.0001$	-	$p<0.0001$	-

Table 5.33: Infradentale to coronoid tip

Dimorphism model	Human		Chimpanzee		Gorilla	
Sex	-	$p<0.05$	-	ns	-	ns
Age	-	$p<0.05$	-	$p<0.0001$	-	ns
Sex+Age	-	ns	-	$p<0.0001$	-	ns

Tables 5.30-5.33 – Random resampling results for indices of bi-mental breadth (Table 5.30), alveolar plane length (Table 5.31), post-M_3 to gnathion (Table 5.32), and infradentale to coronoid process tip (Table 5.33).

Two of these indices, the width across the anterior corpus measured at the *foramen mentale* and the length of the *planum alveolare* of the symphysis, show no significant deviations from the expectations of any of the intraspecific models. The latter

of these, the length of the *planum alveolare*, is perhaps noteworthy given the large differences in the anatomy of the symphyses amongst the Dmanisi specimens (see table 4.9).

The other two indices, the length from the distal-buccal corner of M_3 to *gnathion* and the length from *infradentale* to the superior point of the coronoid process, both show some significance. Both of these measures reflect differences already observed in other measures. The excessive variability in the M_3-*gnathion* measure, significant across all models, is further emphasis for the dramatic differences in posterior dentition length and corpus height between D2600 and D211. The observed variation in *infradentale* to coronoid tip measures are a product of the observed large differences in ramus height (see table 4.4) and relative age of D2600 and D2735. In comparison with a human model, the observed Dmanisi variation in this measure is significant if either age or sex are sampled separately, but when both are considered together, the result falls within the expected range.

Results summary:

For each of the comparative models, traits are present within the Dmanisi group that exceed the expected levels of variation on the basis of both age, sex, and the combined effects of age and sex. In the case of the human comparative model, eleven such traits exist (see table 5.34).

Table 5.34 – Significant differences, human model

Corpus height at canine	Post M_3-gnathion
Corpus height at P_4	Post M_3-infradentale
Corpus height at M_2	Internal breadth at P_3
Symphysis height	P_4/M_1-infradentale
External breadth at M_3	M_2-M_3 mandibular length
Total # of traits: 10 out of 31	

Table 5.34 – List of traits for which the observed variation in the Dmanisi sample exceeds the expected range of variation for the human model.

Generally, these ten traits are focused on several areas of the anatomy already discussed as showing large variation within the Dmanisi sample. Most prominent among these features is an extremely large amount of variability associated with corpus height throughout the entire length of the corpus. Also featuring prominently amongst these measures is the relative difference in posterior dentition size (expanded in D2600 and reduced in D211) and associated structures of the posterior corpus. Despite the large difference in molar size between D211 and D2600, when all three molars are considered simultaneously, the total length of the molar row does not show a significant difference.

Table 5.35 – Significant traits, chimpanzee model

Corpus height at canine	External breadth at M_3
Corpus height at P_4	Post M_3-gnathion
Corpus height at M_2	M_1-M_3 mandibular length
Symphysis height	M_2-M_3 mandibular length
Bi-notch breadth	
Total # of traits: 9 out of 31	

Table 5.35 – List of traits for which the observed variation in the Dmanisi sample exceeds the expected range of variation for the chimpanzee model.

The traits which are unexplained by a chimpanzee model of intraspecific variation are much the same as those observed in comparisons with a human model. The only measure found on this list not observed on the human list is that of M_1-M_3 mandibular length, which merely extends the variation in the posterior dentition throughout the entire

molar row. The variation associated with overall size of the anterior and total dental arcade (Post M_3-infradentale, internal breadth at P_3, P_4/M_1-infradentale) is not excessively variable in this model.

Table 5.36 – Significant traits, Gorilla model

Corpus height at M_2	Post M_3-gnathion
Total # of traits: 2 out of 31	

Table 5.36 – List of traits for which the observed variation in the Dmanisi sample exceeds the expected range of variation for the gorilla model.

Finally, only two variables are not accommodated by any of the three predictions of a model of intraspecific variation based on a gorilla sample. These two, as seen in the previous two models, both relate to the height of the corpus, particularly focused on the posterior expansion of the corpus.

Re-evaluations the Null Hypothesis:

At this point it is necessary to return to the null hypothesis presented at the beginning of this chapter:

> H_0: the variation within the Dmanisi mandibular remains is the result of sampling individuals of different age and sex within a single evolutionary group.

This hypothesis made three predictions.

1. The observed Dmanisi variation fits within the expected range of variation of a comparative model for which sex is known and from which males and females are randomly sampled.
2. The observed Dmanisi variation fits within the expected range of variation of a comparative model for which age is known and from which adults and late adolescent individuals are randomly sampled.

3. The observed Dmanisi variation fits within the expected range of variation of a comparative model for which age and sex are known and from which adult males and late adolescent females are randomly sampled.

If all of these predictions can be rejected, the null hypothesis can be rejected. In the case of the human comparative model, this occurred for eleven of the 31 measures examined. For the chimpanzee model, all of these predictions were rejected for eight of the 31 measures examined. Finally, for the gorilla model, only two of the 31 traits rejected all of the predictions.

The question now is whether these results constitute a rejection of the null hypothesis. While several individual measures are not sufficiently accounted for by the null hypothesis, how many measurements like this constitute a rejection of the null hypothesis for the entire sample? Individually, the measures were considered significant on the basis of one-sided tests of a 0.05 alpha level. However, the entire set of 31 measures can, itself, be considered as a randomly distributed variable. Assuming a normally distributed error, somewhere between one and two measures would be expected to show significance. The validity of this assumption as it relates to the specific distributions of variability for each comparative group will be examined directly in the next chapter. In reality, nearly all of these measures will show a degree of covariation and therefore do not represent independent comparisons.

At this point it is possible to say that in the comparisons made against both a *Homo* and *Pan* comparative model, the null hypothesis can be rejected. Across the complete set of measures examined, a greater amount of variation is present than can be explained solely on the basis of age and sex based on the comparative samples examined

here. When compared with a *Gorilla* model, the observed Dmanisi variation does not exceed the expected level of variation. The implication of these results will be considered in the following chapters.

Summary:

The purpose of this chapter was to address hypotheses of intraspecific variation within the Dmanisi mandibular sample. In particular, to test predictions generated from the null hypothesis related to the expected amount of variation associated with differences in sex, differences in age, and differences with the combined effects of age and sex within the Dmanisi sample. This was done through a series of random resampling analyses involving comparative samples of recent humans, chimpanzees, and gorillas.

Before these analyses were conducted, a brief review of issues pertaining to sexual dimorphism and mandibular growth and development, as they relate to the Dmanisi hypothesis in question, was presented.

Sexual dimorphism is a pervasive and widely discussed issue within hominid evolution. One question of significance is the magnitude of sexual dimorphism in early *Homo* and the ancestral condition with regards to sexual dimorphism for *Homo*. Views are currently divided on these topics between those who view early *Homo* as having less dimorphism and more dimorphism, and those who view low levels or high levels of dimorphism as the ancestral condition. Differing views also exist as to whether the large amount of variation within the Dmanisi sample reflects a large degree of dimorphism or the presence of multiple hominid taxa.

Another problem is how to properly assess dimorphism in fossil samples. Although numerous indices of sexual dimorphism have been generated in the past, a simple male/female ratio (logged and unlogged) was used in the analyses here. This measure is simple, intuitive, and in the context of the pairwise analyses conducted here, an effective measure of sexual dimorphism.

The analyses pertaining to age conducted here deal with age on a relative scale as defined by the dental eruption and wear of individual specimens. Given the observable difference in relative age between the Dmanisi mandibles, how much this difference in age might account for the difference in anatomical variation within the group is of particular interest. The mandible is unique in that it continues to undergo significant morphological changes into adulthood.

The tests of the null hypothesis, that the variation within the Dmanisi sample is the result of sampling individual specimens of different age and sex, focused on 31 linear measures chosen for their availability on the Dmanisi specimens and broad coverage of the mandibular morphology. For each of these measures, a pairwise index of the relative difference between the proposed Dmanisi male and/or adult (D2600) and the subadult female specimens (D211 and D2735) was calculated. The resampling approach determine the likelihood of drawing this value from each of the comparative samples. The results of the tests can be considered with respect to each of the three comparative models of variation; *Homo*, *Pan*, and *Gorilla*.

Of the 31 measures examined, ten traits showed significant differences relative to a human model of variation. These measures focused particularly on aspects of corpus size and posterior tooth size. Similar results, with nine measures showing significant

differences, were observed in comparisons with a chimpanzee model of variation. Again, the areas of significance focused largely on aspects of corpus height and posterior tooth size. For each of these models, the null hypothesis could be rejected. In contrast, when compared with a gorilla model of variation, only two measures showed significant differences. A gorilla model of intraspecific variation could not be rejected.

Chapter six will consider alternative hypotheses aimed specifically at the possibility of the presence of multiple hominid taxa at the Dmanisi site. Chapter six will also make a series of comparisons with

CHAPTER 6

Dmanisi: Interspecific Variation

This chapter is divided into two sections. The first section presents alternative hypotheses for the observed Dmanisi variation then develops a quantitative test of a multiple-species hypothesis. The results of this test are presented as they pertain to both the expected magnitude and expected profile of differences in a mixed-taxa sample. The second section of this chapter considers these results in light of comparisons with the observed level of variation in a fossil sample of *A. boisei*, another Plio-Pleistocene fossil hominid found in deposits penecontemporaneous with Dmanisi in East Africa.

Developing alternative hypotheses:

To summarize the findings of the analyses so far, the hypothesis as initially formulated consisted of an intraspecific based explanation of the Dmanisi variation. The context of the Dmanisi material, both in terms of the *in situ* characterization of the site itself and its evolutionary position in the sequence of hominid evolution, provided support for a single species hypothesis (i.e. the result of intraspecific variation) as the appropriate null hypothesis. The most likely sources of variation within such a sample are derived from resampling a distribution of ages and sexes within a species. The previous analyses presented here have addressed hypotheses related to the

expected variation associated with sexual dimorphism and age-related growth in a series of comparisons with extant humans, chimpanzees, and gorillas. The findings of these analyses have showed a mixed picture based on the thirty-one traits examined within the Dmanisi sample; some traits show a greater level of variation than would be expected in any of the comparisons and other traits show a level of variation consistent with the expectations of some combination of age and/or sex. These results are summarized below in table 6.1 with a listing of the traits for which the observed condition within the Dmanisi sample lies outside of the expected range of variation for each of the comparative groups. It can be seen that for both the human and chimpanzee comparative models, a relatively large number of traits (ten and eight, respectively) cannot be explained by the combined effects of age and sex. For the gorilla model, a relatively minimal number of traits (two) are left unexplained.

Table 6.1 – Dmanisi traits with significant levels of variation

Human	**Chimpanzee**	**Gorilla**
Corpus height at Canine	Corpus height at Canine	Corpus height at M_2
Corpus height at P_4	Corpus height at P_4	Post M_3 to gnathion
Corpus height at M_2	Corpus height at M_2	
Symphysis height	Symphysis height	
External breadth at M_3	Bi-notch breadth	
M_2-M_3 length	Mandible M_1-M_3 length	
Post M_3-gnathion	Mandible M_2-M_3 length	
Post M_3-infradentale	Post M_3-gnathion	
Internal breadth at P_3	External breadth at M_3	
P_4/M_1 to infradentale		
Total # of traits: 10	**Total # of traits: 9**	**Total # of traits: 2**

Table 6.1 – Summary of the results presented in Chapter five, showing which traits are inconsistent with a model of variation for each of the comparative groups, considering the effects of both age and sex.

In the cases of the models of variation provided by comparisons with humans and chimpanzees, the null hypothesis can be rejected. A significant number of variables

exceed the expected range based on the different models. In the case of the gorilla model, while two variables do exceed the expected range, it can be argued that given the total data set of thirty-one variables which were examined, the finding of two significant differences would be expected based on chance alone. However, given the lack of a perceived gorilla level of variation from other localities associated with early *Homo*, a model of variation based on gorillas might be viewed as untenable for this time period of human evolution.

Alternative hypotheses:

Therefore, it is reasonable to consider alternative hypotheses that could explain the observed Dmanisi variation. Two alternative hypotheses immediately emerge as potentially appropriate explanations for the variability within the Dmanisi sample. The first hypothesis is that the Dmanisi variation is representative of multiple hominid taxa present at the site. It has been shown that the variation within the Dmanisi sample, in some aspects, exceeds that present in the lower dimorphism (i.e. human and chimpanzee) comparative models, and therefore could be the result of two, co-mingled hominid species within the sample. This division would most likely be placed between the D2600 specimen (possibly *Homo georgicus* (Gabunia *et al*., 2002; de Lumley *et al*., 2006), and the remaining three mandibles (possibly viewed as basal *Homo erectus/ergaster*; Vekua *et al*., 2002; Rightmire *et al*., 2005). A second hypothesis, however, might suggest that the Dmanisi sample represents a single species, but one which does not fit any of the observed patterns of variation in the comparative samples examined. This hypothesis is

supported by the unique set of anatomical features which unites the sample to the exclusion of other hominid samples.

The hypothesis of a single species, but one with excessive variation, also comes from recognition of the limitations of the employed comparative samples. It would be naïve to think that the observed variation in living humans and living great apes adequately encompasses the variation across large samples of fossil hominids or other fossil primates. Indeed, the fossil record rejects such a notion. For instance, until the emergence of a modern post-cranial anatomy in the Pleistocene, the whole of hominid evolution is characterized by a unique anatomical and locomotor pattern, not present in any living organism (Lovejoy, 2005a; Lovejoy, 2005b).

Furthermore, while hopefully the comparative samples of humans, chimpanzees, and gorillas used here present an adequate representation of the actual patterns of variation in these living taxa, they likely fall short of fully representing the full range and complexity of variation within these groups. Therefore, it is possible the rejection of the null hypothesis of a single species is the result of our comparative samples, and not because the Dmanisi group represents two species.

The goal at this point is to find a strategy which will allow these two alternative hypotheses to be distinguished. The problem with the latter hypothesis, that of excessive variation in a single taxon, is that, by itself, it is largely untestable. By stating that the observed variation in the Dmanisi sample represents a single species, but exceeds the variation boundaries of the available comparative models, the possibility of creating a quantitative test for such a hypothesis has, by definition, been eliminated. Therefore, attention will be focused on the former hypothesis.

Mixed-species sample:

In considering a hypothesis of multiple hominid taxa, the question of interest with regards to the Dmanisi becomes whether or not the pattern of variation in the Dmanisi sample fit expectations of variation for a two-species sample. If not, a two-species model can be rejected. If a two-species model can be rejected, this would provide additional support for the hypothesis of a single species with a large amount of variability. Alone, this hypothesis could still be viewed as somewhat weak, given it derives its support from the rejection of an alternative hypothesis rather than a direct test of its own predictions, but it also has support from analysis in the previous chapter when a gorilla model is examined.

Dealing with mixed taxa samples:

The problems posed by each of these alternative hypotheses has been presented and discussed previously by other researchers. The question of identifying mixed-taxa samples, in particular, has been the subject of much research (Simpson *et al*., 1960; Gingerich, 1974; Cope and Lacy, 1992; Donnelly and Kramer, 1999; Kramer and Konigsberg, 1999; Plavcan and Cope, 2001). A few papers have also dealt with the possibility of excessive or uniquely variable, single-taxon, fossil samples (Kelley and Etler, 1989; Kelley and Plavcan, 1998). The following section will briefly consider this literature.

Most approaches aimed at identifying the presence of multiple taxa within an unknown fossil assemblage rest on as assumption of how variation in structured within a

species. In particular, such approaches require either an assumed or demonstrated threshold amount of variation capable of being accommodated within a single species (Simpson *et al*., 1960; Gingerich, 2001). Assuming a species is delimited by a defined amount of variation, if the variation within the unknown sample exceeds this threshold amount, a hypothesis of multiple species is supported.

The challenge then becomes determining an appropriate metric with which to assess variation and determining an appropriate threshold from which tests can be evaluated. An example and a commonly used metric is the coefficient of variation (C.V.), for which Simpson *et al* (1960) suggest a value of greater than 10.0 as indicative of multiple taxa. This threshold value is based on observed levels of variation across a wide variety of traits and taxa. However, for any individual trait and sample taxon, observed C.V. values may fluctuate considerably. Thus, if the hypothesis in question is set up as a direct comparison between the observed variation in an unknown fossil sample and a known sample of a given taxon (or samples from multiple taxa), the results may reflect how variation is structured within the comparative sample as much as within the unknown sample. Moreover, the C.V. is not the only possible metric with which variation can be described and may not be the most appropriate. As discussed previously, any estimate of C.V. derived from a sample will reflect a certain amount of resampling error, error which is enhanced in very small sample sizes such as that being examined here. Numerous other descriptors of variation have been created and employed, each with its own strengths and weaknesses (Donnelly and Kramer, 1999). The important aspect of choosing a test metric is that it is appropriate for the sample and hypothesis of interest. The method employed here and described below is an attempt to specifically

evaluate a multiple-species hypothesis in the context of the available comparative samples and with a method that takes into account the limitations of a very small sample size.

Another important point is that, as Kelley and Plavcan (1998) note, a rejection of a single-species hypothesis is not, in and of itself, full support for a two-species hypothesis. Alternative hypotheses, such as a two-species hypothesis, are best evaluated when they can be open to the possibility of refutation (Kelley and Plavcan, 1998). Likewise, a rejection of a two-species model is not a direct test of a single-species hypothesis. To consider this situation further, it is helpful to examine the case of *Lufengpithecus*, a late Miocene hominoid from Lufeng, China.

The fossil sample from Lufeng consists of a large sample of hominoid dental material alternatively identified as representing two morphologically similar, but size distinguished taxa (Wu and Oxnard, 1983a; Wu and Oxnard, 1983b; Martin, 1991; Cope and Lacy, 1992; Plavcan, 1993) or a single, extremely sexually dimorphic hominoid species which exceeds the dimorphism observed in extant apes (Wu, 1987; Kelley and Etler, 1989; Kelley and Xu, 1991; Kelley, 1993; Kelley and Plavcan, 1998). The basis for these competing claims is a dental sample with a large range of metric variation which, for some dental characters, is bi-modally distributed with complete separation between the two modes. The question then is whether these two distributions represent different taxa or different sexes within the same taxon. The large amount of variation is equal to or greater than that observed amongst any comparable extant primate. However, Kelley, the most vocal supporter of the single-species, high dimorphism model, adds to the metric characterization of the sample an interpretation of the anatomy of the canines,

which serve to reliably distinguish identifiable male and female individuals (Kelley, 1995; Kelley and Alpagut, 1999). Thus Kelley's argument attempts to combine the observed metrical characterization of the Lufeng sample with an understanding of the observed anatomical characters. More recently, Kelley and Plavcan (1998) use a random simulation procedure to generate artificial, but parametrically controlled, "mixed-taxa" data sets in order to examine the observed Lufeng pattern of variation with hypothetical patterns of variation. Their analysis supports the earlier conclusions by Kelley of a single, highly dimorphic taxon. The method employed here is similar in some ways to that put forward by Kelley and Plavcan, but employs simulations derived from the actual comparative samples rather than artificially generated data. Additionally, any attempt to statistically treat the Dmanisi sample must respect the limitations of its significant sample size limitations.

Nested resampling strategy:

In order to test the two-species hypothesis, a meta-analysis will be conducted whereby a distribution of expected patterns of variation in a mixed-taxa pairing will be generated on the basis of a randomized, two species resampling process. The observed pattern of variation in the Dmanisi sample (in particular, the traits which cannot be explained by a single species model) can then be compared with the simulated distributions in order to test the mixed-taxa hypothesis. This process will be referred to here as a nested resampling procedure.

Three sets of results have been produced by the previous analyses regarding the Dmanisi sample, one for each of the comparative models; *H. sapiens*, *P. t. troglodytes*,

and *G. g. gorilla*. In this analysis, nine sets of results will be produced by simulating the expected pattern of difference for each possible pairwise species comparison (*Homo-Pan*, *Pan-Gorilla*, and *Gorilla-Homo*) against each underlying comparative model (*Homo*, *Pan*, and *Gorilla*). The procedure for this test will essentially repeat that conducted previously when examining hypotheses of age and sex variation, only in these tests, a randomly selected two-species pair will be drawn to serve as a replacement for the original Dmanisi sample.

For example, consider the case involving the initial set of tests of the Dmanisi variation compared with that of a human model of sexual dimorphism. In those tests, the observed variation between the hypothesized Dmanisi male (D2600) and females (D211, D2735) for any given trait within the sample was compared with a distribution of 10,000 randomly drawn male-female pairs of humans. A statistical likelihood could then be calculated for each trait that the proposed hypothesis was consistent with the expected level of variation for the human model. In the test of the two-species hypothesis, the simulated distributions are intended to represent the expected pattern of variation observed in a mixed sample of two species. Therefore, a single individual from two of our comparative samples is randomly chosen (e.g. a chimpanzee and a gorilla). The observed variation between this pair is then calculated for each of the traits in question and compared with the expected level of variation for each of the original comparative models, excluding the individuals which were randomly drawn initially. This process is then repeated 1000 times, each time randomly drawing an initial two-species comparative sample of two individuals with replacement, in order to create a distribution of expected, two-species differences. These results mimic the results of our initial analyses with the

Dmanisi material and allow for comparisons both in regards to the number of traits which are expected to show significant levels of variation in a two species comparison and what profile of traits show such a difference. This analysis is described as a nested resampling procedure because within each of the 1,000 mixed-taxa pair random resampling events, an additional set of 10,000 randomly-sampled distributions are produced from which statistical comparisons can be made. The resampling procedure used in chapter five is then nested within an additional, broader resampling procedure. As in the previous chapter, all analyses were conducted using program code written in the Matlab software package.

The same set of thirty-one traits used in the previous analyses was selected again in order to maintain consistency between the analyses for the purpose of comparison. The two individuals drawn to represent the initial two-species pairing are only selected out of those specimens for whom all of the measurements are available so as to allow for a complete set of observations. These represent the majority of the comparative materials and thus do not play a major role in limiting the resampling procedure.

Each iteration of the nested resampling procedure records *how many traits* show a significant level of variation relative to the comparative model and *which traits* show such variation. Thus it is possible to generate tallies of the expected number of trait differences in every comparison as well as record the traits which are consistent outliers. These results can be obtained for each possible species pair, compared against each possible comparative species, for nine total sets of results. Therefore, this procedure allows for examination of both the magnitude of variation (i.e. the number of traits which show excessive levels of variation) and profile of variation (i.e. which traits consistently

show excessive levels of variation). The hypothesis that the pattern of variation within the Dmanisi sample is the product of resampling a mixed-taxa set of individuals can therefore be broken down into predictions related to both magnitude and profile of variation.

The prediction of the mixed-taxa hypothesis on the basis of magnitude is that the number of traits observed within the Dmanisi sample which exceed that of a single-species model is equal to or greater than that observed for a distribution of randomly drawn mixed-taxa pairings.

The prediction of this hypothesis on the basis of profile is that the set of traits which show significance in the original, Dmanisi single-species model consistently appear as excessively variable in a two-species model and that those traits which are not excessively variable in a single-species model, do not consistently appear as excessively variable in a two-species model.

Results

Results from these tests are broken into two sections, one dealing with predictions related to the magnitude of expected difference and one dealing with predictions related to the profile of expected difference. Additionally, each of these sections will discuss the results as they pertain to each of the three comparative models.

Magnitude of variation:

Comparisons between the Dmanisi group and comparative samples of humans, chimpanzees, and gorillas produced ten, eight, and two unexplained traits (out of a set of

thirty-one total measures) based on intraspecific variation in the previous analysis. The tests presented here are designed to put these numbers into perspective. With these previous results in mind, a random mixed-taxa pairing was drawn, the same thirty-one measures examined, and compared with 10,000 distributions from each comparative group based on a process of random resampling with replacement. This entire procedure was then repeated 1,000 times. For each of these 1,000 iterations, the number of traits which differed significantly from the underlying comparative distribution was recorded. These values were then compared to those observed when a similar procedural test was conducted on the Dmanisi group in order to determine significance. The prediction from the mixed-taxa hypothesis is that an equal or lesser number of traits to that observed in the Dmanisi tests were observed when these comparisons were undertaken. If, in 950 or more of the iterations, more traits differed than were seen to differ in the Dmanisi comparisons, the mixed-taxa hypothesis was rejected.

Table 6.2 lists the results from these tests as they pertain to magnitude of variation.

Table 6.2 – Magnitude of variation results, mixed-taxa pairings

	H. sapiens (10)	*P. troglodytes* (8)	*G. gorilla* (2)
Homo-Pan	15.9*	10.8 (941/1000)	11.9*
Homo-Gorilla	20.4*	15.5*	18.0*
Pan-Gorilla	16.2 (908/1000)	10.3 (680/1000)	12.5*

Table 6.2 – Results for quantitative tests of mixed-taxa hypothesis. Columns list the results for each of the underlying comparative models, with the observed number of trait differences from the Dmanisi group in parentheses. Rows show the results for each of the three possible mixed taxa pairings. The results show the average number of traits which differed significantly from the underlying comparative model. Those marked with an asterisk (*) are statistically significant (>950/1,000, $p<0.05$). Results that are not significant show the number of trials out of 1,000 for which the observed simulation result was greater than that observed in the Dmanisi comparisons.

These results can be interpreted on the basis of the underlying comparative model (*Homo*, *Pan*, *Gorilla*) or the randomly drawn mixed-taxa pairing (*Homo-Pan, Homo-Gorilla, Pan-Gorilla*) involved. The former of these interpretations, that which examines the results based on the underlying comparative model, is examined first.

In the initial analyses, comparisons between the Dmanisi variation and that observed within a human sample yielded ten measures which could not be explained by the expected range of variation based on differences of age and sex. This result of ten measures was lower, on average, than all three possible mixed-taxa pairings compared with a human sample, statistically so in the case of the *Homo-Pan* pairing and *Homo-Gorilla* pairing (see table 6.2). In the case of the *Pan-Gorilla* pairing, although it did not reach significant levels of $p<0.01$, showed a strong tendency towards significance, with more than ten measures showing significant differences in 908 out of 1000 simulations.

Comparisons with the human comparative model are interesting because, morphologically speaking, the Dmanisi remains (and other Pleistocene hominids) follow a human pattern of mandibular morphology to a much greater degree than a great ape pattern. In all of these comparisons, the results show either statistically greater variation in a mixed-taxa pairing relative to the observed Dmanisi variation or a strong tendency towards such significance. These results suggest, relative to a human model, while the Dmanisi sample shows a large degree of variation, the sample does not show the expected magnitude of difference observed in a mixed-taxa sample.

Initial comparisons made on the basis of a *Pan* model of variation found eight traits with a level of variation that could not be accounted for by differences in age and sex. In only one of the three mixed taxa pairings (*Homo-Gorilla*) did the results here

flatly reject a mixed-taxa pairing (see table 6.2). However, in all pairings, the average number of trait differences was greater than the eight observed in the Dmanisi analysis. Furthermore, while the *Homo-Pan* pairing did not achieve significance at the established alpha level of 0.05, it came very close ($p<0.06$). The only result which did not approach a rejection of the hypothesis on the basis of magnitude of variation was that of the *Pan-Gorilla* pairing, in which the mixed-taxa pairing exceed that observed in the Dmanisi comparison in only 680 of a possible 1000 simulations.

As stated previously, the earlier findings based on a comparison between the observed variation in the Dmanisi sample and that expected intraspecific variation based on a gorilla model did not really reject the null hypothesis of a single-species model. Nevertheless, a set of interspecific tests were conducted here. All of the mixed-taxa pairings showed strongly significant results regarding magnitude of variation relative to the observed difference of only two traits in the Dmanisi comparisons (see table 6.2). As would be expected then, the hypothesis of a mixed-taxa sample relative to a pattern of variation from a gorilla model was strongly rejected.

Considering these results together, a somewhat mixed picture emerges. Nine sets of results have been produced related to the alternative hypothesis. As such, interpretations are somewhat difficult. Two conclusions can be drawn, however. The first is that, generally speaking, it appears the hypothesis of the Dmanisi sample representing a two-taxa pairing on the basis of magnitude of variation is not supported. In six of the nine results, this hypothesis can be statistically rejected, and in two of the remaining three results, a strong tendency towards a significant result is observed. Only

in one of nine sets of results, that of a *Pan-Gorilla* pairing compared against a *Pan* model of variation, does the hypothesis not come close to rejection.

This leads into the second observation from these results. If an argument is made that the Dmanisi hominids do represent a mixed-taxa sample, the relationship between the two taxa would likely have to be similar as that observed between *Pan* and *Gorilla*. This is of interest because an extensive literature has documented the relationship between these taxa, discussing not only their morphological similarities and differences (Giles, 1956; Shea, 1983a; Daegling, 1996; Ravosa, 2000), but also the importance of ecological and behavioral variables in creating this pattern of variation (Shea, 1983b). This observation also suggests that, were an argument of taxonomic differentiation within Dmanisi sample presented (i.e. Schwartz, 2000), an important line of evidence with which to test relevant hypotheses would be ecological or dietary information from the Dmanisi site.

Profile of variation:

Results from chapter five provided not only a number of traits within the Dmanisi sample that exceeded the expectations of an intraspecific model but also a specific recognition of which trait these were. Whereas the tests from the previous section were intended to examine the significance of the actual number of differences observed, what has been identified as magnitude of difference here, this section will focus on which traits differ, or the profile of difference.

One might make the argument that in attempting to identify the presence of co-mingled taxa within a sample, the important factor is not how different individual

specimens are, but how these differences are patterned. Do the observed differences form a consistent profile of variation, perhaps associated with an adaptive or allometric shift within the sample? This section will quantitatively explore the issue of whether the observed profiles of differences within the Dmanisi sample are consistent with the expected profile of differences observed in a mixed-taxa sample.

Recall that the simulations conducted in this chapter recorded both the number of traits which differed significantly in each of 1,000 iterations (relative to a randomly drawn distribution of 10,000) and which specific traits these were. Therefore, it is possible to examine which traits, if any, appeared significantly different in a significant number of iterations. In other words, which traits lay outside the expected range of variation in 950 or more of the simulations? Specifically regarding the Dmanisi results, the question is how many of the traits which appeared excessively variable within the Dmanisi sample show up as consistently excessively variable in a mixed-taxa sample? Additionally, how many traits which did not exceed the expected range of variation within the Dmanisi sample show up as consistently excessively variable in a mixed-taxa sample? These two questions are an attempt to identify whether the observations from the Dmanisi sample are consistent with, or inconsistent with a two-species model.

Profile consistency can be defined in a variety of different ways. Two simple definitions are considered here. As a first attempt, the observed Dmanisi pattern was considered consistent with a two-species model if more of the traits which differed significantly within the Dmanisi group appeared significantly different in the random simulations than traits which did not differ significantly in the Dmanisi sample. These results are presented in table 6.3. As in the previous table, columns in the table represent

different underlying comparative models of variation. Rows in the table represent a different mixed-taxa pairing. Results within the table show the number of traits consistent with the observed pattern of variation in the Dmanisi sample on the left side of each column and the number of traits inconsistent with the Dmanisi sample on the right side. The number of traits previously identified as excessively variable is listed in parentheses next to the associated comparative group.

Table 6.3 – Profile of variation results, mixed-taxa pairings

	H. sapiens (10)		*P. troglodytes* (8)		*G. gorilla* (2)	
	consistent	inconsistent	consistent	inconsistent	consistent	inconsistent
Homo-Pan	4	5	2	4	0	4
Homo-Gorilla	6	10	4	4	1	8
Pan-Gorilla	6	1	5	2	1	4

Table 6.3 – Results for the examination of profile differences in a mixed-taxa sample. The columns display results for each of the comparative models with the number of observed differences listed in parentheses. Rows display the results for each of the three possible mixed-taxa pairings. Within each column, results are subdivided into the number of traits which showed excessive variation consistent with what was observed in the Dmanisi sample (left) and the number of traits inconsistent with this pattern (right).

As in the case with the examination of differences in magnitude of variation, the results for the examination of the profile of variation are complicated. Again, the results will be considered with respect to both the comparative model and the individual mixed-taxa pairing. Looking at the human comparative model, it can be seen that analyses from the previous chapter identified ten variables within the Dmanisi sample as inconsistent with a single-species hypothesis of variation. In this analysis, only in the case of the *Pan-Gorilla* pairing do the traits identified as consistent with this profile (six) outnumber the traits identified as inconsistent with the profile (one). In the other two possible pairings, *Homo-Pan* and *Homo-Gorilla*, the inconsistent traits outnumber the consistent traits (five to four and ten to six, respectively). The results of the *Pan* model show a similarly mixed

pattern. In the *Homo-Pan* pairing the number of inconsistent traits (four) outnumbers the consistent traits (two). In the *Homo-Gorilla*, the number of traits are equal (four) between the two sets. Similarly to the *Homo* model, the *Pan-Gorilla* pairing shows a greater number of consistent traits (five) than inconsistent traits (two). As stated in the discussion of the magnitude results, the *Gorilla* model comparisons are perhaps unfair, given that the *Gorilla* model of variation is consistent with a single-species hypothesis. As expected then, all of the possible mixed-taxa pairs show many greater traits inconsistent with the profile than consistent.

Looking at the results across the rows, at the mixed-taxa pairings rather than the comparative models, a similarly mixed picture emerges. None of the models show a profile consistent with a *Homo-Pan* pairing. In the case of the *Homo-Gorilla* pairing, only the *Pan* model of variation yielded results potentially consistent with the observed pattern, although even this result is somewhat equivocal (four and four). The results from these two sets of pairs can perhaps be explained by the strong difference between the human mandibular morphological pattern and the great ape mandibular morphological pattern. The two groups show very different anatomical patterns in the mandible, consistent with different evolutionary histories and different environmental adaptations. In contrast, it is interesting that except for the case of the *Gorilla* model, the *Pan-Gorilla* pairing yields results consistent with a mixed-taxa pattern of variation. This issue is discussed in greater detail below.

One criticism of these results might be in the definition of profile consistency employed. So far, a profile of difference has been considered consistent if the traits observed as being excessively variable in the Dmanisi sample outnumber the traits which

did not. This may not be a fair comparison. Consider again the case of the human model of variation. It was previously identified that ten of the thirty-one measures examined in the Dmanisi sample exceeded the expected ranges of variation. That leaves twenty-one traits which were not excessively variable. In the definition of pattern consistency used above, these two sets of traits were treated equally with respect to pattern consistency. As such, the definition was weighted in favor of rejecting the hypothesis that the pattern of variation observed in the Dmanisi sample is consistent with a mixed-taxa sample. A greater pool of measures inconsistent with the pattern were present than were consistent with the pattern. This problem reaches an extreme degree with the *Gorilla* comparisons, where only two possible measures existed to show consistency, against twenty-nine potential inconsistent measures.

An alternative approach that avoids the problem of inequality in possible consistent/inconsistent measures is to only consider those variables previously identified as being part of the observed pattern of variation. For this definition, the pattern is deemed consistent with the observed Dmanisi pattern of variation if half or greater of the possible traits remained excessively variable.

Looking at the profile of variation with this criterion, the results change somewhat. With this alternate definition, all of the *Pan-Gorilla* and *Homo-Gorilla* comparisons appear consistent with the profile observed in the Dmanisi sample, with at least half of the measures remaining consistent with the pattern of variation. None of the comparative models are consistent with the *Homo-Pan* pairing.

Interpretations of the results relating to the profile of variation are not entirely straightforward. The results themselves are complex and at times appear conflicting.

Additionally, the appropriate definition of what constitutes a consistent profile and what constitutes consistency with a pattern is debatable. Nevertheless, certain observations can be made.

If only the *Homo* and *Pan* comparative samples are considered (excluding *Gorilla* for the reasons outlined previously), the results vary as a function of which mixed-taxa pairing is used, rather than which underlying comparative model is used. The *Homo-Pan* pairing yields results inconsistent with the hypothesis that the profile of variation observed in the Dmanisi sample is best explained by a mixed-taxa hypothesis. Results for the *Homo-Gorilla* pairing also show little evidence of consistency in profile with that observed in the Dmanisi sample. The results for the *Pan-Gorilla* pairing, however, do provide some support for a mixed-taxa interpretation of the profile of variation observed in the Dmanisi sample. This follows the observation made earlier that in terms of magnitude of variation, if a two-species explanation is put forth for the Dmanisi sample, it is most likely a relationship similar to that between *Pan* and *Gorilla*. The results here further suggest that the profile of variation in the Dmanisi sample, particularly that observed between D2600 and the two smaller specimens of D211 and D2735, most likely represents a difference in absolute size, possibly along an allometric scale. Whether or not this supports the notion of two species or male and females of a single species is less clear, although the majority of the evidence appears to line up on the side of the latter of these explanations.

Comparisons with Australopithecus boisei:

One challenge in examining fossil hominid remains is the lack of appropriate comparative models. So far this work has relied on extant humans and great apes, the closest living relatives of fossil hominids and a group of species which displays a variety of different patterns of mandibular morphology. None of these models, however, have provided a clear or close match with the observed variation within the Dmanisi sample. The variation within the Dmanisi sample appears greater than what is observed in extant *Pan* or *Homo* samples, and yet the pattern of variation does not appear to match what is seen in a *Gorilla* sample.

Returning to table 2.1 (reposted below as table 6.4), one possible reason for the lack of concordance between what is observed in the Dmanisi sample and what is observed in the comparative samples appears in the final two columns.

Table 6.4 – Comparative Sample

	Total	Female	Male	Unknown	Dimorphism	Morphology
P. t. troglodytes	61	26	23	12*	Small	Ape
G. g. gorilla	54	31	22	1*	Large	Ape
H. sapiens	90	30	41	20*	Small	Human

Table 2.1 – Comparative extant sample. Total number of specimens, broken down by sex, level of dimorphism, and mandibular morphological pattern. (* - specimens of unknown sex represent individuals which are too young to have been reliably sexed)

With regards to the morphological range of variation encompassed by these groups, the one combination of morphology and dimorphism that is not sampled is a human pattern of mandibular morphology with a high (or at least greater) level of sexual dimorphism. No living group shows the pattern but a comparable group with such a mandibular morphology does exist in the hominid fossil record; *A. boisei*

A. boisei, also sometimes placed into *Paranthropus boisei* (Wood and Richmond, 2000), is a Plio-Pleistocene hominid taxon present in East Africa between approximately 2.5-1.4 MA (Wood and Strait, 2004). *A. boisei* are characterized by their distinctively robust and extremely large masticatory structures (Robinson, 1954; Robinson, 1956; Wood and Lieberman, 2001). *A. boisei* also constitutes a potentially useful fossil comparative sample in that the known specimens are confined to a relatively small geographic region and, according to Wood (1994), show relatively little metric change through time. This helps eliminate further confounding factors when making comparisons with the Dmanisi sample. The *A. boisei* sample is also interesting in that it likely shares a common ancestor with the Dmanisi remains (and other early *Homo* fossils) sometime in the latter half of the Pliocene, and thus is a closely related species.

As a result of their distinctive morphology, for *A. boisei*, more so than many hominid taxa, a reasonable taxonomic consensus exists for the specimens assigned to it. This is particularly true for the dental remains, including the mandibular specimens. A fairly large set of *A. boisei* mandibles is present in the record which, although often quite fragmentary, allows for extensive comparisons with the Dmanisi sample. These comparisons are intended to put the previous results into perspective and perhaps shed some light on conclusions that can be taken away from the Dmanisi remains. They are not intended to represent a formal hypothesis test. In many ways, the two samples are very different. The *A. boisei* sample not only represents individuals scattered across numerous localities in East Africa, it also represents a sample scattered across a long period of time, perhaps a million years or greater. In order to reduce the impact of some of these difficulties, comparisons here will be limited to *A. boisei* specimens from the

extensive deposits in the Koobi Fora region, east Lake Turkana, Kenya (see list, table 6.4). Nevertheless, this sample provides a unique perspective through which the Dmanisi remains can be viewed.

Table 6.5 – Fossil list: *Australopithecus boisei* specimens

KNM-ER 1469	KNM-ER 3954	KNM-ER 728	KNM-ER 729
KNM-ER 1468	KNM-ER 3230	KNM-ER 403	KNM-ER 810
KNM-ER 1806	KNM-ER 3729	KNM-ER 1803	KNM-ER 727
KNM-ER 1808	KNM-ER 3731	KNM-ER 818	KNM-ER 15930
KNM-ER 3229	KNM-ER 404	KNM-ER 726	KNM-ER 16831
KNM-ER 3889	KNM-ER 725	KNM-ER 805	

Table 6.4 – List of *Australopithecus boisei* specimens, all from the Turkana Basin, Kenya, used in the comparisons reported here.

Another challenge with the Dmanisi-*A. boisei* comparisons is that the most of the *A. boisei* specimens are quite fragmentary. Although the total sample is large, few specimens preserve as complete a set of features as found in the Dmanisi remains. In particular, the *A. boisei* sample preserves a large number of lateral *corpora* specimens, with varying degrees of preservation in the dentition, symphysis region, and rami. Given the nature of this sample, the kind of systematic comparisons done in this chapter and the previous chapter are impossible. Instead, simple comparisons of the relative variation within the two groups are examined.

For each of the two samples, the proportional variation, measured as the relative difference between the largest and smallest specimens within each sample, was calculated for a large set of mandibular measures. The set of measures was expanded from the list of thirty-one used in the previous analyses to all possible measures for which comparisons between the samples could be made. These values are discussed in anatomical groups similar to the organization of the previous chapters. Juvenile

individuals (those deemed obviously younger than any of the Dmanisi specimens) were excluded.

The results of these comparisons are visually displayed in figure 6.1 (see below). The figure displays the comparisons, divided into eleven different anatomical regions/categories, with the maximum observed (X_i/X_j) values for each of the groups.

Figure 6.1 – Relative variation within Dmanisi and *A. boisei* samples

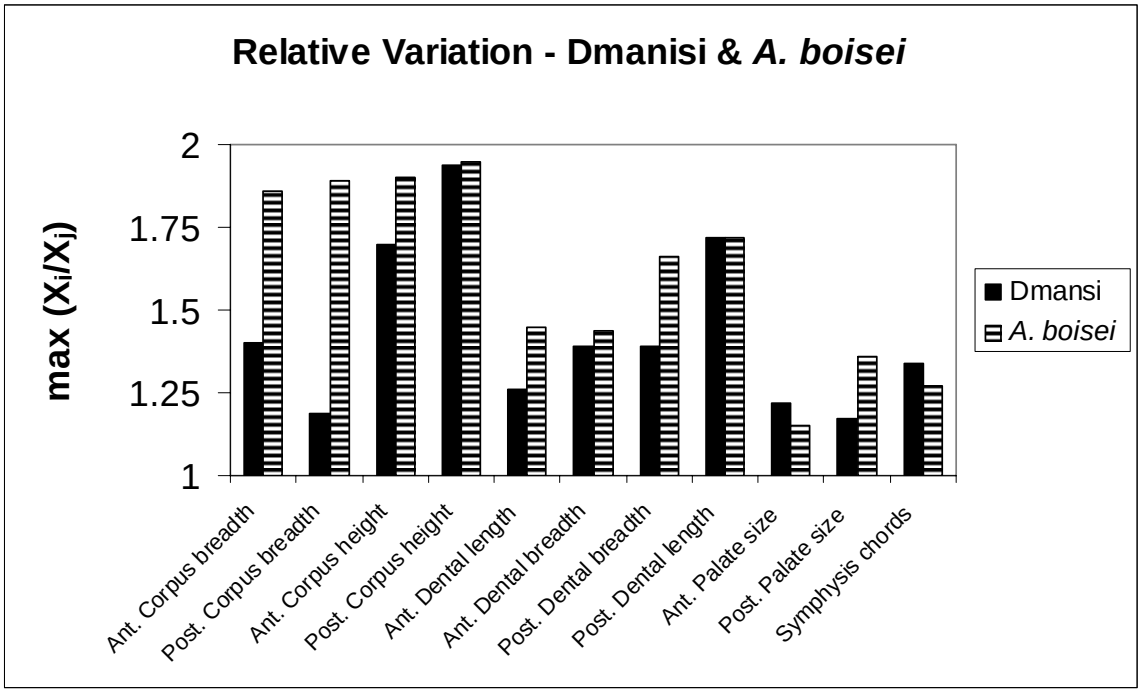


Figure 6.1 – Maximum proportional variation in Dmanisi (solid) and *A. boisei* (hatched) mandibular samples. Anatomical groups are listed across the x-axis with maximum (X_i/X_j) values along the y-axis.

One of the first observations that can be drawn is that, as described and observed in the previous chapters, the Dmanisi sample shows especially high variability in aspects of corpus height and posterior dental size. However, in all of these categories, the observed Dmanisi variation is either met or exceeded by that observed within the *A. boisei* sample. The only categories for which the Dmanisi sample shows greater

observed variation than the *A. boisei* sample are measures of anterior dental arcade size and various symphyseal chord lengths. It should be noted that these two categories are two of the most poorly represented within the *A. boisei* sample owing to the lack of many well preserved symphyses and bilaterally preserved dental arcades.

These comparisons are not meant as a definitive test of the taxonomic integrity of the Dmanisi sample, but rather as another way to understand the Dmanisi variation in a comparative context. In this case, the comparisons are with a penecontemporaneous, hominid taxon. As such, these comparisons support the possibility of the Dmanisi mandibular sample as being representative of a single species, but one with greater variability than observed in recent humans and chimpanzees. The large amount of variation in *A. boisei* is typically thought to represent a greater degree of sexual dimorphism than that observed in recent humans (Brown *et al*., 1993; Suwa *et al*., 1997; Aiello *et al*., 1999; Wood and Lieberman, 2001). While the evidence for such a claim remains equivocal, the Dmanisi remains appear, at least in some characters, to be showing a similar degree of variation.

Summary:

This chapter was intended to present two alternative hypotheses to explain the observed Dmanisi variation and quantitatively evaluate them. One of these stated that the Dmanisi variation is the consequence of the presence of multiple, co-mingled hominid taxa at the site. The second alternative hypothesis is that the Dmanisi variation is the result of a single taxon, but one with greater variation than could be sampled from either

the human or chimpanzee samples used here. Particular attention was focused on the former of these two, that of a mixed-taxa hypothesis for the Dmanisi variation.

A brief review was presented of previous research along these lines, including a review of the story of *Lufengpithecus*, a Miocene hominoid that has been argued to have exceptionally high levels of sexual dimorphism. Also, discussion of the methods used to examine potentially co-mingled fossil samples to determine their taxonomic composition was presented.

Finally, a novel method to deal with this problem, referred to here as a nested random-resampling strategy, was presented and employed to quantitatively assess the magnitude and pattern of variation expected in a mixed-taxa sample based on the comparative data available. This method is an extension of the resampling procedure presented in chapter five, but extended so as to determine whether the results from chapter five for each of the comparative models are consistent with the variation observed in a mixed-taxa pairing.

Using the same set of 31 measures examined in chapter five, this procedure allows for the assessment of both the expected number of traits which will show significant amounts of variation in a mixed-taxa pairing and which traits are expected to show significant differences. If these two factors show results consistent with the results observed in chapter five for the Dmanisi sample, the hypothesis of multiple species is supported. If they show a pattern of variation inconsistent with that observed in chapter five, the results would suggest the Dmanisi sample is not the consequence of co-mingled taxa.

The results for this analysis are complicated, given that there are separate results for each of three possible mixed-taxa pairings (Human-Chimpanzee, Human-Gorilla, Chimpanzee-Gorilla) compared against each underlying model of variation (Human, Chimpanzee, and Gorilla). Given this, the results are complicated to interpret. However, the majority of observations support the notion that a mixed-taxa sample is not a parsimonious explanation for the observed Dmanisi variation. With regards to the magnitude of variation, the number of traits expected to differ significantly in a mixed-taxa pairing, the observed results in chapter five are less than expected for all nine sets of results and significantly so for most of them. Regarding the profile of variation, which traits actually differ, the results are less clear but still show tendency towards an expected profile of trait differences that are not consistent with that observed in the Dmanisi comparisons made in chapter five.

While not a direct test, this provides some support, together with the results derived from chapter five, for the other alternative hypothesis presented, that of Dmanisi representing a single, highly dimorphic taxon.

Finally, to complete the understanding of the observed Dmanisi variation, comparisons were made between the Dmanisi sample and the maximum proportional variation observed in a large set of *A. boisei* fossils. *A. boisei* is a penecontemporaneous hominid taxa from East Africa, and for numerous reasons, provides a strong comparison with the Dmanisi sample. These comparisons suggest that across nearly all aspects of the mandible, even those for which the Dmanisi sample shows extremely high levels of variation, the *A. boisei* sample shows an equal or greater degree of variation, providing further support of a single-taxon explanation for the Dmanisi sample. These comparisons

also provide support for the possibility of greater levels of sexual dimorphism as the primitive condition for early *Homo*.

CHAPTER 7

Summary, Conclusions, and Future Research

This purpose of this chapter is to present a summary of the results of this work, beginning with an outline of the problem, question, and research conducted. The implications of this research will be considered as it pertains to understanding the Dmanisi mandibles, the importance of the Dmanisi site as a whole, and potential significance for the broader understanding of the evolution of early *Homo*. Finally, a few of the questions left unanswered and directions for future research are considered.

The Dmanisi mandibular sample:

As presented in chapter two, the Dmanisi site has emerged over the past fifteen years as a site of critical importance for the understanding of early *Homo* and the dispersal of hominids outside of Africa during the Plio-Pleistocene. Current understandings of the geology place the hominids within rapidly accumulating sediments, deposited in a time interval straddling the Olduvai-Matuyama paleomagnetic boundary at or around 1.77 Ma (Gabunia *et al*., 2001; Ferring and Lordkipanidze, 2003; Mallol, 2004). The preservation of skeletal material is excellent at the site and in addition to the more than fifty hominid elements, a huge sample of a diverse Villefranchian fauna has

been uncovered (Gabunia *et al*., 2000a; Tappen and Vekua, 2003). These remains are found in the context of a basic Oldowan core-flake stone tool assemblage (Gabunia *et al*., 2001; de Lumley *et al*., 2005). This assemblage currently represents the most conclusive and complete evidence for the earliest dispersal of hominids outside of Africa.

The hominid sample is remarkable for the degree of preservation of the material and for the presence of associated elements, cranial and post-cranial, from numerous individuals (Gabunia and Vekua, 1995; Gabunia *et al*., 1999; Gabunia *et al*., 2002; Vekua *et al*., 2002; Jashashvili, 2005; Lordkipanidze *et al*., 2005; Meyer, 2005; Rightmire *et al*., 2005). Thus far, these remains have suggested the need for a dramatic revision of ideas regarding early hominid dispersal and the relationship amongst a wide group of taxa assigned to early *Homo* (e.g. *Homo rudolfensis, Homo habilis,* and *Homo ergaster*) and their connection to specimens classically assigned to *Homo erectus* (Dean and Delson, 1995; Bräuer and Schultz, 1996; Rosas and Bermúdez de Castro, 1998; Gabunia *et al*., 2000b; Schwartz, 2000; Rightmire *et al*., 2005; de Lumley *et al*., 2006). Dated to a time period intermediate within the extensive fossil deposits of early *Homo* from East Africa such as those in the Turkana Basin, Olduvai Gorge, and elsewhere, Dmanisi provides a unique perspective into this dynamic time period during human evolution.

Within this sample, the four preserved mandibles discovered as of the 2005 field season (D211, D2600, D2735, and D3900) present the largest and most striking variation. The first hominid specimen found in 1991, the preserved corpus of D211, presented a unique combination of seemingly primitive and derived features which led different researches to place the specimen anywhere from the Plio-Pleistocene boundary to late Pleistocene in age (Dean and Delson, 1995; Gabunia and Vekua, 1995; Bräuer and

Schultz, 1996; Rosas and Bermúdez de Castro, 1998). In contrast, the second mandible recovered, following the 2000 field season, represents, in many characters, the largest hominid mandible in the Pleistocene fossil record of *Homo* (Gabunia *et al*., 2002). This specimen also contains a unique pattern of exceptional dental wear. Subsequent field seasons produced two additional mandibles, D2735 and D3900, each found *in situ* with associated cranial remains, D2700 and D3444, respectively (Vekua *et al*., 2002; Lordkipanidze *et al*., 2005). The D211 mandible has also subsequently been associated with a cranial specimen, D2282. In contrast to the rather homogenous cranial remains associated with these specimens, the mandibular sample is exceptionally diverse.

Anatomically speaking, the picture presented by the Dmanisi sample is complicated. Many features, such as the morphology of the premolars, the robusticity of the corpus, and the development of certain aspects of the symphysis place them solidly within the range of variation of contemporaneous East African specimens such as KNM-WT 15000, KNM-ER 992, or OH 13. Other aspects of their anatomy, however, such as pronounced development of the *tori mandibularis* and orientation and form of the *foramen mandibularis* suggest a relationship with specimens much later in time, including later *Homo erectus* and *Homo heidelbergensis*. Other characters present both pictures, such as the molar morphology, with D2600 showing characteristic early *Homo* expansion of the posterior dentition, particularly mesial-distal expansion, and D211 showing exceptional (for this time period) reduction of the posterior dentition. Even within the sample, the D2735 specimen, intermediate between D211 and D2600, aligns itself more closely with the former in some characters and the latter in other characters.

The primary goal of this work was to present a thorough description and comparisons of the preserved mandibular sample with the aim of developing an appropriate and testable hypothesis for the observed variation. Also, the goal was to examine variation in a systematic and hierarchical fashion beginning with models of intraspecific variation. This approach was informed by both the context of the Dmanisi site and the anatomy of the mandibular sample.

One factor of importance within the Dmanisi sample is the distribution of age within the sample. Two of the specimens, D2600 and D3900, are clearly adults, likely older adults on the basis of the extreme dental attrition in both individuals. The remaining two specimens are each in the process of M_3 eruption and can be classified as late adolescent individuals. Using known patterns of mandibular growth and development in humans and recent apes, this observed difference in relative age is clearly one factor contributing to the Dmanisi variation.

Another possible source of variation is sexual dimorphism within the sample. Ongoing debate exists as to the level of sexual dimorphism within the hominid lineage, including early *Homo* (Kramer, 1993a; Lieberman *et al*., 1996b; Lockwood, 1999; Reno *et al*., 2003; Plavcan *et al*., 2005; Reno *et al*., 2005). The pattern of the size differences and the combination of unique, shared anatomical features within the sample, support dimorphism as a possible explanation and reasonable hypothesis for the Dmanisi variation. Furthermore, given the context of the site it is appropriate to independently test a model of sexual dimorphism prior to considering explanations based on higher order, phylogenetic sources of variation.

A hypothesis of intraspecific variation:

Based on the anatomy of the Dmanisi specimens and the context of the site a null hypothesis for the observed variation was presented as follows:

> H_0: the variation within the Dmanisi mandibular remains is the result of sampling individuals of different age and sex within a single evolutionary group.

In order to test this hypothesis, three predictions were generated and quantitatively examined. These predictions are:

1. The observed Dmanisi variation fits within the expected range of variation of a comparative model for which sex is known and from which males and females are randomly sampled.
2. The observed Dmanisi variation fits within the expected range of variation of a comparative model for which age is known and from which adults and late adolescent individuals are randomly sampled.
3. The observed Dmanisi variation fits within the expected range of variation of a comparative model for which age and sex are known and from which adult males and late adolescent females are randomly sampled.

A probabilistic, random resampling strategy was employed in order to test these predictions using samples of extant *Homo sapiens*, *Pan troglodytes troglodytes*, and *Gorilla gorilla gorilla* as comparative models of age and sex related variation. Individual specimens were randomly drawn with replacement 10,000 times in order to produce a distribution of the expected range of variation against which the observed Dmanisi

variation could be compared and a functional p-value generated for each of the comparative models and each of the linear measures examined. The proportional, pairwise variation between male/female, adult/late adolescent, and adult male/late adolescent female was used as a test statistic for each of the three predictions, respectively. For any given measure, if all three of the predictions were rejected, the null hypothesis was considered rejected. If any of the three predictions could not be rejected, the observed variation was considered as being parsimoniously explained by either a difference in sex, age, or the combination of the two.

Results of the analyses of intraspecific variation presented in chapter five were mixed based on the comparative model employed. Using a *Gorilla* model of variation, only two of thirty-one measures examined lay outside the expected range of variation based on intraspecific factors. This was considered within the range of expected variation based on a model of repeated examination and the null hypothesis was not rejected. For both the *Homo* and *Pan* models, however, a sufficient number of significant differences existed, ten and eight, respectively, to reject the null hypothesis. As might have been predicted on the basis of the anatomical descriptions, the measures which could not be accounted for by a model of intraspecific variation consisted primarily of variables related to corpus height and the development of the posterior dentition, two areas of excessive variation within the Dmanisi group.

A hypothesis of interspecific variation:

Chapter six presented two alternative hypotheses for consideration. The first of these alternative hypotheses was that rather than being explained by a model of

intraspecific variation, the variation within the Dmanisi mandibular assemblage was the result of a mixed-taxa sample. The second alternative hypothesis stated that the Dmanisi sample still represented a single taxon, but which, for numerous potential reasons, presented greater variation than could be sampled out of a comparative group of extant *Homo sapiens* or *Pan troglodytes troglodytes.* The latter of these alternative hypotheses, while worthy of consideration and discussion, is unfortunately, by definition, impossible to directly test.

Instead, a quantitative test of the mixed-taxa hypothesis was conducted, whereby the observed pattern of variation in the Dmanisi sample was compared with the expected pattern of variation, considered in terms of both magnitude and profile, of a mixed-taxa assemblage. A nested resampling procedure was developed in order to test this hypothesis. Based on the same resampling procedure conducted in chapter five, this procedure replaced the observed variation of the Dmanisi sample with the "observed variation" of a randomly drawn mixed-taxa pairing. The procedure was "nested" in the sense that the entire procedure used in chapter five to examine intraspecific variation, was repeated with random replacement of the mixed-taxa pairing 1,000 times in order to generate expected models of simulated interspecific variation with regards to both the number of expected differences and which specific measures formed the profile of observed variation.

Nine sets of results were produced based on the comparison between three possible mixed-taxa pairings (*Homo-Pan*, *Homo-Gorilla,* and *Pan-Gorilla*) and three underlying, comparative models of variation (*Homo*, *Pan,* and *Gorilla*). Magnitude of variation was treated as the number of traits which showed significantly greater than

expected variation. The profile of variation was treated was evaluated on the basis of traits which consistently showed significant levels of variation and whether or not these traits were part of the observed set of excessively variable within the Dmanisi sample. Results for both of these categorizations of variation were considered with regards to the underlying comparative model and the mixed-taxa pairing involved.

Results for the analysis of magnitude showed that all nine sets of results produced, on average, a greater number of significant differences than observed in any of the comparative tests involving the Dmanisi sample. Six of the nine were statistically significant on the basis of the nesting resampling strategy employed; two of the remaining showed a strong tendency towards significance, and only one of the nine showed no sign of significance (although still showed more differences, on average, than observed within the Dmanisi sample). Regarding the breakdown by comparative model, all of the comparisons with an underlying gorilla model showed a significantly greater than expected number of differences. This is perhaps not surprising as the Dmanisi variation did not really exceed the expectations of a gorilla model of variation. Two of the three pairings (*Homo-Pan* and *Homo-Gorilla*) showed a significantly greater number of differences when compared against a human model. The other pairing, *Pan-Gorilla*, approached, but did not reach significance ($p<0.1$). Only with the *Pan* model of variation were results less clear. The *Homo-Gorilla* pairing produced a significant result, the *Homo-Pan* pairing a near significant result ($p<0.06$), and *Pan-Gorilla* a non-significant result ($p<0.35$).

Results for the profile of variation were somewhat less clear. The profile of variability for the Dmanisi sample was defined on the basis of what traits showed

significantly more variation than could be accommodated with an intraspecific model of variation. As such, the determination of which results were consistent with this definition and which were not varied for each of the comparative models, *Homo*, *Pan*, and *Gorilla*. Overall consistency was based on the preponderance of traits showing significant levels of variation consistent and inconsistent with this pattern. In order to account for potential bias in the number of "available consistent or inconsistent" traits, pattern was considered on the basis of both consistent and inconsistent traits and on solely consistent traits. Both sets of evaluations yielded similar, although complex results.

As with the examination of magnitude of variation, none of the results were consistent with a mixed-taxa sample on the basis of a gorilla model of variation. For the other two models the outcome depended on the mixed-taxa pairing chosen. A *Homo-Pan* pairing was inconsistent with the pattern of variation observed within the Dmanisi sample for all cases. A *Homo-Gorilla* pairing was also inconsistent with the Dmanisi pattern, although less strongly so. However, a *Pan-Gorilla* mixed-taxa pairing showed a greater tendency towards consistency with the Dmanisi sample than inconsistency.

Taken together, these results support the notion that the variation within the Dmanisi sample is not consistent with a mixed-taxa sample on the basis of the comparative materials available. The pairwise differences observed between the Dmanisi mandibles do not closely associate with the expected pattern of variation when individuals of two species are randomly drawn and compared. The rejection of the mixed-taxa hypothesis provides further support for the hypothesis that the Dmanisi variation reflects the presence of a single hominid taxon at Dmanisi with greater expected variation than a comparable sample of humans or chimpanzees. This conclusion is

further supported by the anatomy of the Dmanisi mandibles, which show a suite of unique features which serve to unite the sample to the exclusion of other Lower Pleistocene hominid mandibular samples. Included in these traits are a distinct *torus mandibularis*, characteristically swollen *tuberculum marginale anterius*, evenly rounded and projecting *tuber symphyseos* without any development of the *tuberculae lateralis*, and a similar pattern of *foramina*. In contrast, the traits that distinguish the Dmanisi mandibles are largely confined to only two areas, the height of the corpus and development of the posterior dentition.

The single taxon argument can also be viewed from a comparative perspective involving the maximum observable pairwise differences in the Dmanisi sample relative to the known sample of *A. boisei* from East Africa. When these comparisons are viewed it is clear that even those anatomical regions which show the greatest variation within the Dmanisi sample fit within the observed range of variation in *A. boisei*. This not only suggests that such a range of variation is not untenable in a Plio-Pleistocene hominid sample, but also support the possibility that a large degree of dimorphism is the ancestral condition for both early *Homo* and *A. boisei*.

If a mixed-taxa argument is advocated, the results presented in chapter six provide marginal support for the notion that the relationship between the taxa involved would be akin to that observed morphologically between extant chimpanzees and gorillas. Numerous studies have shown a strong allometric relationship the cranio-dental anatomy of *Pan* and *Gorilla*. However, this result could also be a reflection of a strong size differentiation between the Dmanisi specimens not related to phylogenetic differences.

Conclusions:

This research began with a single question; how can the mandibular variation from Dmanisi be best explained in a systematic, hypothesis driven manner? The results here suggest that the Dmanisi sample most likely represents the remains of a single taxon, but one displaying greater amounts of variation than extant samples of humans and chimpanzees. This conclusion is based on both qualitative and quantitative assessments of the anatomy of this sample.

Anatomically, the Dmanisi mandibles show a large amount of variation. Contained within this variation is a combination of unique, shared features and widely divergent features. All of the specimens show distinctively expressed *tori mandibularis*, *tuberculae marginale anterius*, and a similar pattern of foramina. In addition, strong similarities are present in the shape of the dental arcade, occlusal morphology of the premolars, and some aspects of the dental wear. Against this set of similarities are several dramatic differences. The morphology of the dental roots is quite divergent and is accompanied by equally divergent differences in the size of the posterior dentition, particularly M_3. Differences in corpus height (but not corpus breadth) between D2600 and the remaining specimens are also dramatic. Some aspects of the morphology, such as the symphysis, so both similarities (e.g. development of the *tuber symphyseos*) and differences (e.g. the orientation and structure of the *planum alveolare* and *tori transverse superiori*), further complicating the anatomical picture.

Quantitatively, some of the variation can be explained by the likely effects of continued growth within some of the specimens (particularly of D2735) and the possible effects of sexual dimorphism. However, for an intraspecific model to fully account for

the observed Dmanisi variation, either a model of variation on par with that observed in gorillas or an explanation for the excessive variation relative to extant human and chimpanzees is required.

A model of increased intraspecific variation:

One of the questions worth further discussion is the issue of what could be contributing to the large variation within the Dmanisi sample. One possibility, albeit a mundane one, is the difficulties associated with resampling. The methods employed within this work are designed to maximize the ability to make definitive claims regarding the variability of the sample while simultaneously recognizing the limiting effects of sample size and possible sample differentiation (e.g. age, sex). In order to accomplish this, attention was focused on the relationship of any two of the specimens, taken to be a randomly drawn pair from a larger sample, rather than any metrical assessment of the variability in the sample as a whole. Nevertheless, a sample size of four (and three in most quantitative aspects) poses certain insurmountable problems. For example, the possibility always exist that one the members of our randomly drawn fossil sample is derived from the tail of the actual distribution and thus beyond the reach of most statistical approaches. Given the Dmanisi sample contains one of the largest (D2600) and one of the smallest (D211) hominid mandibles in the Lower Pleistocene, at least with regards to certain metrical characters, the possibility even exists that the sample is simultaneously derived from both ends of a distribution! Taken in isolation, parsimony would suggest a division of these two into distinct categories on the basis of such observations. However, when the entirety of the sample is considered, parsimony

suggests that, although there are strong differences within the group, they are representatives of the same group.

The evidence in favor of this argument come from multiple sources. First, the stratigraphic context of the material suggests they most likely represent a single hominid taxa. The hominid remains from the site consist of multiple associated elements from different individuals, scattered across an area of only a few square meters, and without a gap in fossil material between the individuals. The ecology of extant great apes suggests the presence of sympatric hominid species, while possible, is unlikely. The anatomy of the mandibles also provides evidence that they are a single hominid species. They contain unique features which serve to unite them as a sample to the exclusion of other hominid samples. Finally, while the metric variation is greater than expected for a comparable sample of humans or chimpanzees (although not gorillas), the pattern of differences does not match that expected from a mixed taxa samples.

Problems of resampling strategy could also affect the comparative samples used. A second explanation for the observation of excessive variation within the Dmanisi sample relative to either humans or chimpanzees is that the comparative samples of humans and chimpanzees may not adequately represent the variation within these taxa. Specifically, the comparative samples might under represent the actual expected variation within these taxa. The distributions of values for most of the characters examined in these analyses appear to show a strongly normal distribution, suggesting this is not the case. However, for parts of the analysis which involved extensive subdivision of the total sample, such as those which sample only “adult males” and “late adolescent females”, the effects of resampling error were likely greater. Nevertheless, most of the results based on

such sub-divided analyses which yielded significant results produced values well outside the expected distribution, suggesting that even with a larger sample the results would not change dramatically. An expanded comparative sample would be nice, but would be unlikely to dramatically change the conclusions.

A more intriguing explanation for the high degree of variation is an increased level of sexual dimorphism amongst *Homo* in the Lower Pleistocene. For reasons outlined previously with regards to the difficulty of estimating levels of dimorphism in fossil samples, it would be difficult to mount such an argument solely on the mandibular sample from Dmanisi. The potential to incorporate analyses of the cranial, dental, and post-cranial remains from Dmanisi, however, discussed in greater detail below, provide some cause for optimism.

The possibility that the variation within the Dmanisi sample is the consequence of an increased level of sexual dimorphism relative to extant humans and chimpanzees is of significance for broader interpretations of early *Homo*. Increased sexual dimorphism in the Dmanisi hominids supports the notion that the ancestral condition for both early *Homo* and *A. boisei* is relatively high dimorphism. If this is true, it is of obvious importance for the interpretation of much of the early *Homo* material from East Africa for which the taxonomic and sex classification are often debated. Higher than expected levels of sexual dimorphism could suggest evolutionary models for this time period which place a greater emphasis on the importance of taxonomic differentiation are misguided. If this is true, it would also support the notion that the reduction in sexual dimorphism seen in more recent humans is the result of a gradual process, similar

perhaps to that observed in dental reduction and brain expansion during the Pleistocene, rather than a sudden transition.

Significance of Dmanisi for issues of early Homo:

One final question is the significance of these results for other issues pertaining to early *Homo*. Dmanisi provides a unique perspective on an issue classically discussed solely in the context of the African fossil record. The question of who, when, and why the earliest members of our genus, *Homo*, appeared on the evolutionary landscape has always been one of rich inquiry and ongoing controversy. The continual discovery over the past century in South and East Africa of rich fossil assemblages dated between 1.5 and 2.5 million years in age has continually pushed and reshaped ideas regarding the emergence of the genus *Homo* (Wood, 1993; Wood and Collard, 1999b; Wood and Collard, 1999a). Initial ideas of the earliest members of our genus as a transitional species between the Australopithecines and classic *Homo erectus* (Leakey *et al*., 1964; Tobias, 1965; Tobias, 1966; Tobias, 1991), always controversial, has only grown more so as the range of variation encompassed by these early fossils has grown. This is a problem not only for the taxonomy of early *Homo*, but also for an understanding of the evolutionary model which gave rise to the genus *Homo* and began the processes of brain expansion, tool use, and range dispersal which characterize Pleistocene human evolution.

While extensive fossil variation within individual early *Homo* localities has been known for many years (e.g. OH 9 and OH 12), Dmanisi provides the strongest evidence of the full range of this variation from a single, narrowly confined fossil location. As such, it provides a valuable perspective from which to understand this variation. If, as I

have suggested, the Dmanisi mandibular variation is reflective of the presence of adolescent females and an old adult male individual (and possible old adult female in D3900), it shows the full developmental range of variation and provides a sense of the expected intraspecific variation for penecontemporary fossil deposits from East and South Africa.

Dmanisi, as the earliest well dated hominid site with extensive *in situ* fossil and archaeological material outside of Africa, poses interesting questions as to when this expansion out of Africa began and which, amongst the Plio-Pleistocene hominid groups, were the first to leave. In this regard, the issues of early hominid dispersal and the transition to early *Homo* become intertwined. Is the expansion out of Africa witnessed in the terminal Pliocene-early Pleistocene the product of an ecological shift in the relationship between hominids and their environment? And if so, does this ecological shift occur simultaneously with the emergence of *Homo*, or is it a later development within the *Homo* lineage. If the former is true, it suggests either a later emergence of *Homo* (i.e. after 2 million years) or an as of yet undocumented hominid presence in Pliocene deposits outside of Africa.

This also poses questions for the uncertain group of fossils found in deposits in Africa dated between 2-2.5 MA. If the latter of these statements is true, it suggests an earlier appearance of the genus *Homo*, perhaps in accord with the earliest appearance of modified stone tools at 2.5 MA. This view leaves unanswered, however, the question of "why" regarding expansion out of Africa. As the fossil evidence stands at the moment, there are few dramatic differences in body size, brain size, or stone tool assemblages between the Dmanisi site and terminal Pliocene sites known from East Africa (Semaw *et*

al., 1997; Asfaw *et al*., 1999; de Heinzelin *et al*., 1999; Cameron, 2003). The complicated issues of biogeography, ecology, and taxonomy during this time period all become intertwined with the issue of what defines the genus *Homo* and what evolutionary forces led to its emergence (Wood and Collard, 1999). These are all questions of considerable interest that can only be answered by continual work at fossil sites such as Dmanisi and other terminal Pliocene-early Pleistocene localities outside of Africa.

Unresolved questions:

As alluded to earlier, much of the importance of the Dmanisi material is likely yet to be realized. With so much of the hominid material the product of recent and ongoing excavations, a complete understanding of the material will not be available until research on the various cranial, dental, and post-cranial remains are integrated. Already, multiple individual specimens from Dmanisi preserve multiple cranial, dental, and post-cranial elements.

The advantages of integrating analyses from multiple elements are many. Problems of sample size, while not fully alleviated, are eased when multiple elements from single individuals are present. Multiple elements from a single individual increase the accuracy of estimates of body size, sexual dimorphism, and age of individuals. This increased accuracy potentially allows for more detailed hypotheses about developmental and morphological systems.

As an example, consider the case of sexual dimorphism discussed throughout this work. The presence of adult male and female specimens, together with multiple sub-

adult specimens from the same site, presents a unique opportunity to examine questions of ontogeny, allometry, and the development of sexual dimorphism in the Lower Pleistocene hominid record. Information on these topics would also inform understandings of the evolutionary processes involved with the differentiation of early *Homo* and the evolutionary transition towards increasing brain size, body size, and dental reduction which characterize the evolution of Pleistocene *Homo*.

Another interesting question for future inquiry is the unusual dental wear of the specimens. As outlined in chapter three, the D2600 specimen displays the greatest wear gradient across the molars of any Lower Pleistocene fossil hominid (and possibly any comparable fossil hominid). Additionally, the specimen shows a distinctive set of wear complexes across the anterior and posterior dentition. On top of this, the D3900 mandible, which is affiliated with the adult D3444 cranium, preserves a completely edentulous mandibular (and maxillary) dental arcade. Nothing in the pattern of alveolar resorption, aside from the extreme level of resorption, is suggestive of any process other than normal dental attrition and loss as seen in recent human populations.

The dental wear of these two adult specimens raises many questions about the diet of the Dmanisi hominids. Unfortunately, the lack of any preserved dental enamel on either of these specimens does not allow for most methods of comparative microwear analysis (Puech *et al*., 1983; Lalueza *et al*., 1996; Lucas, 2004; Ungar, 2004; Scott *et al*., 2006; Ungar *et al*., 2006). The development of methods capable of providing information on the dental use and diet of these specimens would be of great significance.

As stated at the beginning of this work, the time period associated with the emergence of the genus *Homo* has been, and continues to be, an area of rich inquiry in

Paleoanthropology. This transition is the critical link between our Australopithecine past and a morphological and behavioral complex which characterizes Pleistocene human evolution. Our understanding of this time period will continue to evolve as we find new fossils at site such as Dmanisi, but also as our understanding of these fossils and the methods we employ to gain an understanding of them evolve as well.

APPENDIX A: Dmanisi mandibles

Figure A1.1 – D211: superior

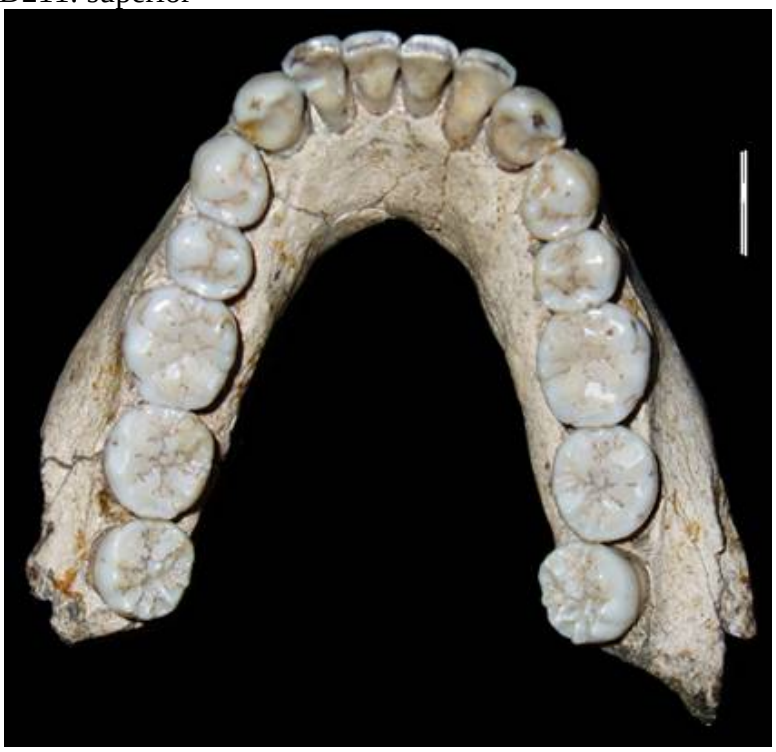


Figure A1.2 – D211: Lateral, right

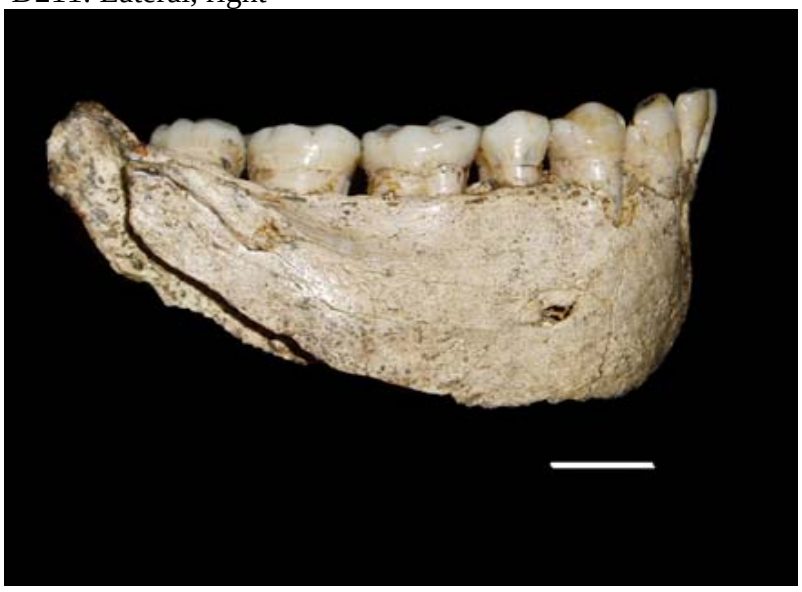


Figure A1.3 – D211: Lateral, left

Figure A1.4 – D211: Anterior

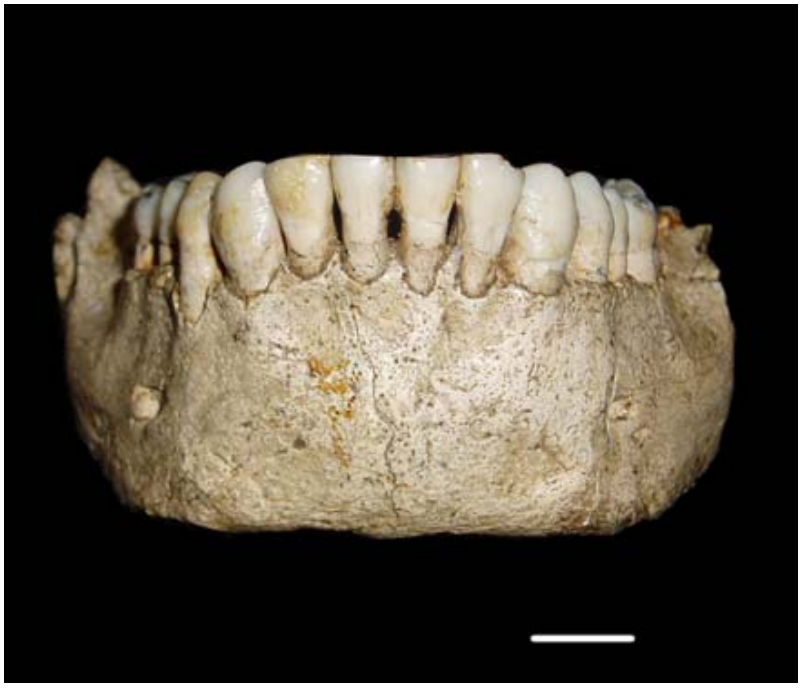


Figure A1.5 – D211: Inferior

Figure A2.1 – D2600: Superior

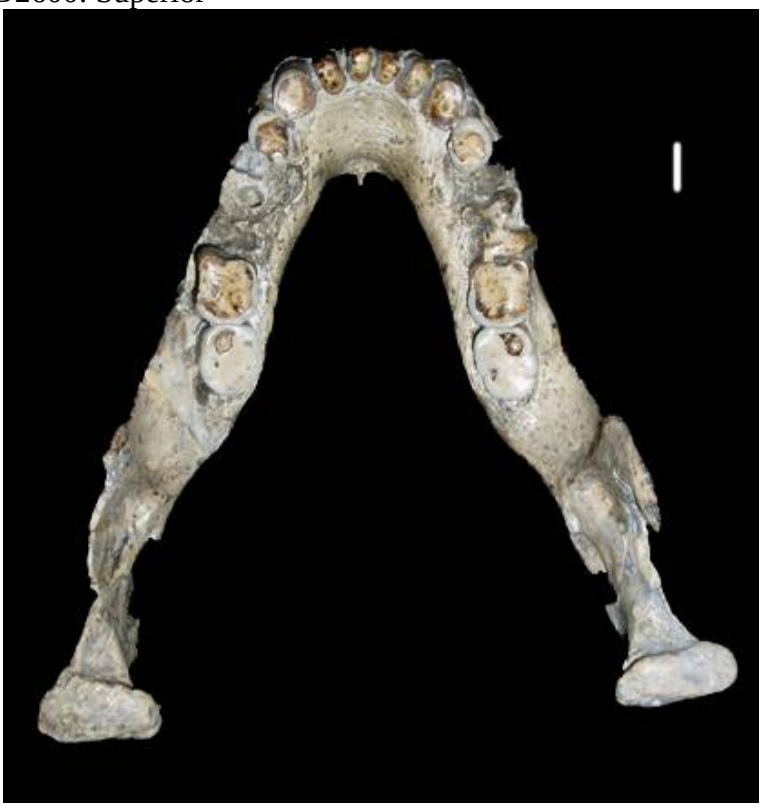


Figure A2.2 – D2600: Lateral, right

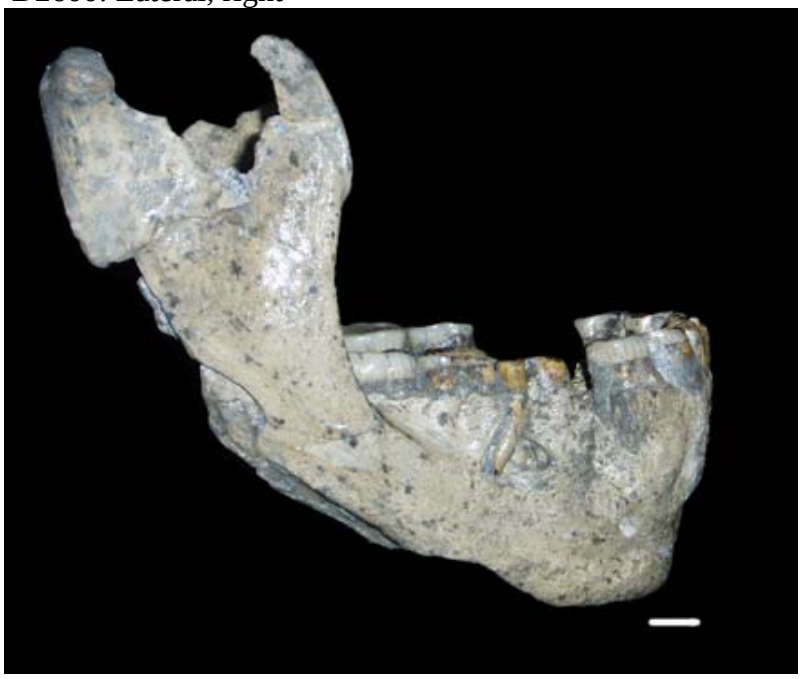


Figure A2.3 – D2600: Lateral, left

Figure A2.4 – D2600: Anterior

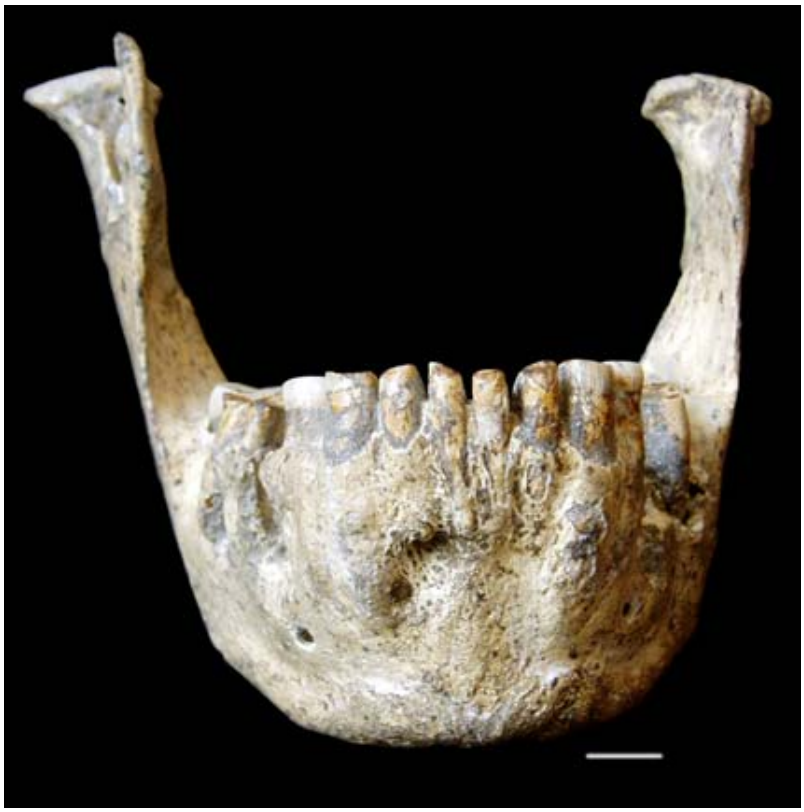


Figure A2.5 – D2600: Inferior

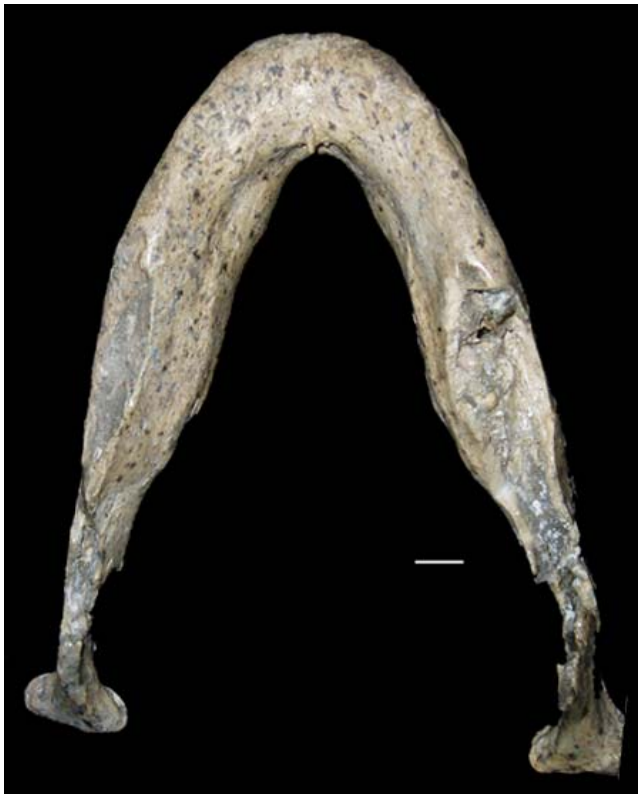


Figure A3.1 – D2735: Superior

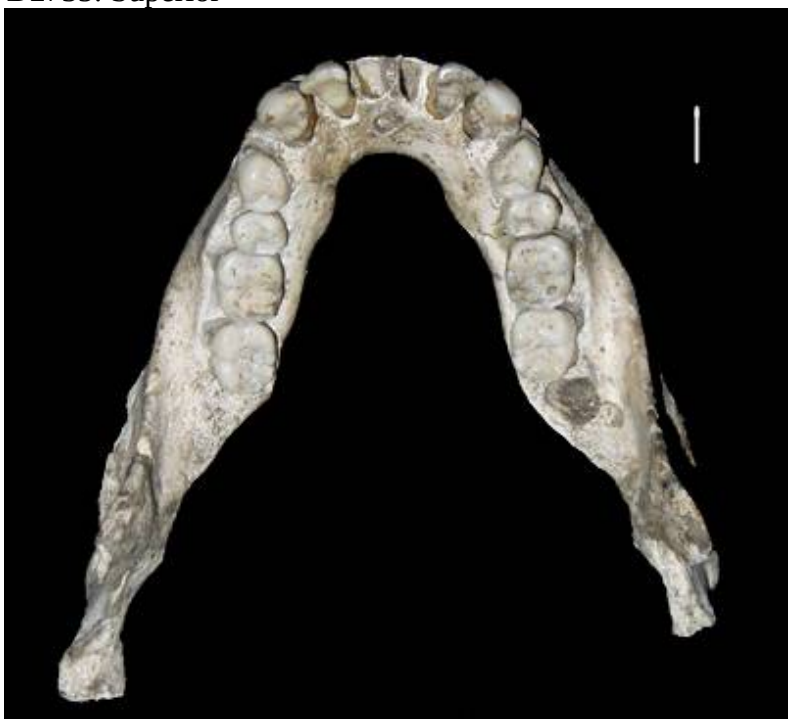


Figure A3.2 – D2735: Lateral, right

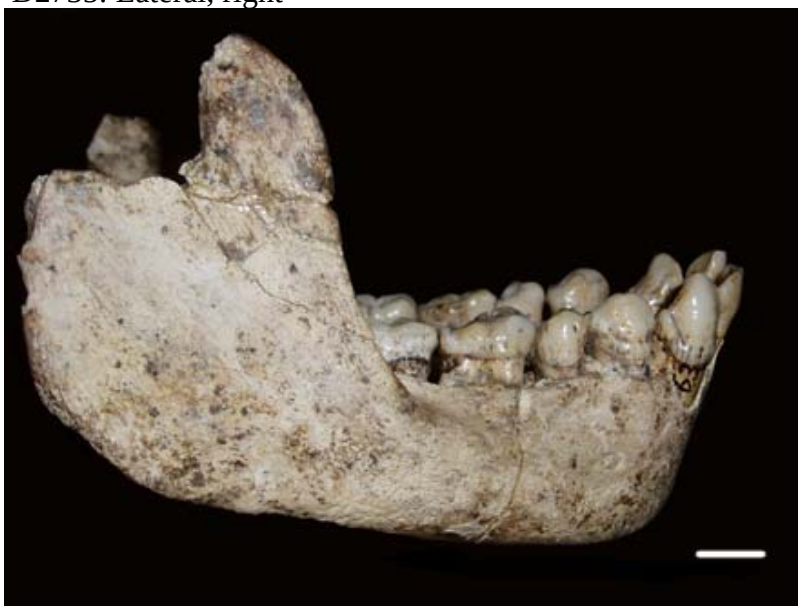


Figure A3.3 – D2735: Lateral, left (canines and incisors removed)

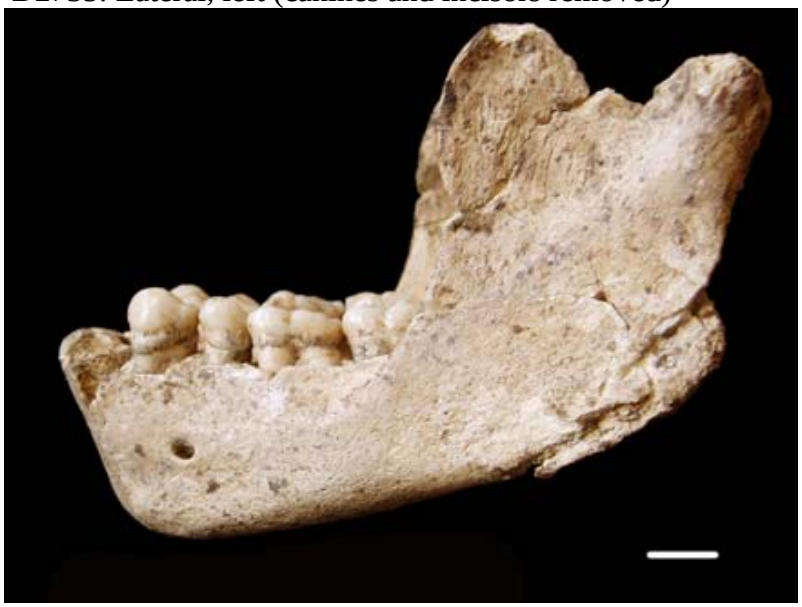


Figure A3.4 – D2735: Anterior

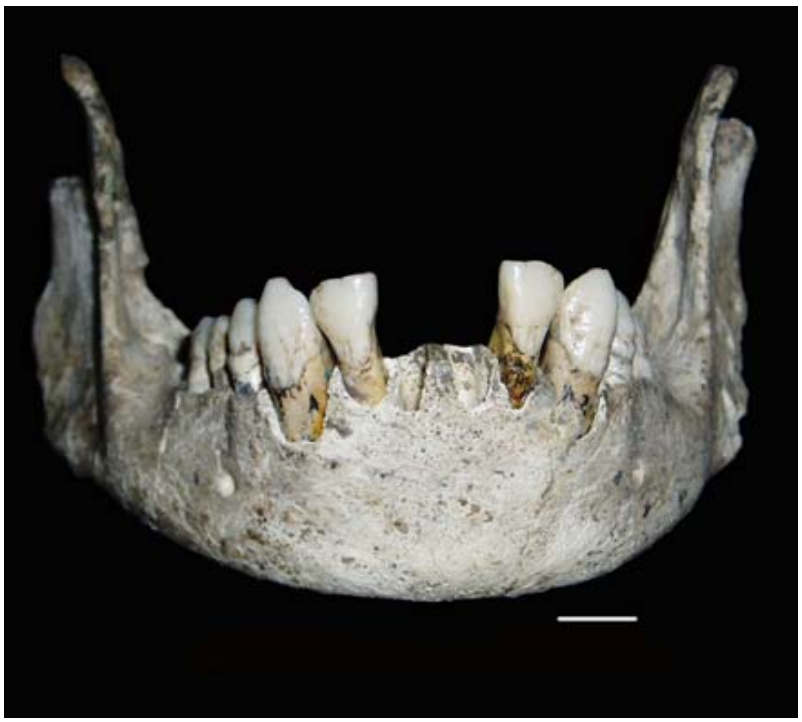


Figure A3.5 – D2735: Inferior

Figure A4.1 – D3900: Superior

Figure A4.2 – D3900: Lateral, right

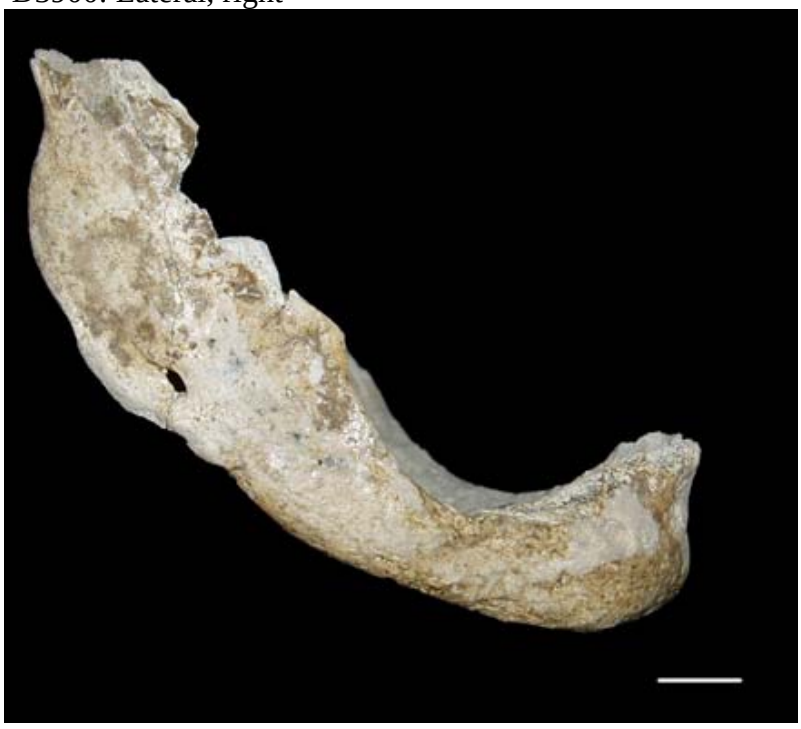


Figure A4.3 – D3900: Anterior

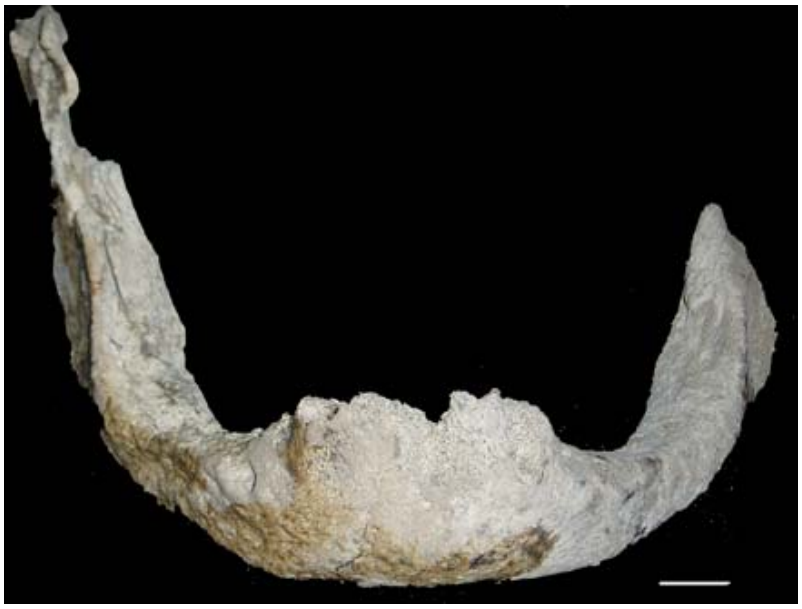


Figure A4.4 – D3900: Inferior

APPENDIX B: Dmanisi metric data

All values listed below represent the bilateral average when such a value is available and appropriate for the given measurement. If only a right-side measure (*) or left-side measure (**) is available, they are indicated by asterisks. All measurements are recorded in millimeters.

Measurement	D211	D2600	D2735
Body breadth at symphysis	17.2	22.7	16.1
Body breadth at *foramen mentale*	17.7	21.4	19.6
Body breadth at I_2	17.1	21.6	16.4
Body breadth at C	18.2	23.1	17.3
Body breadth at P_3	18.0	22.4	18.9
Body breadth at P_4	17.3	21.5	19.6
Body breadth at M_1	17.5	19.8	20.7
Body breadth at M_2	21.1	21.4	22.3
Body breadth at M_3	-	22.7	-
Body breadth at post-M_3	-	22.6	-
Body height at symphysis	31.0	50.0	34.0
Body height at *foramen mentale*	26.3	42.0	26.5
Body height at I_2	28.2	44.5	29.6
Body height at C	27.6	45.3	26.6
Body height at P_3	27.0	44.1	26.9
Body height at P_4	-	41.5*	24.7
Body height at M_1	-	41.0*	22.3
Body height at M_2	-	36.5	20.9
Body height at M_3	-	-	-
Mandibular length I_1-I_2	10.4	11.9	12.8
Mandibular length I_1-C	18.5	21.2	25.1
Mandibular length C-P_4	24.8	28.6*	29.4
Mandibular length C-M_1	38.9	43.2	43.4
Mandibular length C-M_2	51.1	56.7	55.6
Mandibular length C-M_3	61.5	71.5	-
Mandibular length P_3-P_4	16.8	19.2*	17.9
Mandibular length P_3-M_1	30.4	34.0	31.0
Mandibular length P_3-M_2	43.2	47.9	44.8
Mandibular length P_3-M_3	53.4	62.0	-
Mandibular length P_4-M_2	33.9	35.5	33.9
Mandibular length P_4-M_3	44.9	52.9	-
Mandibular length M_1-M_2	26.8	28.3*	26.4

Measurement	D211	D2600	D2735
Mandibular length M_1-M_3	37.1	44.9*	-
Mandibular length M_2-M_3	23.0	30.8	-
Infradentale to P_4-M_1	33.7	39.7*	40.3
Infradentale to post-M_3	66.9	78.4	-
Gnathion to post-M_3	65.8	83.2	-
Foramen mentale to center of base	12.8	15.8	13.1
Foramen mentale to alveolar margin	13.8	24.0	12.4
Bimental breadth	45.3	45.2	50.2
External breadth at I_1 (distal-buccal corner)	10.7	11.3	12.0
External breadth at I_2 (distal-buccal corner)	21.2	24.7	25.0
External breadth at C (distal-buccal corner)	36.1	40.6	41.2
External breadth at P_4 (distal-buccal corner)	49.0	-	52.8
External breadth at C	30.6	36.8	34.0
External breadth at P_3	42.5	48.8	49.8
External breadth at P_4	48.7	-	53.5
External breadth at M_1	56.7	-	59.2
External breadth at M_2	60.9	69.0	61.3
External breadth at M_3	60.0	70.0	-
Internal breadth at C	21.9	22.3	24.9
Internal breadth at P_3	26.4	32.3	31.3
Internal breadth at P_4	31.0	-	36.2
Internal breadth at M_1	36.3	-	37.8
Internal breadth at M_2	40.5	44.0	40.5
Internal breadth at M_3	44.1	47.1	-
Infradentale to sup. trans. torus	21.2	28.5	23.5
Infradentale to inf. trans. torus	-	44.8	33.6
Sup. trans. torus to symp. base	14.1	16.9	13.3
Planum alveolare length	17.3	24.6	17.3
Mandibular orale to *fossa genioglossi*	21.8	34.2	24.2
Depth of *fossa genioglossi*	1.4	1.3	0.6
Mandibular orale to gnathion	30.3	46.1	33.9
Biramus breadth at ramus root	77.4	85.8	81.1
Biramus breadth at alveolar margin	80.0	94.1	81.8
Max. bicondylar breadth	-	133.3	-
Posterior bicondylar breadth	-	112.0	-
Internal condylar breadth	-	86.3	-
Binotch breadth	-	107.5	89.4
Bicoronoid breadth	-	103.8	95.0
Bigonial breadth	-	-	102.8

Measurement	D211	D2600	D2735
Posterior biramus breadth at alveolar margin	-	-	106.5
Min. ramus length (A-P)	-	-	37.4
Infradentale to coronoid tip	-	114.3*	94.0*
Condylar height above occlusal plane	-	57.6	-
Condylar height above basal plane	-	82.6*	-
Coronoid height above occlusal plane	-	56.7*	36.0*
Coronoid height above basal plane	-	94.1*	59.3*
Condylar length	-	12.0	-
Condylar breadth	-	23.6	-
Mid-condyle to opposite C	-	140.4	-
Mid-condyle to opposite P_3	-	136.6	-
Mid-condyle to opposite P_4	-	133.2	-
Mid-condyle to opposite M_1	-	129.6	-
Mid-condyle to opposite M_2	-	123.7	-
Mid-condyle to opposite M_3	-	115.9	-
Mid-condyle to coronoid tip	-	34.5*	-
Gonion to gnathion	-	-	93.8
Gonion to infradentale	-	-	101.5
Infradentale to post-C (midline)	10.4	13.5	16.8
Infradentale to post-M_1 (midline)	39.6	42.3	43.4
Infradentale to post- M_2 (midline)	52.0	56.5	55.6
I_1 breadth	6.2	7.1	-
I_1 length	4.3	4.7	-
I_2 breadth	7.2	9.0	7.3
I_2 length	4.6	5.5	5.1
C breadth	8.2	10.3	9.3
C length	7.4	9.0	9.0
P_3 breadth	9.0	7.4	10.3
P_3 length	7.3	8.9	7.2
P_4 breadth	8.7	-	9.4
P_4 length	6.3	-	6.7
M_1 breadth	10.3	11.4	11.0
M_1 length	11.0	13.7	11.2
M_2 breadth	10.3	12.3	10.4
M_2 length	10.7	13.1	10.9
M_3 breadth	9.5	13.2	-
M_3 length	9.7	16.7	-

APPENDIX C: Program files for Matlab

Age and Sex resampling programs:
(used in the analyses for Chapter 5)

1) Gorilla program

```
for x=1:31;

f=1;
for i=1:54                          {this section separates female gorillas}
   if  gor_sex(i)==1                {gor_sex=array identifying males and females}
      gorf(f,1)=gorilla(i,x);       {gorilla(i,x)=matrix of gorilla trait values}
      f=f+1;
   end
end

ftwo=1;                             {the data contains missing values marked
for i=1:(f-1)                              as "-9", this section removes
   if gorf(i,1)~=-9                 those values}
      gorff(ftwo,1)=gorf(i,1);
      ftwo=ftwo+1;
   end
end

clear gorf

m=1;
for i=1:54                          {this section and the next repeat the
   if  gor_sex(i)==2                       previous two sections, but isolate
      gorm(m,1)=gorilla(i,x);              males instead of females}
      m=m+1;
   end
end

mtwo=1;
for i=1:(m-1)
   if gorm(i,1)~=-9
      gormm(mtwo,1)=gorm(i,1);
      mtwo=mtwo+1;
   end
end

clear gorm
msex=mtwo-1;                        {marks the number of males and
fsex=ftwo-1;                               females for each trait}
clear mtwo
clear ftwo
```

```
clear ic=1;
for i=1:msex                                {this section creates a distribution
   for j=1:fsex                             of all possible male/female vlaues}
      gorexdist(c)=(gormm(i)/gorff(j));
      c=c+1;
   end
end

gormean=mean(gorexdist);                    {calculates various metrics of interest}
resultsg(1,x)=gormean;
gorstd=std(gorexdist);
resultsg(2,x)=gorstd;
sexmax=(max(gormm))/(min(gorff));
resultsg(3,x)=sexmax;
sexmin=(min(chimm))/(max(gorff));
resultsg(4,x)=sexmin;
msex;
resultsg(5,x)=msex;
fsex;
resultsg(6,x)=fsex;

randsextest1=0;                     {this section conducts the resampling by sex test}
randsextest2=0;
for i=1:10000
malerand=randperm(msex);
femrand=randperm(fsex);
   if ((Dman(2,x))/(Dman(1,x)))>(chimm(malerand(1))/(chiff(femrand(1))))
      randsextest1=randsextest1+1;
   else
      randsextest1=randsextest1;
   end
   if ((Dman(2,x))/(Dman(3,x)))>(chimm(malerand(2))/(chiff(femrand(2))))
      randsextest2=randsextest2+1;
   else
      randsextest2=randsextest2;
   end
end
randsextest1;
resultsg(7,x)=randsextest1;
randsextest2;
resultsg(8,x)=randsextest2;

clear randsextest1 randsextest2
clear c
clear gormm
clear gorff

y=1;                                        {the following sections repeat the above
for i=1:54                                        procedures, but sample randomly on
   if  gor_cage(i)==2                             the basis of age categories, rather
      gory(y,1)=gorilla(i,x);                     than sex}
      y=y+1;
   end
end

ytwo=1;
```

```
for i=1:(y-1)
   if gory(i,1)~=-9
      goryb(ytwo,1)=gory(i,1);
      ytwo=ytwo+1;
   end
end

clear gory

a=1;
for i=1:54
   if  gor_cage(i)>2
      gora(a,1)=gorilla(i,x);
      a=a+1;
   end
end

atwo=1;
for i=1:(a-1)
   if gora(i,1)~=-9
      gorab(atwo,1)=gora(i,1);
      atwo=atwo+1;
   end
end

clear gora
y=ytwo-1;
a=atwo-1;
clear ytwo
clear atwo
clear i

c=1;
for i=1:a
   for j=1:y
      gorexage(c)=(gorab(i)/goryb(j));
      c=c+1;
   end
end

gormean=mean(gorexage);
resultsg(9,x)=gormean;
gorstd=std(gorexage);
resultsg(10,x)=gorstd;
maxage=(max(gorab))/(min(goryb));
resultsg(11,x)=maxage;
minage=(min(chiab))/(max(goryb));
resultsg(12,x)=minage;
y;
resultsg(13,x)=y;
a;
resultsg(14,x)=a;

randagetest1=0;
randagetest2=0;
for i=1:10000
```

```
yrand=randperm(y);
arand=randperm(a);
   if ((Dman(2,x))/(Dman(1,x)))>(gorab(arand(1))/(goryb(yrand(1))))
      randagetest1=randagetest1+1;
   else
      randagetest1=randagetest1;
   end
   if ((Dman(2,x))/(Dman(3,x)))>(gorab(arand(2))/(goryb(yrand(2))))
      randagetest2=randagetest2+1;
   else
      randagetest2=randagetest2;
   end
end
randagetest1;
resultsg(15,x)=randagetest1;
randagetest2;
resultsg(16,x)=randagetest2;

clear randagetest1 randagetest2
clear y a i
clear gorab
clear goryb

yf=1;                                          {this final set of sections again repeats
for i=1:54                                            the resampling procedure, but now
   if  gor_cage(i)==2 & gor_sex(i)==1                 combining both age and sex}
      goryf(yf,1)=gorilla(i,x);
      yf=yf+1;
   end
end

ytwo=1;
for i=1:(yf-1)
   if goryf(i,1)~=-9
      goryofe(ytwo,1)=goryf(i,1);
      ytwo=ytwo+1;
   end
end

clear goryf
yf=ytwo-1;
resultsg(17,x)=yf;

am=1;
for i=1:54
   if  gor_cage(i)>2 & gor_sex(i)==2
      goram(am,1)=gorilla(i,x);
      am=am+1;
   end
end

atwo=1;
for i=1:(am-1)
   if goram(i,1)~=-9
      goradma(atwo,1)=goram(i,1);
      atwo=atwo+1;
```

```
   end
end

clear gora
am=atwo-1;
resultsg(18,x)=am;

maxagesex=(max(goradma))/(min(goryofe));
resultsg(19,x)=maxagesex;
minagesex=(min(goradma))/(max(goryofe));
resultsg(20,x)=minagesex;

randagesextest1=0;
randagesextest2=0;
for i=1:10000
yrand=randperm(yf);
arand=randperm(am);
   if ((Dman(2,x))/(Dman(1,x)))>(goradma(arand(1))/(goryofe(yrand(1))))
      randagesextest1=randagesextest1+1;
   else
      randagesextest1=randagesextest1;
   end
   if ((Dman(2,x))/(Dman(3,x)))>(goradma(arand(2))/(goryofe(yrand(2))))
      randagesextest2=randagesextest2+1;
   else
      randagesextest2=randagesextest2;
   end
end
randagesextest1;
resultsg(21,x)=randagesextest1;
randagesextest2;
resultsg(22,x)=randagesextest2;

clear randagesextest1 randagesextest2
clear yf am i
clear goradma
clear goryofe

end

save results resultsg -ascii -tabs  {exports the file in tabular format}
```

Identical programs were used for the chimpanzee and human samples, substituting the appropriate identifying variables for each group.

Nested reresampling programs:
(used for the analyses in Chapter 6)

1) Gorilla and Chimp mixed-taxa pair program

```
y=0;
for z=1:1000
   gorrand=randperm(54);          {random arrays are generated of equal size as the gorilla
   chirand=randperm(61);                  and chimp samples}
   for r=1:54;
      if min(gor_tot((gorrand(r)),:))~=-9          {the randomly chosen gorilla must have all of
         testsamp(1,:)=(gor_tot((gorrand(r)),:));          the available measures, no "-9"s}
         pick1=gorrand(r);                         {testsamp becomes the test pair}
         break
      end
   end

   x=1;                                          {the remainder of the gorilla sample is isolated}
   for r=1:54
      if r~=pick1
         gorother(x,:)=gor_tot(gorrand(r),:);
         x=x+1;
      end
   end

   for r=1:61;                                   {the process is repeated for the chimp sample}
      if min(chi_tot((chirand(r)),:))~=-9
         testsamp(2,:)=(chi_tot((chirand(r)),:));
         pick2=chirand(r);
         break
      end
   end

   for x=1:31;
   f=1;
   for i=1:53
      if  gorother(i,x)~=-9
         gorf(f)=gorother(i,x);
         f=f+1;
      end
   end

   msex=f-1;

   randsextest1=0;                               {the resampling test is conducted, in this case
   for i=1:10000                                        against a gorilla model}
   malerand=randperm(msex);
      if ((testsamp(2,x))/(testsamp(1,x)))>(gorf(malerand(1))/(gorf(malerand(2))))
         randsextest1=randsextest1+1;
      else
         randsextest1=randsextest1;
      end
   end

   if randsextest1>9500 | randsextest1<500
```

```
   testoutg(z,x)=1;
else
   testoutg(z,x)=0;
end

difftallyg(z)=sum(testoutg(z,:));

clear randsextest1 malerand
clear c x f r i
clear chif
clear msex

end

clear pick1 pick2

gorrand=randperm(54);
chirand=randperm(61);

for r=1:54;                                          {the entire process is repeated against a chimpanzee
   if min(gor_tot((gorrand(r)),:))~=-9                     model of variation}
      testsamp(1,:)=(gor_tot((gorrand(r)),:));
      pick1=gorrand(r);
      break
   end
end

for r=1:61;
   if min(chi_tot((chirand(r)),:))~=-9
      testsamp(2,:)=(chi_tot((chirand(r)),:));
      pick2=chirand(r);
      break
   end
end
x=1;
for r=1:61;
   if r~=pick2
      chiother(x,:)=chi_tot(chirand(r),:);
      x=x+1;
   end
end

for x=1:31;

f=1;
for i=1:60
   if  chiother(i,x)~=-9
      chif(f)=chiother(i,x);
      f=f+1;
   end
end

msex=f-1;

randsextest1=0;
for i=1:10000
```

```
malerand=randperm(msex);
   if ((testsamp(2,x))/(testsamp(1,x)))>(chif(malerand(1))/(chif(malerand(2))))
      randsextest1=randsextest1+1;
   else
      randsextest1=randsextest1;
   end
end

if randsextest1>9500 | randsextest1<500
   testoutc(z,x)=1;
else
   testoutc(z,x)=0;
end

difftallyc(z)=sum(testoutc(z,:));

clear randsextest1 malerand
clear c x f r i
clear chif
clear msex

end

clear pick1 pick2
gorrand=randperm(54);
chirand=randperm(61);

for r=1:54;                                    {finally, the process is repeated a third time for a
   if min(gor_tot((gorrand(r)),:))~=-9                human comparative model}
      testsamp(1,:)=(gor_tot((gorrand(r)),:));
      pick1=gorrand(r);
      break
   end
end

for r=1:61;
   if min(chi_tot((chirand(r)),:))~=-9
      testsamp(2,:)=(chi_tot((chirand(r)),:));
      pick2=chirand(r);
      break
   end
end

for x=1:31;

f=1;
for i=1:90
   if  lib_tot(i,x)~=-9
      humf(f)=lib_tot(i,x);
      f=f+1;
   end
end

msex=f-1;

randsextest1=0;
```

```
   for i=1:10000
   malerand=randperm(msex);
      if ((humsamp(2,x))/(humsamp(1,x)))>(humf(malerand(1))/(humf(malerand(2))))
         randsextest1=randsextest1+1;
      else
         randsextest1=randsextest1;
      end
   end

   if randsextest1>9500 | randsextest1<500
      testouth(z,x)=1;
   else
      testouth(z,x)=0;
   end

   difftallyh(z)=sum(testouth(z,:));

   clear randsextest1 malerand
   clear c x f r i
   clear chif
   clear msex

   end

   clear pick1 pick2

y=y+1
end

for i=1:31
   traittallyh(i)=sum(testouth(:,i));
   traittallyg(i)=sum(testoutg(:,i));
   traittallyc(i)=sum(testoutc(:,i));
end

clear i z
```

This entire program is repeated for the other two possible mixed-taxa pairings, human-chimpanzee and human-gorilla.

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