ASSESSING PHENOTYPIC VARIATION AND ECOLOGICAL VERSATILITY IN SELECTED CATARRHINE PRIMATES

by

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DISSERTATION ABSTRACT

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Generalist and specialist species can be broadly distinguished by their ecological tendencies to utilize many available resources, or a selected few. Those organisms with more ecological versatility may have an advantage in the face of environmental fluctuation or rapid ecological change (Turley and Frost 2018; Antón, Potts, and Aiello 2014; Kuzawa and Bragg 2012; Davidson, Jennions, and Nicotra 2011; Ash and Gallop 2007). Developmental plasticity may provide a mechanism for fluctuating environmental pressures to impart increased phenotypic variation to an adult population (Antón et al 2016; West-Eberhard 2003). The aim of this dissertation is to evaluate whether more ecologically versatile species will exhibit greater phenotypic variation.

Eighty-one skeletal traits were analyzed across cranial, dental, and postcranial anatomic regions, using a total sample of 4084 individuals in six selected catarrhine primate species. To do this, I reported measures of variation for each skeletal trait (sample variation, standard deviation, and the coefficient of variation), assessed variation using principal components analyses, and ultimately tested for significant differences between taxa using general linearized models.

The main hypothesis of this dissertation, that ecological versatility positively correlates with phenotypic variation, was not supported among the majority of skeletal features examined. Where significant results did occur, such as cranial differences between male Pan troglodytes and Homo sapiens (Chapter One), where Homo sapiens displayed more variation, or long bone length differences in Papio and Theropithecus (Chapter Two), where P. hamadryas displayed more variation, the patterns were subtle and sometimes contradictory. Chapter Three results indicate that sample sizes required for accurately detecting patterns of phenotypic variation range from 30-52 individuals for molar areas, 10-16 individuals for femoral lengths. These sample sizes are substantially larger than those offered by Antón, Potts, and Aiello (2014), indicating that the ability to detect increased intra-taxon variation within more ecologically versatile species may be beyond currently available hominin fossil sample sizes. Future investigations should focus on traits which are developmentally plastic, such as long bone lengths, as informative for understanding the adaptive relationship between ecological versatility and phenotypic variation.

A complete list of specimens used in this study is available in Supplemental Files.

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This dissertation is dedicated to my mom, the original Dr. Eller.
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TABLE OF CONTENTS

Chapter Page

SUPPLEMENTAL FILES

CHAPTER I: INTRODUCTION, ECOLOGICAL VERSATILITY AND PHENOTYPIC VARIATION

Ecological versatility and related concepts (including terms such as generalism, heterotrophy, eurytopism, or adaptability) have been in common use across the life sciences since at least the latter half of the 20th century, when scholars published theoretical prospectuses on niche evolution (Levins, 1968), variation in mammals (Yablokov 1974), shifting balance theory (Wright 1982), and mammalian habitat theory (Vrba 1992). Mostly, ecological versatility refers to an organism having an ability to take advantage of a wide variety of environmental opportunities, perhaps even thriving in fluctuating ecologies (Bell 2010; Devictor, Julliard, and Jiguet 2008; Levins 1968). Generalist and specialist species refer to a broad definition of how organisms navigate their ecologies, whether by taking advantage of a large variety of available resources or by homing in on a selected few (Krebs and Davies 1993). Some studies suggest that ecological versatility, including diverse diets and habitat occupation, is correlated with an increased population-level phenotypic variation (Davidson, Jennions, and Nicotra 2011; Kussell and Leiber 2005; Lande and Shannon 1996; Yablokov 1974). Some assert that versatility as a trait has selective advantage, particularly in highly unpredictable or fluctuating environments (Lande 2014; Grove 2011; Potts 1998a; Lachmann and Jablonka 1996).

The variability selection hypothesis (VSH) has been offered as an integrated perspective on the evolutionary effects of changing landscapes and climates on populations of early *Homo* in eastern Africa around 2 million years ago (Antón *et al* 2016; Potts and Faith 2015; Antón, Potts, and Aiello 2014; Potts 2013, 2012, 2002, 1998a,b). The VSH asserts that early Homo populations may have had a selective advantage to surviving fluctuating environments, relative to contemporaneous australopiths (Potts 2013, 2012, 1998a). The hypothesis directly relates diverse habitats, phenotypic variation, and adaptive advantage in human evolution, and has been used to study such processes as social learning (Borg and Channon 2012), genetic inheritance modelling (Grove 2011), and ecological refugia use (Stewart and Stringer 2012). Another directly testable prediction of VSH (see Antón, Potts, and Aiello 2014), provided adequate samples, is that a more ecologically versatile primate species may display more phenotypic variation than less ecologically versatile species.

This dissertation reflects my interests in the adaptive significance of generalism; the hypothesis that humans, some primates, and other mammals may have convergently evolved ecologically versatile lifeways in response to a fluctuating environment. My theoretical perspective focuses on the role of environmental factors, and those effects on the skeletal phenotype. Specifically, I investigate anatomical signatures of ecological versatility, including an increase in phenotypic variation among putatively versatilist catarrhine primate species. Further I assess the likelihood of detecting these signatures in the hominin fossil record, as has been previously proposed (Antón, Potts, and Aiello 2014).

Catarrhine primates are an ideal group within which to evaluate these hypotheses, given the ecological variation across old world monkeys and apes, and existing hypotheses on the role of ecological versatility in human evolution. Primate study species

(*Homo sapiens*, *Pan troglodytes*, *Papio hamadryas*, *Theropithecus gelada*, *Macaca fascicularis*, and *Macaca nemestrina*) are analyzed as pairs, where one member of each pair is less ecological versatile than the other. **Table 1** summarizes their ecological profiles, where putative versatilist species are highlighted in gray.

In Chapter One, I evaluate phenotypic variation in 28 traits of the cranium and dentition across six catarrhine species. Craniodental materials are commonly found in fossil assemblages, yet cranial bones are known to be more variable across study taxa than dentition. Skeletal traits are linear measures of the cranium and molars; these were analyzed as two anatomic regions (cranial, dental) among a total sample of 4042 individuals. Statistical analyses include direct comparisons on measures of variance (sample variance, standard deviation, and coefficient of variation), principal components analysis, and generalized linear models to determine the magnitude of difference in variation between species pairs.

In Chapter Two, I evaluate standing phenotypic variation in measures of the limb long bones to determine if more ecologically versatile primates display increased postcranial variation. Postcranial materials are less common and more difficult to associate with known individuals in the fossil record; yet, postcranial elements are more likely to vary across study taxa than does craniodental material due to the duration and quality of long bone growth. I include 53 linear measures of the humerus, radius, femur and tibia within six sampled catarrhine species (n=113). Assessment includes reporting measures of variance, and visualizing variation with principal components analyses. Significant difference between study pairs were analyzed using generalized linear models.

In Chapter Three, I use extant skeletal material, craniodental and postcranial, in hominoids *Pan troglodytes* and *Homo sapiens* to evaluate the sample sizes necessary to observe the increased phenotypic variation among more ecologically versatile species predicted by variability selection. Using the framework of VSH, Antón, Potts, and Aiello (2014) report the variation in several morphological features to argue that early *Homo spp.* tend to be more variable than australopith species. One potential concern with their analysis is that available early hominin sample sizes are limited. I evaluate the sample sizes necessary to test for differences in variance between populations using the several of the anatomic characters of Antón, Potts, and Aiello (2014; see Table 1) where I have equivalent skeletal data.

Across these studies, factors which affect measures of variation (such as sexual dimorphism, body size, sample size, measurement type) and obscure relevant biological comparisons are examined and discussed. These potential confounding factors are important considerations when attempting to reliably and accurately detect significant sample variance differences between distinct populations. This dissertation contributes original data and analyses for understanding the ways in which population variation can, under proper conditions, reveal patterns of adaptive significance among catarrhines.

CHAPTER II:

CRANIODENTAL VARIATION AND ECOLOGICAL VERSATILITY IN SELECTED CATARRHINE PRIMATES

Introduction

Concepts of ecological versatility (including terms such as generalism, heterotrophy, eurytopism, or adaptability) have been in common use across the life sciences since at least the latter half of the 20th century, when scholars published theoretical prospectuses on these concepts including niche evolution (Levins, 1968), variation in mammals (Yablokov 1974), shifting balance theory (Wright 1982), and mammalian habitat theory (Vrba 1992). More recent work using similar concepts has largely focused on evolutionary consequences of a fluctuating environment, i.e. how survival in a variable environment may be correlated with increased behavioral, genetic, or morphological diversity (Lande 2014; Kussell and Leiber 2005; Lachmann and Jablonka 1996; Lande and Shannon 1996).

Although often used heuristically, ecological versatility and related terms mostly refer to an organism having an ability to take advantage of a wide variety of environmental opportunities, perhaps even thriving in fluctuating ecologies (Devictor, Julliard, and Jiguet 2008; Kussell and Leiber 2005; Levins 1968). The ecological tendency of some organisms to ‘specialize’ in a few resources (such as food type, or habitat) when others have a more ‘generalized’ approach has been observed for decades

(Krebs and Davies 1993). This concept has been used to refer to a variety of organisms including temperature range tolerances in ocean life (Kolbert 2016), to some particularly hardy species of rats, birds, grasses, monkeys, and humans (Sullivan 2004, rats; Morante-Filho, Arroyo-Rodríguez, and Faria 2016, birds; Davidson, Jennions, and Nicotra 2011, grass; Richard, Goldstein, and Dewar 1989, macaques; Potts 1998b, humans). Thus, ecological specialists should benefit from environments that tend to be more stable and homogeneous through time and space, while ecological versatilists should benefit in heterogeneous environments (Devictor, Julliard, and Jiguet 2008; Östergård and Ehrlén 2005; Marvier, Kareiva, and Neubert 2004.; Kassen 2002; Futuyma and Moreno 1988).

Yet, the ambiguity of the terms, and the diverse organisms to which they are applied, makes operationalizing ecological versatility a difficult task. Some researchers use this concept largely to mean behavioral changes in response to environmental change; for example, Borg and Channon's (2012) study of increased social learning in variable environments, or Richard, Goldstein and Dewar's (1989) weed macaques concept used to challenge phylogeny in deference to behavioral ecology types. Others are documenting physiological changes; for example, Stoessel, Kilbourne, and Fischer (2013) report on increased morphological variation across 236 bird species by ecology type, or see Davidson, Jennions, and Nicotra's (2011) study of adaptational plant morphology and developmental plasticity. These are not mutually exclusive. It is useful to think of both behavioral adaptability (sociobehavioral traits involved in diverse food acquisition and habitat occupation), and phenotypic plasticity (the ability or tendency of an organism to alter its phenotype either temporarily or permanently relative to its environment) as equal and intersecting aspects of ecological versatility (Jablonka and Lamb 2014; Pigliucci and Müller 2010).

Extant nonhuman primates reflect a range of ecological versatility and provide an opportunity to examine the relationship between ecological versatility and phenotypic variation in our close relatives. Most modern species of arboreal primates travel in groups which are restricted to increasingly fractured forest ranges, with limited or seasonally available food sources (IUCN 2018; Mittermier 1988). Indeed, almost 70% of modern primates are threatened with extinction in the wild, or worse (IUCN, 2018). Only a few species have widespread populations, occur in both arboreal and terrestrial environments, and are able to supplement wild foods with human-cultivated, human-manufactured, and/or provisioned food sources (IUCN 2018; Rowe and Myers 2016). Those primate species which exhibit more ecological versatility may also exhibit increased phenotypic variation. Here, ecological versatility is defined as a suite of features including: dietary diversity, widespread habitat occupation, and social complexity usually in large groups; a less ecologically versatile primate would tend to have a restricted habitat, a limited dietary breadth, and smaller group sizes (concept derived from Potts' versatilist traits, see Potts 1998a).

Using three pairs of catarrhine species (*Homo sapiens* and *Pan troglodytes*, *Papio hamadryas* and *Theropithecus gelada*, *Macaca fascicularis* and *Macaca nemestrina*), I compare a more ecologically versatile species with a closely related species who is less ecologically versatile. Using sixteen measurements of the cranium, and twelve measurements of the molars, phenotypic variation between taxa is evaluated to determine if increased craniodental variation is positively correlated to ecological versatility.

Background

Measuring Variation

Standing phenotypic variation in a population is the total amount of variation in metric characteristics of the adult phenotype, such as a range of tail lengths or hindlimb widths. The amount of standing variation within a population is determined by a number of factors, including genetic variation and nutritional status (Yablokov 1974). In rapidly changing environments, or where a single breeding population's range covers a diverse array of habitats, there may be a selective advantage to maintaining polytypic traits (Grove 2014; Potts 2012; Davidson, Jennions, and Nicotra 2011; Levins 1968). Populations with more polytypic traits, more standing population variation, or both, may be able to buffer individuals from the oscillating pressures of an unpredictable or highly variable environment (Kuzawa and Bragg 2012; Potts 1998a; Levins 1968). In other words, more phenotypic variation can be the result of and the defense against a fluctuating environment.

In order to assess the hypothesized correlation of an increase in phenotypic variation relative to an increase in ecological versatility, it's important to distinguish between similar terms used here: *variation*, *variability* (or *variable*), and *variance*, as each reflect an aspect of understanding differences within a population. *Variation* is the range of qualitative or quantitative diversity displayed by a population, and this term is usually applied to a specific trait or suite of traits (*e.g.*, Davidson, Jennions, and Nicotra 2011; Yablokov 1974; Simpson, Roe, and Lewontin 1960). Variation is best understood here as a specific amount of differences within a population at a given time. *Variance* is a statistical property, measuring the amount of variation in the population (Sokal and Rohlf

1995; Simpson, Roe, and Lewontin 1960). *Variability* can be defined as the presence of differences among individuals within a breeding population (Yablokov 1974; Simpson, 1944). Variability, and the related adjective *variable*, describes a potential to vary, or the characteristic of being capable of change. Rates of inter-population variability can be compared across differing populations, using equivalent traits, to reveal informative populational characteristics (Yablokov 1974, pg. 262). Of interest in this study is the amount of phenotypic variation which can be detected (using measures of statistical variance) across sampled species. Further, phenotypic variation is focused on dimensions of size, and not necessarily shape.

Defining the Skeletal Phenotype

Here, assessments of phenotypic variation are focused on craniodental materials for two central reasons. First, extant craniodental materials are relevant to hypotheses on primate ecological versatility which are derived in part from hominin craniodental fossil evidence (Antón, Potts, and Aiello 2014). Second, although there may be utility in describing "phenotypic variation" in the abstract sense for theoretical argument, operationalization of this term requires consideration of the inherent variability of any given aspect of the phenotype. Utilizing both cranial and dental material allows for exploration of varying aspects of the phenotype.

Although craniodental materials are sometimes analyzed together, we should expect the sociobehavioral aspects of ecological versatility (diversity among dietary and habitat acquisition) to impact aspects of the phenotype differently based on factors such as tissue type and developmental variability. For example, the intermembranous developed bones of the cranium react differently to environmental pressures than do fully occluded molar crowns (White and Folkens 2011; Irish and Scott 2015). Erupted permanent dentition doesn't remodel; therefore, dentition should be less influenced by ontogenetic plasticity than the cranial measures (Irish and Scott 2015; Aiello and Wood 1994). A versatilist trait, like dietary diversity, where foods of differing hardness are consumed may impact the growing cranium (and thus adult cranial shape/size) due to a breadth of regular mastication forces but may not significantly change adult molar size. Thus, we should expect that molar crown variation (a trait under investigation here) is more likely to reflect standing genetic diversity alone, while cranial size variation is more likely to reflect both standing genetic variation and variation derived from the environment, i.e., developmental (phenotypic) plasticity. Additionally, measures of molar occlusal surfaces should produce less variation in catarrhine primates than cranial measures do, because of the relative anatomical conservation of molars across catarrhines and between the sexes (Delson *et al* 2000; Delson and Szalay 1980).

Sampled Catarrhine Primates

Modern primates reflect a range of ecological versatility. Some extant primates have widespread populations, occurring in multiple environments, while most species of primates are restricted to smaller ranges and specialized habitats (Rowe and Myers 2016; Groves 2011). We can recognize extant species with versatilist traits by their large and varied spatial distributions, broad dietary habits, and flexible socio-ecological patterns. The species pairs under study here are *Homo sapiens* and *Pan troglodytes*, where *H. sapiens* is the more ecologically versatile species; *Papio hamadryas* and *Theropithecus gelada*, where *P. hamadryas* is the more ecologically versatile species; as well as, *Macaca fascicularis* and *Macaca nemestrina*, where *M. fascicularis* is the more ecologically versatile species; **Table 1** summarizes their ecological profiles, where putative versatilist species are highlighted in gray.

Ecological versatility in study species is determined by three main factors: size of geographic distribution, level of habitat diversity, and level of dietary diversity. Geographic distribution size, the area in which the species occurs, is considered "large" if the range spans a single continent or more, "small" if restricted to a single locale. Habitat diversity, the extent to which the species occupies heterogenous environments, is considered "high" if the species is known to occupy at least three distinct ecologies and "low" if the species occurs in a single ecology type. Dietary diversity, a general scale of dietary breadth, considers omnivores as regular consumers of grains, fruits, and meats to be "high" in diversity; heavy preference for any one food type is considered "low" dietary diversity.

Table 1: ***Ecological Summaries of Selected Catarrhines***[1]

	Geographic Distribution	*Habitat Diversity*	*Dietary Diversity*
Homo sapiens	Large	High	High
Pan troglodytes	Med-Small	Medium	Medium
Papio hamadryas	Large	High	High
Theropithecus gelada	Small	Low	Low
Macaca fascicularis	Large	High	High
Macaca nemestrina	Medium	Low	Medium

[1] Geographic distribution from Rowe and Myers 2016, IUCN 2018; Habitat diversity from Rowe and Myers 2016, Wilson and Reeder 2005; Dietary diversity from Rowe and Myers 2016.

Here, all three putative versatilists occupy at least a million square miles continuously: Humans occupy every temperate continent on the planet, *Papio hamadryas* (sensu lato) occupies a broad swath of Africa, and *Macaca fascicularis* occurs across much of southeast Asia, continuing into mainland China to the north (Rowe and Myers 2016, IUCN 2018). *Theropithecus gelada* and *Macaca nemestrina* considered “low” in habitat diversity because they are restricted to a single ecology type, the grasslands and the rainforest, respectively (Wilson and Reeder 2005). *Pan troglodytes* occupies a relatively small geographic ranges in central and western Africa, and there are populations in both forest and savannah habitats (Rowe and Myers 2016).

Study pairs were assigned for comparability in phylogeny and body size, in addition to ecological profiles. Species were matched as pairs on phylogeny as closely as possible to reduce non-relevant information from phenotypic shape and genetic distinctions. Matching pairs as closely as possible for body size also reduces non-relevant variation from the comparisons, because absolute size is related to total variation (Yablokov 1974; Simpson, Roe, and Lewontin 1960). These six species were also chosen because of their relative availability in museum collections, availability of published data relevant to this project, and extensive ecological descriptions in the literature.

Materials and Methods

Craniodental Samples

To determine if more ecologically versatile species are more phenotypically variable, craniodental skeletal measurements were obtained among six catarrhine species. The total sample size is 4042 individuals, with 3531 individuals contributing cranial data, 675 individuals contributing dental data, and 164 individuals contributing both; see **Table 2** for sample information. All specimen source information is available in **Appendix A: Specimen Source List**; this appendix includes all specimens used throughout this dissertation.

Twenty-eight linear measures were derived from the cranium and molars; see **Appendix B: Craniodental Measurement Protocol** for the complete measurement list and description. This protocol was specifically created to ensure comparability across studies, maximizing the utility of newly created data and the existing reliability of traditional methods. Each measurement is cross-referenced with previously utilized skeletal measurement protocols to ensure comparability to previous work (*esp.* Frost *et al* 2003; Aiello and Wood 1994; Howells 1973). To ensure meaningful biological comparability across taxa, only standard anatomic landmarks and homologous molar measures are used. With few exceptions where no alternatives were possible, sample specimens were originally collected from the wild with geographic origin and subspecies designations documented.

Table 2: ***Sample specimens, by taxon***

Taxon	***Cranial***	***Dental***
Homo sapiens	2524	42
Pan troglodytes	193	86
Papio hamadryas	511	380
Theropithecus	42	57
Macaca	243	61
Macaca	18	49
Total	**3531**	**675**

Sixteen cranial distance measures encompass aspects of the neurocranium, splanchnocranium, and basicranium. All measures are based on standard anatomical landmarks, and therefore the measures are homologous across study species. Cranial data is obtained from previously collected and/or published data; individual data collectors are listed in **Appendix A**. Cranial data were obtained from public datasets including PRIMO, Morphosource, and Howells' cranial measurements (1973). Other specimens were provided by individual researchers with permission, including cranial data shared by K. McNulty, J. Arenson, and M. Anderson. Previously obtained cranial measurements are either calculated as linear distances from digitized Microscribe 3DX landmarks by the author or, in the case of Howells' data, is directly from published caliper measurements. Although cranial data are combined from different methodologies, previous studies have shown that combined digitized scans and caliper measures are interchangeable in many studies (Cooke and Terhune 2015).

Twelve dental measures include those of the upper and lower permanent molars, buccolingual and mesiodistal maximum distances. Dental data was obtained by the author, using Mitiyuto digital calipers accurate to 0.01mm, and from previously collected and/or published data shared with permission by J. M. Plavcan. Both previously collected and original data were obtained by caliper measures; individual specimen data collectors are listed in **Appendix A**. Mesiodeistal maxima are directly equivalent between taxa, but buccolingual measures are slightly adjusted for old world monkeys due to varying sizes of the two lophs. Following Freedman (1957), two buccolingual measures, one across the mesial loph and another across the distal loph, are collected on cercopithecids (*i.e. Papio, Theropithecus,* and *Macaca*), but are averaged together to be comparable with hominoid measures.

Analyses

Data Transformations

Measures of variance are relatively simple, yet sensitive, calculations (Sokhal and Rolfe 2001; Simpson, Roe, and Lewontin 1960). Determining the standing phenotypic variation in a sample, and comparing it to another biological sample, requires reducing the amount of variation from expected but irrelevant sources. Several steps were taken to reduce the amount of variation from known sources that are not the focus of this investigation, such as absolute scale, ontogenetic stage, allometry, sexual dimorphism, and sample size.

Absolute size differences between individuals may produce variation among the group which is unrelated to ecological differences between species. Each skeletal measure was divided by the geometric mean of all variables for that individual to control for absolute scale (e.g. Mosimann and Malley 1979). This procedure does not remove the influence of allometry on shape, however, morphological shape itself is not being analyzed here, other than its influence on general morphological variation. Therefore, in one set of analyses all data were adjusted across the total sample using the geometric mean. Values divided by the geometric mean in this way are referred to as "adjusted values" or "adjusted data" throughout this dissertation.

All measurements were taken on adults; assessment of "adult" status was based on observed full eruption of the third molar. Furthermore, all analyses were run with sexes pooled as well as separately by sex to control for differing levels of sexual dimorphism. Finally, measures of variation can be sensitive to differences in sample size, although there is no generally recognized guideline on precisely when unequal sample sizes negatively affect results (Keppel 1993). To determine if sample size was a contributing factor to overall of patterns of variation across taxa, regressions were performed in MS Excel on sample size (n) per species/sex group as compared to the summed CV statistic for each.

Measuring Variation

To describe the variation of the population overall, several measures of variance are reported including sample variance, standard deviation and coefficients of variation, each based on both raw and adjusted data.

Variance (σ^2) is defined as the sum of the squared distances of each term from the population mean (μ), divided by the number of terms in the sample ($N - 1$) (Sokal and Rohlf 1995). This statistic squares the distances of each term from the population mean, thus variance is exponentially bigger than the scale of the original terms. Trends in sample variation are therefore easy to see, but this statistic is sensitive to the size of the distribution and may not be directly comparable between samples of differing sizes. This statistic is also used in pairwise F-tests. Standard deviation of a population (σ) is the square root of the sum of the squared distances of each term from the population mean (μ), divided by the number of terms in the sample ($N - 1$). This statistic is related in absolute numbers relative to the original terms, and is independent of the mean, but is also sensitive to the size of the distribution (Sokal and Rohlf 1995).

The coefficient of variation (CV) conveys the standard deviation relative to the mean and is more robust relative to distribution size. Also known as relative standard deviation (RSD), and the coefficient of variation (CV), or (V), this statistic expresses the relationship between the standard deviation (σ) and the mean (μ) as a ratio. This statistic is argued to be a more revealing tool when studying variation, as the relational nature of this statistic conveys information about the level of variance given the population mean and is divorced from any particular unit of measure (Yablokov 1974; Simpson, Roe, and Lewontin 1960). Due to the unique information presented from each statistic, all three are reported using both raw and adjusted data for a total of 6 measures of variation for each species, by sex and by anatomic region. The most robust measure, CV, is used to rank species by total variation in tables of results.

Assessing Variation

In order to visually assess variation by taxon and among anatomic regions, principal components analysis (PCA) was used as an ordination and data reduction technique and performed separately on cranial and dental data in PAST (Hammer *et al* 2001). PCAs allow sample groups to be compared without bias; the amount of variation explained with each component reveals whether factors of interest (like ecological versatility).

To more generally test the hypothesis that ecologically versatile species will exhibit more variance in adult skeletal traits than less versatile species, a generalized linear model (GLM) was applied to all six study taxa simultaneously, to determine if the mean variation of each taxon was different from each other (GLM). Each GLM was run on pooled sex, males only, and females only. Each GLM procedure was repeated for all three measures of variance, Sample Variance, Standard Deviation, and Coefficient of Variance; these measures were also taken from geomean adjusted data to correct for the effects of absolute body size. Each anatomic region (cranial, dental) was analyzed separately. These tests were performed in *SAS: Statistical Analysis Software v9.4* using the GLM Procedure.

If the GLM showed differences among taxa, or among taxon/sex categories, then pairwise T-tests with a Bonferroni correction were conducted to test how the taxa ranked relative to each other. A Bonferroni correction adjusts the threshold of significance for pairwise T-tests by the number of groups being distinguished; a significant result within a GLM may not actually signal a difference among groups once the alpha level has been lowered by the number of groups tested. Therefore, this pairwise comparison is a conservative test of relative mean differences between groups.

These analyses allowed for direct comparisons of the measures of variance for each taxon and both sexes. Strong support for the main hypotheses (that ecological versatility is positively correlated with increased phenotypic variation) would feature a pattern of results which include 1) significant differences in measures of variance observed between study pairs, 2) versatilist species (*H. sapiens*, *P. hamadryas*, *M. fascicularis*) consistently exhibit higher means of their measures of variance than their less ecologically versatile pair partners (*P. troglodytes*, *T. gelada*, *M. nemestrina*), and 3) modern humans consistently exhibit more variation than other study species.

Results

First, I report patterns of variation between species pairs, and between anatomic regions, for all study species using three measures of variation (sample variation, standard deviation, and coefficient of variation). Summations and means of measures of variance are presented in **Table 3** (Dentition) and **Table 4** (Crania); these are reported within species as pooled sex values, and as sex separate values. All measures of variance are listed by individual measurement within species in **Appendix C**. To illustrate the effect of absolute size, unadjusted data is also reported. To determine if sample size is affects patterns of variation, regressions on sample size were performed. Next, to visually assess variation by species and among anatomic regions, scatter plots (**Figs. 1-6**) produced by principal components analysis are reported on cranial and dental data, presented as both pooled and single-sex values. Eigenvalues for each PCA are reported in text. Finally, generalized linear models (GLMs) were performed on all study taxa to determine if the measures of variance for each taxon are significantly different from each other. Reported here are the results of thirty-six GLMs (including two anatomic regions, three sex classes, and six measures of variance), shown by compiled p-values (**Table 5**), and highlighted results in **Figure 7**. Results for all GLMs (with box plots) are available in **Appendix D**.

Measures of Variation

Tables 3 and **4** report the means and sums of each measure of variation. These measures are themselves compelling estimates of how much variation is within each species while also observing a number of potentially confounding factors: the effect of absolute body size on variation, sexual dimorphism, and the differing values between the statistical measures of variation. For example, across species it is observable that cranial samples (**Table 4**) vary more than do dental samples (**Table 3**). Further, all measures of variation are smaller when performed on data transformed by the geometric mean to control for absolute body size.

Table 3. Summations and averages of measures of variance in molar traits, by species/sex[1]

			Unadjusted, reported in mm						Adjusted by geometric mean[2]					
			Sample Variance		Standard Deviation		Coefficient of Variation		Sample Variance		Standard Deviation		Coefficient of Variation	
Taxon	**Sex**	**N**	**Sum**	**Mean**	**Sum**	**Mean**	**Sum**	**Mean**	**Sum**	**Mean**	**Sum**	**Mean**	**Sum**	**Mean**
H. s.	P[3]	42	8.571	0.714	9.933	0.828	92.195	7.683	0.030	0.002	0.580	0.048	58.219	4.852
	F	20	8.188	0.682	9.723	0.810	92.943	7.745	0.034	0.003	0.597	0.050	60.184	5.015
	M	22	7.629	0.636	9.190	0.766	83.332	6.944	0.026	0.002	0.543	0.045	54.279	4.523
P. t.	P	86	6.368	0.531	8.584	0.715	80.968	6.747	0.024	0.002	0.527	0.044	52.815	4.401
	F	50	5.351	0.446	7.855	0.655	75.111	6.259	0.024	0.002	0.529	0.044	53.055	4.421
	M	36	6.864	0.572	8.931	0.744	82.615	6.885	0.022	0.002	0.508	0.042	50.858	4.238
P. h.	P	380	18.373	1.531	14.414	1.201	127.923	10.660	0.036	0.003	0.626	0.052	60.917	5.076
	F	140	17.793	1.483	14.122	1.177	132.394	11.033	0.034	0.003	0.613	0.051	59.424	4.952
	M	240	13.868	1.156	12.422	1.035	105.999	8.833	0.035	0.003	0.615	0.051	60.047	5.004
T. g.	P	57	7.984	0.665	9.426	0.785	84.673	7.056	0.035	0.003	0.615	0.051	59.620	4.968
	F	18	3.547	0.296	6.316	0.526	61.774	5.148	0.047	0.004	0.683	0.057	66.278	5.523
	M	39	6.138	0.511	8.287	0.691	72.565	6.047	0.028	0.002	0.556	0.046	53.910	4.492
M. f.	P	61	3.386	0.282	6.181	0.515	96.216	8.018	0.022	0.002	0.479	0.040	46.641	3.887
	F	29	3.003	0.250	5.793	0.483	93.868	7.822	0.024	0.002	0.494	0.041	47.895	3.991
	M	32	2.347	0.196	5.192	0.433	78.424	6.535	0.018	0.002	0.447	0.037	43.860	3.655
M. n.	P	49	4.119	0.343	6.728	0.561	82.184	6.849	0.020	0.002	0.468	0.039	45.789	3.816
	F	23	4.192	0.349	6.763	0.564	85.207	7.101	0.022	0.002	0.476	0.040	46.680	3.890
	M	26	2.869	0.239	5.641	0.470	67.470	5.622	0.017	0.001	0.439	0.037	43.115	3.593

[1] Summations and averages are pooled totals for all twelve molar traits (measures of variance by trait in Appendix C).

[2] Scaled data has been adjusted to correct for size, where adjusted data is "trait/geometric mean of individual=scaled trait".

[3] The designation "P" represents pooled sex samples.

***Table 4. Summations and averages of measures of variance in cranial traits, by species/sex*[1]**

			Unadjusted, reported in mm						**Adjusted by geometric mean[2]**					
			Sample Variance		**Standard Deviation**		**Coefficient of Variation**		**Sample Variance**		**Standard Deviation**		**Coefficient of Variation**	
Taxon	**Sex**	**n**	**Sum**	**Mean**	**Sum**	**Mean**	**Sum**	**Mean**	**Sum**	**Mean**	**Sum**	**Mean**	**Sum**	**Mean**
H. s.	P[3]	2524	518.573	32.411	85.030	5.314	100.265	6.267	0.044	0.003	0.786	0.049	76.939	4.809
	F	1156	387.252	24.203	73.913	4.620	91.458	5.716	0.043	0.003	0.774	0.048	76.175	4.761
	M	1368	441.073	27.567	78.815	4.926	92.141	5.759	0.044	0.003	0.782	0.049	76.246	4.765
P. t.	P	193	1569.504	98.094	136.856	8.554	194.534	12.158	0.133	0.008	1.312	0.082	133.446	8.340
	F	103	1249.089	78.068	123.306	7.707	178.282	11.143	0.118	0.007	1.238	0.077	125.224	7.826
	M	90	1941.103	121.319	150.634	9.415	210.898	13.181	0.151	0.009	1.387	0.087	141.672	8.854
P. h.	P	511	1560.338	97.521	121.717	7.607	171.577	10.724	0.169	0.011	1.332	0.083	118.140	7.384
	F	175	605.619	37.851	79.832	4.989	130.154	8.135	0.102	0.006	1.095	0.068	100.675	6.292
	M	336	1018.579	63.661	101.214	6.326	142.017	8.876	0.128	0.008	1.200	0.075	108.212	6.763
T. g.	P	42	574.628	35.914	79.658	4.979	130.001	8.125	0.071	0.004	0.913	0.057	84.362	5.273
	F	13	159.125	9.945	44.543	2.784	88.289	5.518	0.041	0.003	0.729	0.046	69.200	4.325
	M	29	206.953	12.935	50.610	3.163	88.839	5.552	0.049	0.003	0.799	0.050	78.284	4.893
M. f.	P	243	312.605	19.538	60.777	3.799	145.951	9.122	0.087	0.005	1.062	0.066	109.309	6.832
	F	96	151.484	9.468	44.216	2.764	124.159	7.760	0.072	0.005	0.983	0.061	106.321	6.645
	M	147	210.422	13.151	51.368	3.210	124.603	7.788	0.070	0.004	0.965	0.060	100.717	6.295
M. n.	P	18	766.260	47.891	91.607	5.725	170.510	10.657	0.107	0.007	1.084	0.068	102.252	6.391
	F	8	236.509	14.782	55.829	3.489	129.722	8.108	0.044	0.003	0.760	0.048	85.928	5.371
	M	10	614.956	38.435	82.121	5.133	145.505	9.094	0.101	0.006	1.038	0.065	94.350	5.897

[1] Summations and averages are pooled totals for all sixteen cranial traits (measures of variance by trait in Appendix C).

[2] Scaled data has been adjusted to correct for size, where adjusted data is "trait/geometric mean of individual=scaled trait".

[3] The designation "P" represents pooled sex samples.

To determine if sample size was a contributing factor to overall of patterns of variation across taxa, regressions were performed in MS Excel on sample size (n) per species/sex group as compared to the summed CV statistic for each. Across this study, sample sizes of species/sex groups range from 8 (*M. nemestrina* female dentition) to 2524 (pooled sex modern human crania). All sample sizes used in these analyses are reported in **Table 1** (Dentition) and **Table 2** (Crania). Among molars, unscaled total variance had a significant correlation with sample size (p=0.00(a=0.05); R^2=0.55) but scaled molar total variance did not (p=0.11; R^2=0.15). Cranial total variance did not significantly correlate with sample size in either unscaled (p=0.10(a=0.05); R^2=0.15) or scaled data (p=0.13; R^2=0.13). In each sample, an individual is represented by either 16 cranial measures, or 12 dental measures; thus, even the smallest sample size analyzed (*M. nemestrina* female dentition) contains 96 data points. Concerning analyses of variation, scholars have remarked that although no lowest threshold of sample size seems to exist, sets below 20 datum points tend to behave more erratically (Gilbert and Grine 2010; Keppel 1993). Thus, these considerations are sufficient for determining the samples comparable despite unequal sample sizes.

Among molars, sample size was a significant factor in sample variation (as measured by summed sample variance per species/sex) for unscaled data (p=0.04 (a=0.05); R^2=0.36), but the relationship disappeared and among scaled data (p=0.19; R^2=0.17). Among cranial measures, neither unscaled (p=0.18 (a=0.05); R^2=0.17) nor scaled data (p=0.81 (a=0.05); R^2=0.01) was correlated with body size. Although the molar variation in general seems to in some part be correlated with overall size, cranial data does not indicate a clear relationship between variation and size. This is likely due to the complexity of cranial shapes, where these shapes are more responsible for variation in the sample than absolute size. In both regions, however, these analyses indicate that the scaling procedure used here is sufficient to adjust for variation between species/sex groups due to absolute scale in both cranial and dental data sets.

Principal Components Analyses

To visualize overall variation in these samples, scatter plots from principle components analyses (PCAs) are included for cranial (**Figures 1-3)** and dental (**Figures 4-6**) data, with 95% confidence ellipses. PCAs highlight the amount of variation in a sample without assumptions of the source of the variation, and therefore, are informative for comparatively assessing the entire study sample. These data represent complete measurement sets for each individual, which have been scaled for body size by transforming the data by the geometric mean, within each study species.

Among dental samples (**Figure 1**; n=511), PC 1 explained 78.35% of the variation (Eigenvalue 0.066), while PC 2 explained only 6.93% of the variation (Eigenvalue 0.006). This result indicates that the majority of the variation is explained by PC1, and that source is likely the sex/species categories. **Figures 2 and 3** show the single sex PCAs, and here, it is discernable that although the shapes of the ellipses differ, their respective elliptical areas appear to be similarly sized, especially among the monkey taxa. Among hominoids, it does appear plausible that humans (in blue for all PCA figures) may be more dentally variable than *Pan troglodytes*, particularly among males (**Figure 3**).

Figure 1: **PCA Scatter Plot, Dental**

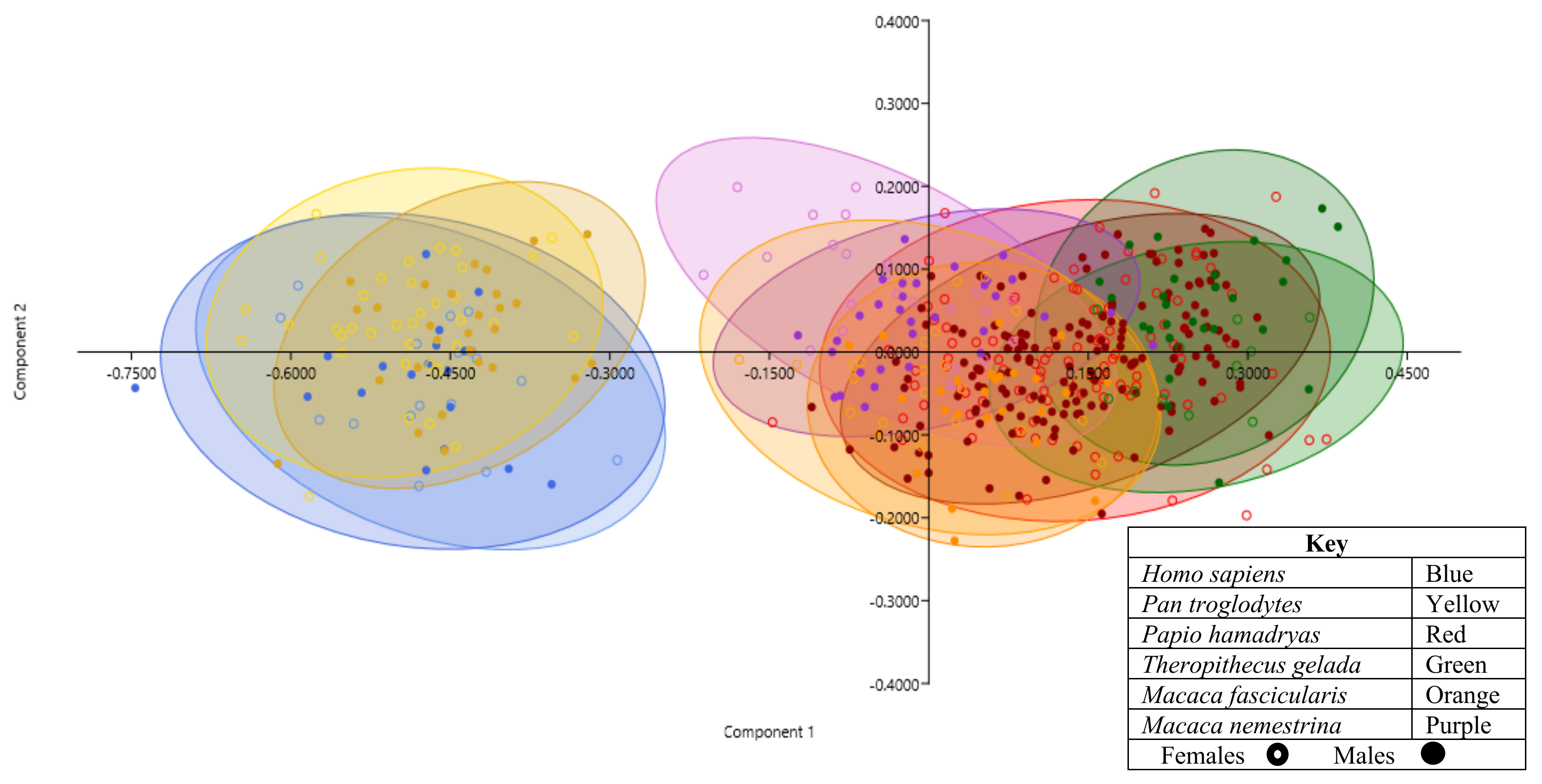
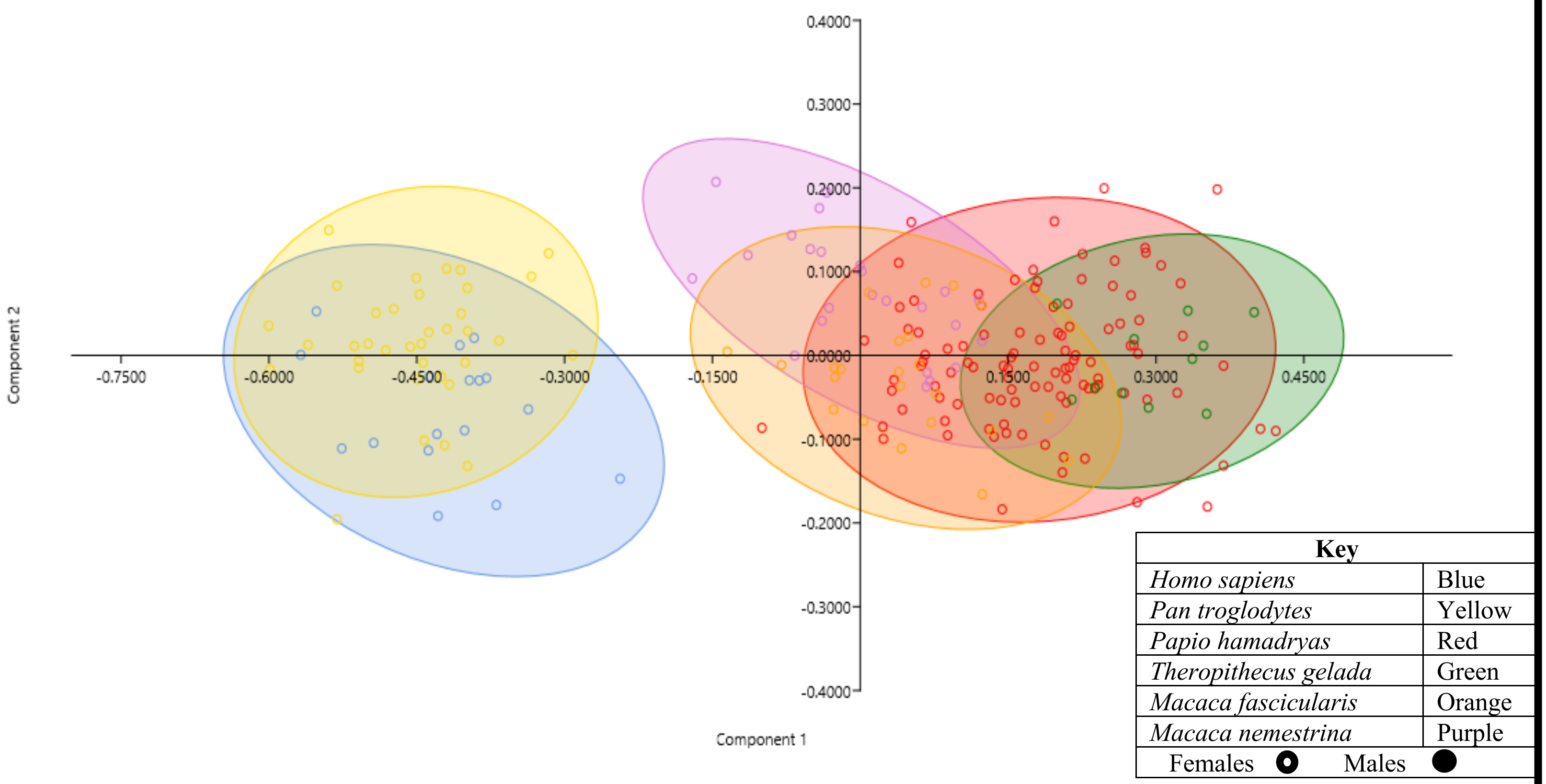


***Figure 2*: PCA Scatter Plot, Dental, Females only**



Key	
Homo sapiens	Blue
Pan troglodytes	Yellow
Papio hamadryas	Red
Theropithecus gelada	Green
Macaca fascicularis	Orange
Macaca nemestrina	Purple
Females ⦿	Males ●

***Figure 3*: PCA Scatter Plot, Dental, Males only**

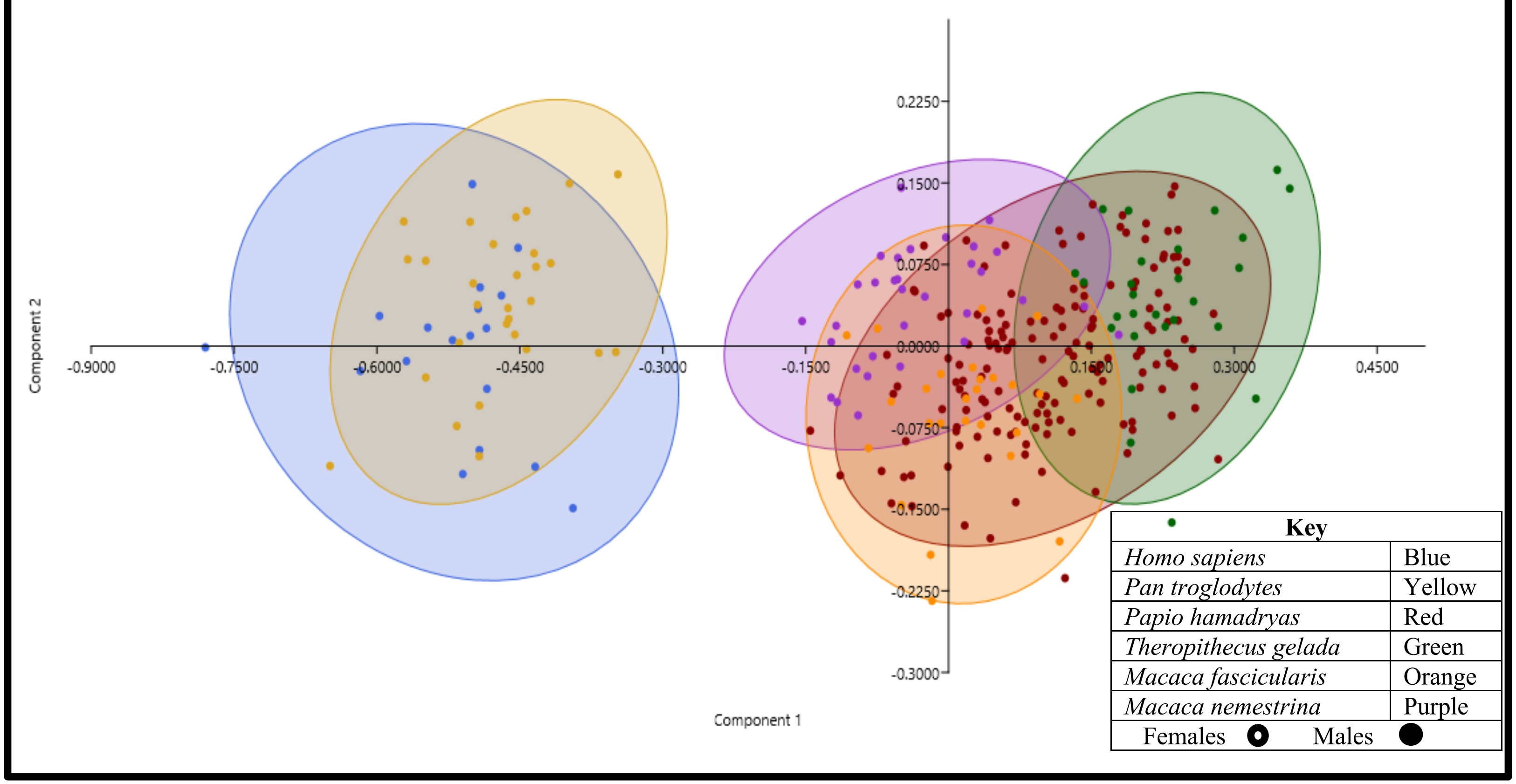
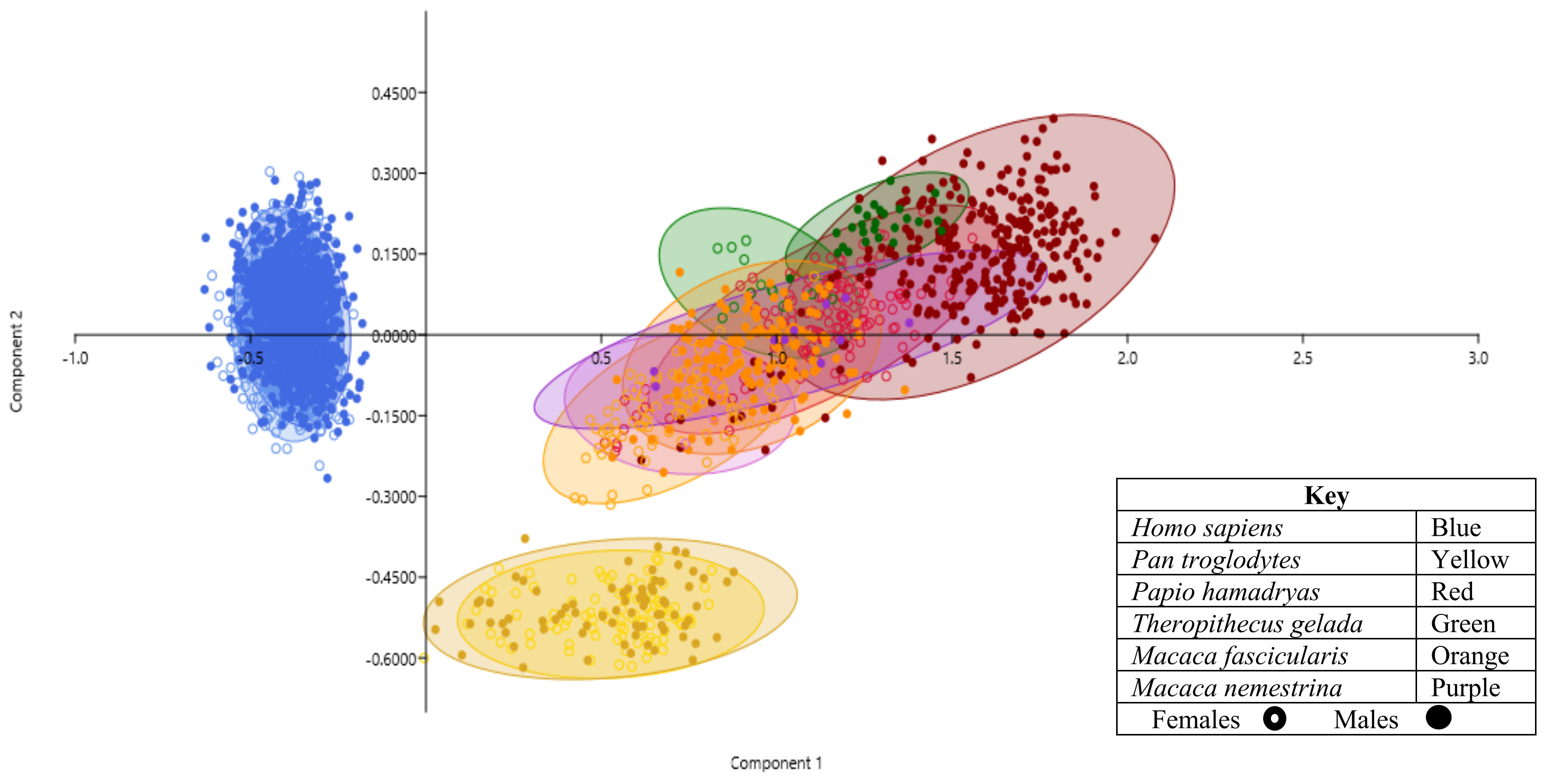
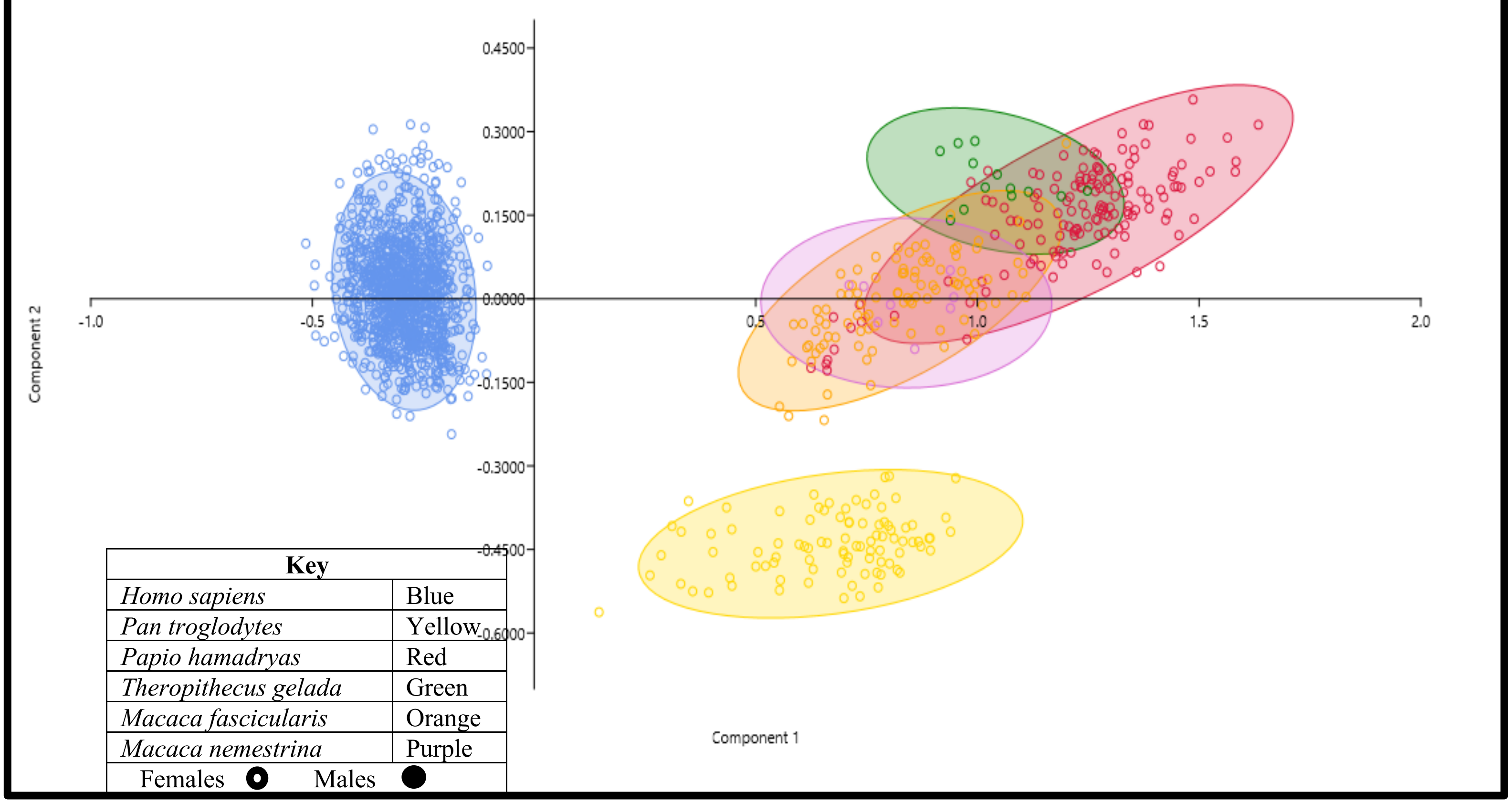


***Figure 4*: PCA Scatter Plot, Cranial**



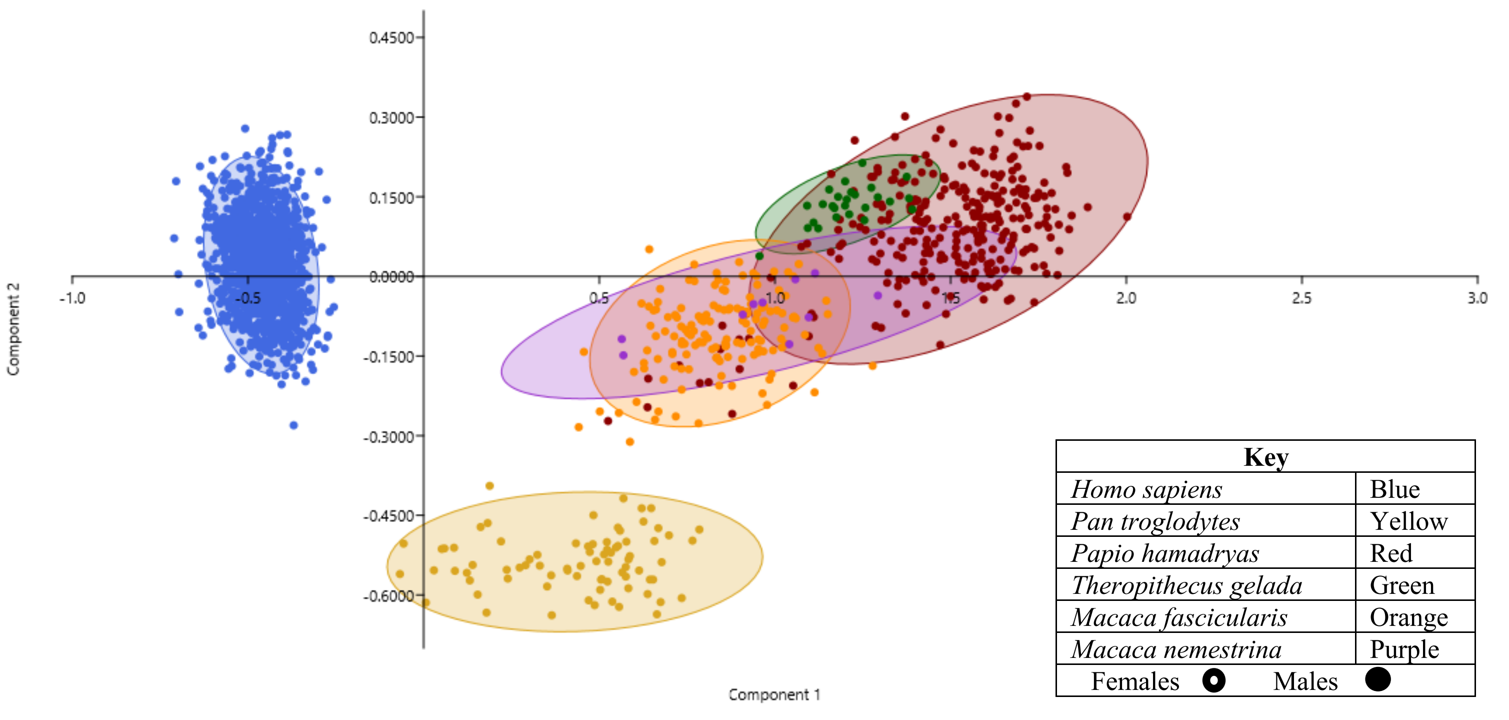
Key	
Homo sapiens	Blue
Pan troglodytes	Yellow
Papio hamadryas	Red
Theropithecus gelada	Green
Macaca fascicularis	Orange
Macaca nemestrina	Purple
Females ⊙	Males ●

***Figure 5*: PCA Scatter Plot, Cranial, Females only**



Key	
Homo sapiens	Blue
Pan troglodytes	Yellow
Papio hamadryas	Red
Theropithecus gelada	Green
Macaca fascicularis	Orange
Macaca nemestrina	Purple
Females ⊙	Males ●

Figure 6: **PCA Scatter Plot, Cranial, Males only**



Within all cranial samples (**Figure 4**; n=3429), PC 1 explained 87.14% of the variation (Eigenvalue 0.473), while PC 2 explained only 4.31% of the variation (Eigenvalue 0.023). This result indicates that the overwhelming majority of the variation is explained by the sex/species categories; a stronger association than among the dental data. **Figures 5 and 6** show single sex scatter plots for all cranial variables. Here, it is easier to discern that while the shapes of the ellipse per taxon are not equal, their respective areas are similar, indicating that the amount of variation across taxa is similar.

Combined, these analyses suggest several important factors. First, cranial and dental data are likely to return differing results on the question of sample variation; humans appear more dentally variable, but less cranially variable, than *Pan troglodytes*, for example. Second, species/sex categories explain the majority of variation. This was expected, and therefore species pairs chosen to be similar to each other in phylogeny and body size remain the most directly informative comparisons. Third, and most importantly, after absolute size and sexual dimorphism are minimized within samples, levels of variation appear similar between taxa. This pattern does not appear to support our main hypotheses that ecologically versatile species are more variable.

Generalized Linear Models

Generalized linear models (GLM) were performed on all study taxa simultaneously to determine if the measures of variance for each taxon are significantly different from each other, regardless of pairings; **Table 5** reports the results (p-values) of the GLM procedures.

Table 5: ***Measures of Variance among Anatomic Regions, Sex Categories***

Results of Generalized Linear Models (a = 0.05)						
Group	*Samp Var Unadj. data*	*Samp Var Adj. data*	*Stan Dev Unadj. data*	*Stan Dev Adj. data*	*Coef Var Unadj. data*	*Coef Var Adj. data*
Pooled, Cranial	**0.0414**[1]	0.2039	**0.0216***[2]	0.1546	**0.0045***	0.1017
Female, Cranial	**0.0002***	**0.0305**	**<.0001***	**0.0153**	**0.0034***	0.1135
Male, Cranial	**0.0005***	0.0723	**<.0001***	**0.0397**	**<.0001***	**0.0322***
Pooled, Dental	**<.0001***	0.1615	**<.0001***	0.092	**<.0001***	**0.0044***
Female, Dental	**<.0001***	0.1095	**<.0001***	0.1909	**<.0001***	0.0949
Male, Dental	**<.0001***	**0.041**	**<.0001***	**0.0436**	**<.0001***	**0.0004***

[1] Significant GLM results are in bold type.

[2] Significant differences detected within pairwise comparison groupings are marked with an asterisk.

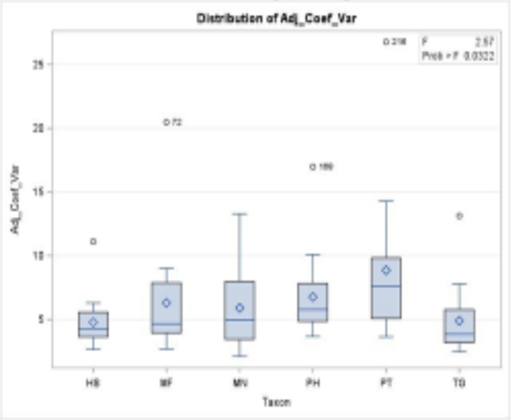
Significant results (a = 0.05) are in bold; bolded p-values with asterisks are those GLM results which also had significant groupings within the pairwise comparisons. Measures of variance on unadjusted data are all significant; this is expected, because absolute body size is a large source of variation. Further, all but one test on unadjusted data also shows significant differences between groups. Although many GLMs detected significant differences among taxa, pairwise comparisons show meaningful distance between groupings to be much rarer. All box plots resultant from GLM procedures, and their groupings within the pairwise comparison, are available in **Appendix D**.

Of the eighteen GLM results on adjusted data, only three show significant groupings within the pairwise comparisons, and all are under the measure coefficient of variance (**Table 5**). The sample groups are ‘male crania’, where *Pan troglodytes* has a significantly higher mean than modern humans (HS), and the sample groups ‘pooled dental’ and ‘male dental’, where *Papio hamadryas* cannot be distinguished from most other taxa. **Figure 7** displays the box-plot results of the GLM procedures, and their pairwise comparison groupings, for these three analyses.

Figure 7: Coefficient of Variance GLM procedures, with Bonferroni corrections, on geomean adjusted datasets.

Cranial: Coefficient of Variance, Males

Generalized Linear Model (*α* = 0.05)

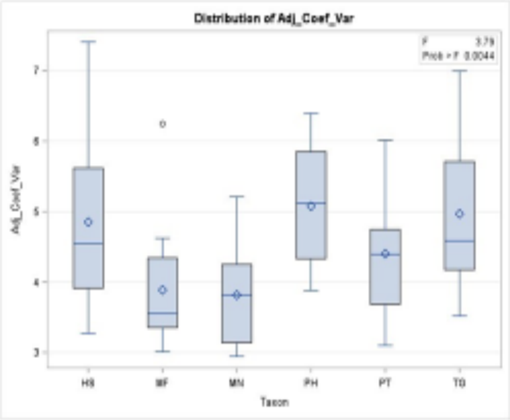


Bonferroni Correction
***α* = 0.05; Critical Value of t = 3.01557**

CVAMC	Minimum Significant Difference	3.9899		
Bon Grouping		Mean	N	Taxon
	A	8.855	16	PT
B	A	6.763	16	PH
B	A	6.295	16	MF
B	A	5.897	16	MN
B	A	4.893	16	TG
B		4.761	16	HS

Dental: Coefficient of Variance, Pooled

Generalized Linear Model (*α* = 0.05)

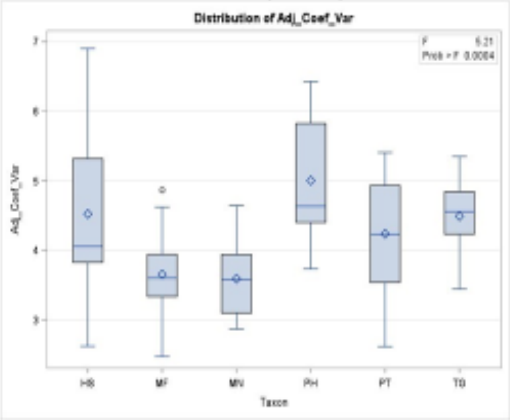


Bonferroni Correction
***α* = 0.05; Critical Value of t = 3.04579**

CVAPD	Minimum Significant Difference	1.2233		
Bon Grouping		Mean	N	Taxon
	A	5.0764	12	PH
B	A	4.9685	12	TG
B	A	4.8517	12	HS
B	A	4.4012	12	PT
B	A	3.8869	12	MF
B		3.8159	12	MN

Dental: Coefficient of Variance, Males

Generalized Linear Model (*α* = 0.05)



Bonferroni Correction
***α* = 0.05; Critical Value of t = 3.04579**

CVAMD	Minimum Significant Difference	1.0291		
Bon Grouping		Mean	N	Taxon
	A	5.0039	12	PH
B	A	4.5233	12	HS
B	A	4.4926	12	TG
B	A	4.2381	12	PT
B		3.6549	12	MF
B		3.5928	12	MN

Boxplots derived from the GLM procedures show a visual display of the variation between all six taxa (**Figure 7**). The results shown here are the overall most informative ones from these procedures, because of two factors. First, the measure of variance under analyses (CV: the coefficient of variation) is the most robust measure in use here because this statistic weighs the standard deviation by the mean of that sample. Second, these data have been adjusted by the geometric mean to remove the influence of absolute size. Groupings based on pairwise comparisons are also included here, showing the significant differences between taxa within a sample. These three results summarized the inconsistency of the entire dataset with regard to the hypothesis that more ecologically versatile species are more variable than less versatile species; *Pan troglodytes* has the most variable cranial data, while *Papio hamadryas* displays the most variation in dental data. Modern humans are not consistently distinguishable by measures of variance from other taxa.

Discussion

Standing phenotypic variation is a characteristic of populations which can inform studies of adaptation (Yablokov 1974). Measuring standing phenotypic variation in a population is a relatively easy task. However, accurately anticipating and accounting for known sources of variation is difficult, and essential, to avoiding false positives. Depending on the inquiry, known sources of variation may need to be assessed. Here, the goal was to assess if phenotypic variation is greater in ecologically versatile catarrhines, and therefore many steps were taken to ensure analyses were accurately summarizing population variation trends. Even after controlling for known sources of variation, however, the effects of anatomic region and cranial shape were both important contributing factors. It is plausible that molar and cranial samples behave differently enough as to be incomparable across regions. Molar variation tended to be an order of magnitude smaller than cranial variation across the study population; this is an interesting result for comparing variance between regions but confounding when discerning differences between taxa. Confounding factors are also present with regard to cranial shape, where differing rates of sexual dimorphism can falsely inflate patterns of variation between taxa. These effects were removed in the present study were hypothesis testing required, but that is not possible for many other studies where demographic information is not known.

Considerations of sample size and absolute body size affecting the variation present in a sample have likely been adequately addressed for the purposes of this analysis. Sample sizes in both anatomical regions are sufficiently large to not effect variation in any significant way. Sexual dimorphism can be controlled within analyses by separating sexes where relevant. Absolute body size does impact variation, in that bigger bodies have more variance relative to their size, but once body sizes are scaled across taxa that effect is significantly diminished. Finally, it should be noted that anatomic regions do display differences in variance, regardless of other confounding factors. Across taxa and measures of variance, molars tend to vary less than the cranium. This was expected, given supporting literature on craniodental variation reported in relevant taxa (Aiello and Wood 1994; Delson 2000).

Results presented here do not show support for the hypothesis that more ecologically versatile primate species exhibit more phenotypic variation within craniodental features. The measures of variance (**Tables 3, 4**) and PCA scatterplots (**Figs.**

1-6) indicate the weakness of any variation pattern relative to ecological versatility. Versatilist species are not easily discernible from less ecologically versatile species. For example, among baboons, the highland restricted *Theropithecus* is comparatively variable with the widespread and dietarily diverse *Papio hamadryas*. GLM procedures show that *P. hamadryas* does display slightly more variation than *T. gelada*, but this result was not consistent across sexes or anatomic regions (**Table 4**, **Figure 7**). If ecological versatility were strongly associated with phenotypic variation, these results should have *P. hamadryas* far outranking *Theropithecus*, if for no other reason than standing genetic diversity. Further, all analyses reveal that modern *H. sapiens* are arguably less variable than chimpanzees. PCA scatter plots (**Figures 1-6**) help visualize modern human variation relative to other species and indicate that humans may indeed be the least variable sample in this study. GLM procedures confirm any ambiguity that modern humans do not display more variation than *Pan troglodytes*. One possible conflating issue is that while *P. troglodytes*' habitat range is significantly smaller than that of *H. sapiens*, there is evidence that chimpanzee genetic diversity may exceed that of modern humans (Stone *et al* 2001; Deinard and Kidd 1999). However, since higher genetic diversity in *Papio hamadryas* (as evidenced by existence of multiple subspecies) than in *Theropithecus gelada* did not correlate with increased phenotypic variation, assuming this is the cause of difference between modern humans and chimpanzees should be met with caution. Again, given the amount of difference in ecological versatility between modern humans and chimpanzees, it would be expected by the main hypothesis here that modern humans were easily more variable than chimpanzees. This is not supported in these analyses.

Conclusion

Variation is the raw material on which selective pressures act (Darwin 1859). Therefore, variability, a measure of population variation can be indictive of selective pressures; these two characteristics (population variability and selective pressure) are related (Yablokov 1974). Some scholars argue variability itself is a characteristic that can be altered as part of an adaptive strategy, allowing populations to display a narrow or wide range of phenotypic (or genotypic) traits simultaneously (Grove 2014; Lande 2009; Potts 1998a; Vrba 1992). There may be an advantage for a diverse population in the face of environmental diversity or change (Turley and Frost 2018; Antón, Potts, and Aiello 2014; Borg and Channon 2012; Kuzawa and Bragg 2012; Davidson, Jennions, and Nicotra 2011; Bell 2010; Ash and Gallop 2007).

The main hypothesis of this paper, that ecological versatility positively correlates with phenotypic variation, was not supported among craniodental features of selected extant catarrhine primates. Craniodental features were chosen because a) they are more frequent in museum collections and public databases and b) they are known to be more phenotypically conserved than postcranial material. However, postcranial features (particularly of the long bones) are known to be more developmentally plastic than craniodental features (Ruff et al 2019; Trinkhaus, Churchill, and Ruff 1994; DeRousseau and Reichs 1987). Developmental plasticity may be a more active buffering process to combat environmental flux than standing phenotypic variation in adults (Pfenning et al 2010; Jablonka and Lamb 2004; West Eberhard 2003; Lande and Shannon 1996). If so, this effect may present in postcranial elements more readily than craniodental elements, due to the duration and nature of long bone growth (Cunningham, Scheuer, and Black 2016).

Known sources of variation in populations, which do not relate directly to ecological versatility, include body size, sex, sexual dimorphism, and age of the individual, along with the anatomic region were under examination. In this study, specimens were only included if these variables were known, thus allowing them to be removed when necessary for hypothesis testing. However, in many settings, such as studies of fossil assemblages, these demographic variables are not always known, or knowable. Further, sample sizes are often much smaller, which could artificially increase sample variance estimates (Sokal and Rohlf 2012). Given the relative weakness of the correlation between ecological versatility and phenotypic variation under known conditions, it would require careful vetting of data to witness the pattern at all. Yet, it is the act of reconstructing past environments which can be most informative of evolutionary history and therefore should be combined with extant data to compare demographic expectations.

CHAPTER III:

POSTCRANIAL VARIATION AND ECOLOGICAL VERSATILITY IN SELECTED CATARRHINE PRIMATES

Introduction

Exposure to fluctuating environments may be correlated to an increase in population-level phenotypic and/or genetic variation (Antón, Potts, and Aiello 2014; Lande 2014; Potts 2013, 2012; Kusell and Leiber 2005; Lande and Shannon 1996). Such a correlation has been advanced for decades; for example, Yablokov (1974) argues that standing phenotypic variation - the total amount of variation in metric characteristics of the adult phenotype - in mammalian populations can indicate the amount and directionality of selective pressures. A number of factors determine the amount of standing variation within a population, including genetic variation, limb use or disuse, and nutritional status (Schlichting and Pigliucci 1998; Yablokov 1974; Simpson 1944). A population responding to somewhat predictable, yet variable environmental fluctuations should exhibit increased intra-taxon diversity as selective pressures become less unidirectional (Lande 2014; Pfenning et al 2010; Kussell and Leiber 2005; Lachmann and Jablonka 1996). In rapidly changing environments, or where a single breeding population's range covers a diverse array of habitats, there may be a selective advantage to maintaining polytypic traits (Grove 2014; Potts 2012; Davidson, Jennions, and Nicotra 2011; Lande and Shannon 1996; Levins 1968). Populations with more polytypic traits, more standing variation, or both, may be able to buffer individuals from the effects of the environment (Turley and Frost 2018; Sanchez and Schoch 2013; Kuzawa and Bragg

2012; Potts 1998; Levins 1968). In other words, more phenotypic variation can be the result of, and potentially the adaptive response to, a fluctuating environment.

The idea that ecological versatility positively correlates with increased phenotypic variation has not yet been directly tested in extant primates. In order to examine the relationship between ecological versatility and phenotypic variation among extant nonhuman primates, catarrhines are ideal because they exhibit a range of ecological versatility. For example, almost 70% of all primates today are determined to be “Near Threatened with Extinction” in the wild, or worse; the IUCN recognizes four categories approaching complete extinction (IUCN 2018). This is because most living primate species are arboreal, and travel in groups restricted to increasingly fragmented forest habitats (IUCN 2018; Mittermeier 1988). Some species do have widespread populations, occurring in both arboreal and terrestrial environments, and consuming variable diets that are often supplemented with cultivated or manufactured foods (IUCN 2018; Rowe and Myers 2016; see DeRousseau and Reichs 1987). The relative success of these species may reflect enhanced tolerance to environmental fluctuation (see Hill and Winder 2019 for operationalizing this in the study of baboons). The aim of this project is to test the hypothesis that more ecologically versatile species will exhibit greater phenotypic variation, as measured in skeletal variation. Following Potts' (1998a) concept of versatilist traits, for the purposes of this analysis ecological versatility is defined as a suite of features including: 1) dietary breadth, 2) widespread geographic distribution, and 3) occupation of heterogeneous habitats.

In Chapter One, the hypothesis that ecological versatility and phenotypic variation are positively associated was tested using cranial and dental measures; here, the same question is posed to postcranial samples. In each of three pairs of catarrhine species (*Homo sapiens* and *Pan troglodytes*, *Papio hamadryas* and *Theropithecus gelada*, *Macaca fascicularis* and *Macaca nemestrina*), I compare the putatively more ecologically versatile species with a closely related, but less ecologically versatile species.

Background

The set of phenotypes which can be produced by a genotype exposed to differing environmental conditions during growth is called the developmental reaction norm or DRN (Schlichting and Pigliucci 1998). Under fluctuating environmental conditions, expanding DRNs may be more advantageous than changes in protein-coding genes (Kelley, Panhui, and Stoehr 2012; Beldade, Mateus, and Keller 2011; Pigliucci and Müller 2010; Müller 2007; Pigliucci 2001), which would result in greater variation in adult body shapes and sizes.

Jablonka and Lamb (2014) discuss a synthesis of evolutionary perspectives that focus on the multi-dimensional reality of inheritance, including intergenerational models of learned behavior (such as human language) accompanied by physiological change. They attempt to resolve the unproductive (and false) dichotomy that the source of inherited information must be either genetic or environmental. For example, among primates deemed ‘adaptable’ (a group that largely coincides with those defined by the IUCN as ‘least threatened’, and in some instances ‘invasive’) a shared trait is the occupation of diverse habitats. When adjusting to novel, unpredictably fluctuating, or patchy environments, organisms employ both behavioral and physiological strategies including changes in immune-response, dietary preference, and substrate use; for example, see Stewart and Stringer's (2012) study on the use of refugia during periods of climatic flux in human evolution, or Parsons' (1983) book on strategies of colonizing species. These strategies could result in long-term phenotypic change; especially if, for example, the novel environment is introduced during the organism's developmental stages (Turley and Frost 2018; Turley, Simons, and Frost 2018; West Eberhard 2003; Lachmann and Jablonka 1996). These modes of inheritance include learned behaviors (such as dietary preference and acquisition) that juveniles receive from adults, and in some cases, reiterative physiological responses (Jablonka and Lamb 2014; West-Eberhard 2005, 2003). Given that accumulated variation may be the result of both genetic (regulatory or protein coding, time allowing) and environmental inheritance when an organism experiences fluctuating environments, it is reasonable to anticipate that primates exposed to (either developmentally or evolutionarily) fluctuating environments on a consistent basis should display more phenotypic variation, when examined as a group, than those in more stable, specialized niches (Lande 2014, 2009; Stoessel, Kilbourne, and Fischer 2013; Pfenning et al 2010; Lande and Shannon 1996).

Kuzawa and Bragg (2012) lay out expectations under which phenotypic, especially developmental, plasticity could facilitate genetic evolution. First, a population moves into a novel environment. Then, plasticity facilitates an improved "fit" between phenotype and environment within the lifetime of an organism. Over subsequent generations, Kuzawa and Bragg argue, natural selection acts on the genetic architecture of the newly expressed trait to improve on either the plasticity of the phenotype or the efficiency of the new phenotype. These expectations of developmental plasticity fall in line with other hypotheses about evolution in changing environments (Turley and Frost 2018; Antón *et al* 2016; Forsman 2015; Antón and Snodgrass 2012; West-Eberhard 2005, 2003, 1989, 1986; Potts 1998; Lachmann and Jablonka 1996; Matsuda 1987; Parsons 1983; Levins 1968). Studies in other fields have already engaged this strategy: Davidson and colleagues (2011) tested the idea that invasive plant species would exhibit more phenotypic plasticity. Comparing several lines of morphological variation during growth, they found that invasive species were frequently more plastic than noninvasive species. However, heightened developmental plasticity wasn't always associated with a measurable fitness benefit, and less plastic species maintained greater fitness homoestasis in resource strapped environments (Davidson, Jennions, and Nicotra 2011). Similarly, a 2013 study by Stoessel, Kilbourne, and Fischer surveyed 236 avian species for correlative patterns between morphological variation and what they call 'ecological plasticity'. They found that while a few traits did exhibit increased variation with more ecological plastic species, such as femoral length, they concluded these traits could not clearly be associated with ecology to the exclusion of limb function (Stoessel, Kilbourne, and Fischer 2013).

Postcranial long bones may be particularly informative skeletal elements, because their long postnatal growth period can reveal the consequences of a fluctuating environment in the adult phenotype (Sanchez and Schoch 2013; Trinkhaus, Churchill, and Ruff 1994; DeRouseeau and Reichs 1987). Many dimensions of postcranial bones are subject to environmental pressures, both during periods of growth and beyond (Ruff *et al* 2019; Turley and Frost 2018; Cunningham, Scheuer, and Black 2016; White, Black, and Folkens 2011). Maximum lengths of long bones are not achieved until adulthood, when the epiphyseal growth plate is fused to the diaphysis (Cunningham, Scheuer, and Black 2016). This period of growth lasts for years in most primates, and therefore long bone lengths can be influenced by changes in physical activity or nutritional status (for example, Ruff *et al* 2019; DeRousseau and Reichs 1987).

These developmental factors ultimately contribute to the overall length and robusticity of long bone lengths in adults; Trinkhaus, Churchill, and Ruff (1994) show that variation in humeral diaphysis dimensions is particularly sensitive to biomechanical loading. Long bone lengths, along with maximum proximal and distal dimensions of the ends, and the area of the articular surfaces have all been shown to correlate strongly with individual body size and substrate (Ruff *et al* 2019; Eller, Guthrie, and Frost 2012; Delson *et al* 2000). Enthesial surfaces also vary within populations, as individual use affects these dimensions most strongly (Turley and Frost 2018). Therefore, linear measures of the postcranial long bones are expected to vary more within a population which copes with multiple habitats and varied resource availability (see Turner *et al* 2016 for long bone dimensional changes in the cercopithecine monkey *Chlorocebus*). A robust analysis of postcranial dimensions should reveal differences in the amount of intra-taxon variation between species that regularly encounter diverse ecological pressures and those species with more limited ecological versatility.

Materials and Methods

Study Species

To determine if more ecologically versatile species are more phenotypically variable, linear postcranial measurements were obtained for three pairs of extant catarrhine species. As in Chapter One, the species pairs are *Homo sapiens* and *Pan troglodytes*, where *H. sapiens* is the more ecologically versatile species; *Papio hamadryas* and *Theropithecus gelada*, where *P. hamadryas* is the more ecologically versatile species; and finally, *Macaca fascicularis* and *Macaca nemestrina*, where *M. fascicularis* is the more ecologically versatile species. **Table 1.1** summarizes their ecological profiles, where putative versatilist species are highlighted in gray; it should be noted this table is reproduced from Chapter 1, where more detail on ecological profiles can be found. Study pairs were assigned for comparability in phylogeny and body size, in addition to ecological profiles. These species were also chosen because of their representation in museum collections, availability of published measurements, and detailed ecological descriptions in the literature.

Skeletal Protocol

Phenotypic variation in the adult skeleton is documented with a linear measurement protocol of 53 measures, including measurements of the humerus (14), radius (10), femur (17), and tibia (12). Limb bones should reveal information about environmental pressures because as bony elements they have long periods of growth and high cellular growth rates, especially at the epiphyses (Cunningham, Scheuer, and Black 2016). These specific skeletal elements were chosen because they represent two proximal segments of the limb (humerus and femur) and two distal limb segments (radius and tibia), and therefore they reflect the forelimb and hindlimb. Further, they are commonly found in fossil assemblages, at least in fragments. While none of these qualities are under investigation here specifically, the amount of variation encapsulated within these four bones should give a reasonable proximation of the appendicular skeletal variation.

The measurement protocol includes linear measures designed to capture the overall size and variation of the element. Maximum lengths of each bone are recorded, along with breadths across distal and proximal ends, and enthesial lengths (muscle attachment sites along the diaphysis). These measures were chosen to capture phenotypic variation of the long bones generally, and include characteristics known to be affected by environmental influence, such as long bone length (Guthrie 2011; Elton 2001). This protocol has the dual goals of ensuring comparability across studies by including traditional measurements and ensuring meaningful biological comparability across taxa by including anatomical landmarks as frequently as possible. Each measurement is cross-referenced with previously utilized skeletal measurement protocols to ensure comparability to previous work (see **Appendix E** for complete protocol and measurement references). All measures were taken on the left element, if possible, with calipers and/or osteometric boards.

Table 1 reports the sample size for each element per species, by sex, with a total of 113 individuals; "P" represents the pooled sex value. A complete list of all specimens, including institutional identification numbers and coder name, is given in **Appendix A.** Some samples used here were retrieved from public datasets; examples include Terry Collection and PRIMO.

Table 1: Study Sample Individuals and Elements

Taxon	Sex	Total N	Humerus	Radius	Femur	Tibia
Homo sapiens	P	18	18	18	18	18
	M	9	9	9	9	9
	F	9	9	9	9	9
Pan troglodytes	P	15	15	15	15	15
	M	6	6	6	6	6
	F	9	9	9	9	9
Papio hamadryas	P	38	23	33	19	35
	M	25	15	23	13	24
	F	13	8	10	6	11
Theropithecus gelada	P	16	13	12	10	12
	M	10	8	7	5	7
	F	6	5	5	5	5
Macaca fascicularis	P	16	11	12	11	12
	M	7	5	6	5	6
	F	9	6	6	6	6
Macaca nemestrina	P	10	3	10	4	9
	M	6	2	6	2	5
	F	4	1	4	2	4

Sex-split tallies are labeled (P) pooled, (M) male, (F) female; total N represents the number of individuals in the sample; each bony element column tallies the number of elements per species/sex.

Other specimens are provided by individual researchers with permission, including data shared by S. Frost, and E. Guthrie. In perfect practice, a complete individual would total 53 measures covering 4 bony elements. However, individuals are sometimes missing elements, or a measurement was not taken due damage or the remaining presence of soft tissue. Missing data is addressed per analytic technique, as warranted, as explained in more detail below. Specimens included under study were determined to be adult by one of two methods a) where possible, associated dental eruption was used to establish adult if the second molar was fully erupted, and b) epiphyseal growth plates were fused, or obliterated.

Data Analysis

As in Chapter 1, I include three types of analyses to report the variation in the sample. First, I explore the data visually using principal components analyses. Next, I report measures of variance per bony element, per species. Lastly, I conduct analyses of variance to determine if species are significantly different to each other.

Principal Components Analyses

To explore patterns of variation by taxon and among bony elements, principal component analysis (PCA) was used as an ordination and data reduction technique and performed separately on each bony element in *PAST* (Hammer *et al* 2001). PCAs allow for direct comparisons among the variation within subsamples, where 95% confidence ellipses indicate the variation of the subsample using the area (size) of the ellipse. The size of the ellipse represents the largest possible two-dimensional slice through a high dimensional space. Specimens which were missing more than half of their expected data points, or those which did not include any measure of long bone length, were excluded entirely from principal components analyses. Those records which contain large amounts of unavailable data would skew the PCA results significantly, and because lengths are physically larger measures than distal or proximal ends, these measures tend to weigh heavily in the overall PCA. Small amounts of missing data were estimated in *PAST* using iterative imputation, where missing values are filled with column averages and then regression values for the missing data are computed reiteratively until convergence is reached (Hammer *et al* 2001). Any subgroup (sex/species group) where the "n" is less than 3 were not grouped with ellipses but instead are reported as individuals.

Measures of Variation

I report three measures of variation: sample variance (SV), standard deviation (SD), and coefficient of variation (CV) to quantify phenotypic variation for all 53 variables. Measures of variation are reported within each taxon, and bony element, and were performed on both pooled and single sex samples.

Postcranial size differences are notable between sexes and among taxa in this study, and therefore the data is presented as raw values and as adjusted by the geometric mean. This adjustment makes variation more comparable across diverse sizes. For each bone, each measurement is divided by the geometric mean for that individual by element, and then three measures of variance of each element are taken from the adjusted data. For individuals with missing data, the geometric mean was calculated using the species/sex average for any missing measurements, to avoid falsely weighting that statistic. These imputed species/sex averages were not used for any other calculations. This process was repeated for each element in each species/sex group where possible; all steps were completed in *MS Excel*. Data analyses in Chapter One revealed that while adjusting the data with the geometric mean does reduce the variation created by size differences between groups, it does not change the relative scale of variation inherent in the total sample.

Analyses of Variation

To test the hypothesis that ecologically versatile species are more variable in adult skeletal traits than less versatile species, an ANOVA for unbalanced samples was applied to all six study taxa simultaneously, to determine if the means of the measures of variance for each taxon were different to one another. Tests were performed in *SAS: Statistical Analysis Software v9.4* using a generalized linear model procedure with Bonferroni corrections. If the ANOVA showed differences among taxa by producing a significant p-value, then pairwise T-tests with a Bonferroni correction were conducted to test how the taxa ranked relative to each other. These analyses allowed for statistical comparisons between the measures of variance for each taxon. A Bonferroni correction adjusts the threshold of significance for pairwise T-tests by the number of groups being distinguished, because a significant p-value from the generalized ANOVA may not actually signal a difference among groups once the alpha level has been lowered by the number of groups tested. Therefore, this pairwise comparison is a conservative test of relative mean differences between taxa. Each ANOVA procedure with pairwise Bonferroni corrections was repeated for all three measures of variation: sample variance, standard deviation, and coefficient of variation. These measures are reported on both unadjusted and geomean adjusted data, and as both pooled and single sex samples.

First, each bony element (humerus, radius, femur, and tibia) was analyzed separately, including all variables for that element (14, 10, 17, and 12, respectively). These analyses give the most information about variation within each skeletal element. However, due to the differing sizes of both samples and measurement sets, these elements alone cannot describe overall skeletal variation. To provide a view across total skeletal variation, ANOVAs were also performed on a standardized set of ten measures each from across all four elements; this set is termed “skeletal, total”. Further, width and length variables across all four elements were compiled and analyzed separately as: "skeletal, lengths" consisting of two length variables per bone; and "skeletal, widths" with eight variables of proximal and distal aspects. These skeletal variables allow the measures to be as standardized as possible across bony elements, where sources of variation (e.g., long bone length, unequal bone measurement sets) are differentially contributing to phenotypic variation.

Results

Principal Components Analyses

A principle components analysis was conducted on the geomean transformed variables for each bony element to reduce and ordinate the data (**Table 2**). **Figures 1-4** show scatter plots of PC1 vs. PC2 for the six sampled species, with sexes pooled for each element: humerus, radius, femur, and tibia. Split sex scatter plots, and complete eigenvalues per PCA, are reported in **Appendix G**. **Figures 1-4**, and **Table 2**, show several patterns which are important to note. First, the bony elements do not return the

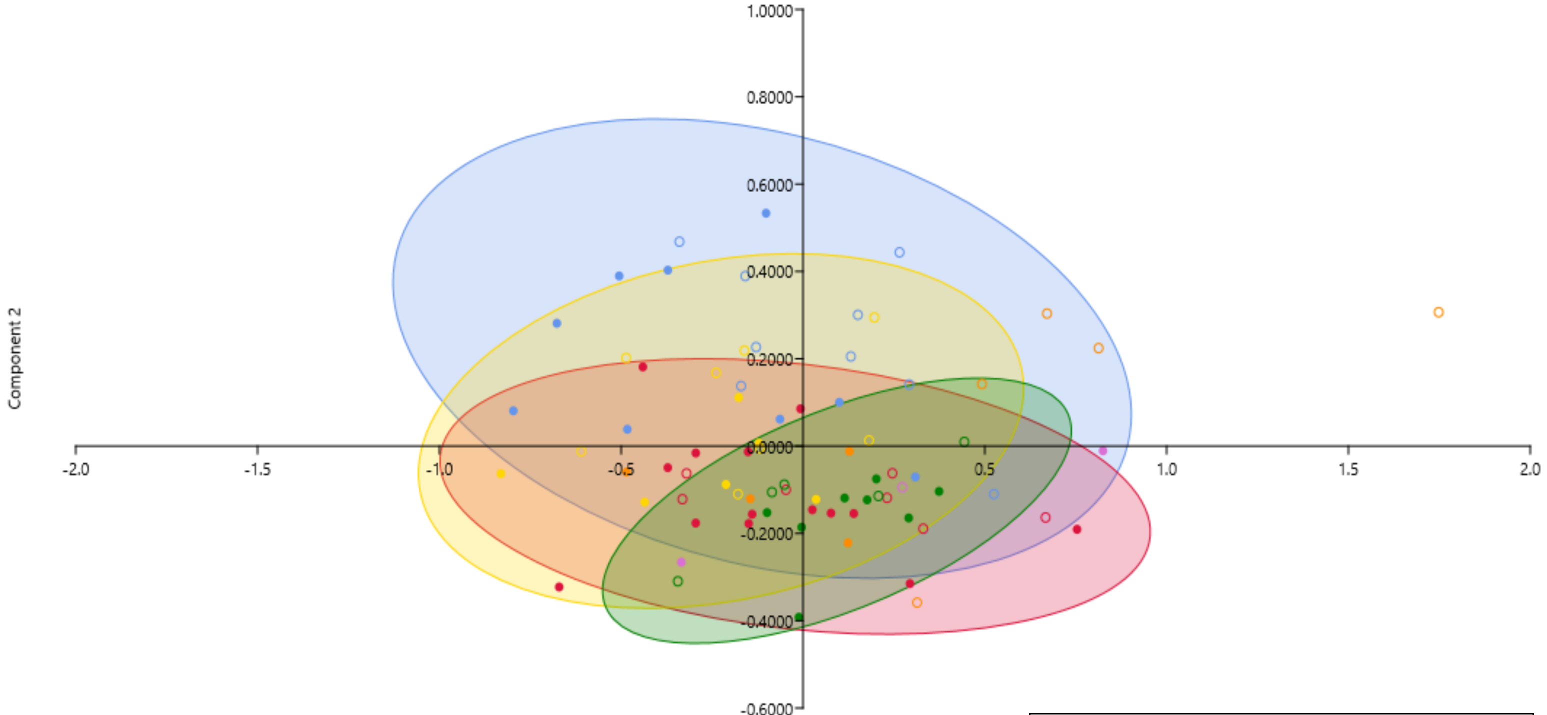
Table 2:
First three eigenvalues of pooled sex PCAs

	PC	***Eigenvalue***	***% variance***
Humerus	1	0.1716	72.783
	2	0.0424795	18.017
	3	0.00836758	3.5491
	PC	***Eigenvalue***	***% variance***
Radius	1	0.90889	91.269
	2	0.0679089	6.8193
	3	0.00991483	0.99563
	PC	***Eigenvalue***	***% variance***
Femur	1	0.75491	84.866
	2	0.0895821	10.071
	3	0.00834635	0.93829
	PC	***Eigenvalue***	***% variance***
Tibia	1	0.777344	96.025
	2	0.0114036	1.4087
	3	0.00586926	0.72503

same results. The first principle component of the humeral set (**Table 2**) explains substantially less variance in the sample than PC1 does in the other three elements. The second notable observation from these plots is that there does seem to be a consistent relationship among some taxa. For example, *Papio hamadryas* appears to display consistently more variation than *Theropithecus gelada*, especially in the forelimb. Only in the tibia does *P. troglodytes* display more variation than *H. sapiens*, while in the other elements a comparison between the two suggests equivalent levels of variation. Unfortunately, these patterns are difficult to assess in the macaque samples using this method, but they reiterate those found in the measures of variance reported in **Table 3**. That is, while individual bony elements are not returning consistent results, there is some indication that more versatile species display more variance, especially in the forelimb. The humeral data suggests *Homo sapiens* display the most variation, while *Papio hamadryas* has the most radial variation. In the hindlimb, both *H. sapiens* and *M. fascicularis* show the most femoral variation, yet in the tibia *Pan troglodytes* and *P. hamadryas* appear the most variable taxa. Overall, there is no indication that any one taxon displays consistently more variation across all four elements.

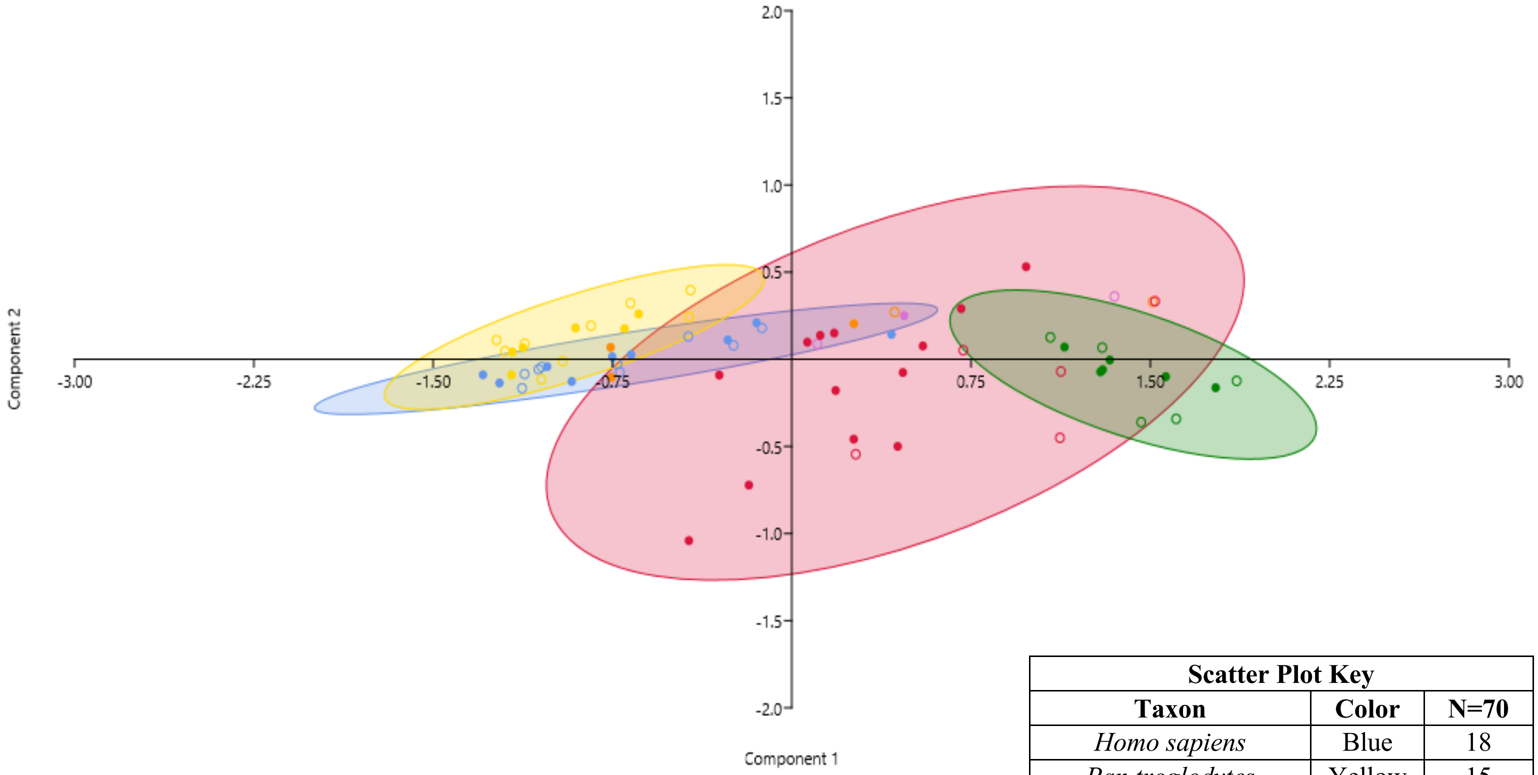
It is important to note that individuals missing more than 50% of the variables, or long bone lengths, were excluded entirely from these analyses (see sample sizes reported in **Figures 1-4**). This is because the iterative imputation method, recommended by *PAST* for use in principal components analysis with missing data, may overestimate components when too much data is missing (Hammer *et al* 2001, pg. 98). Therefore, while some data presented in these analyses are estimated, this method should not alter the overall pattern of the results.

Figure 1: Humerus, Principal Components Analysis, Pooled Sex



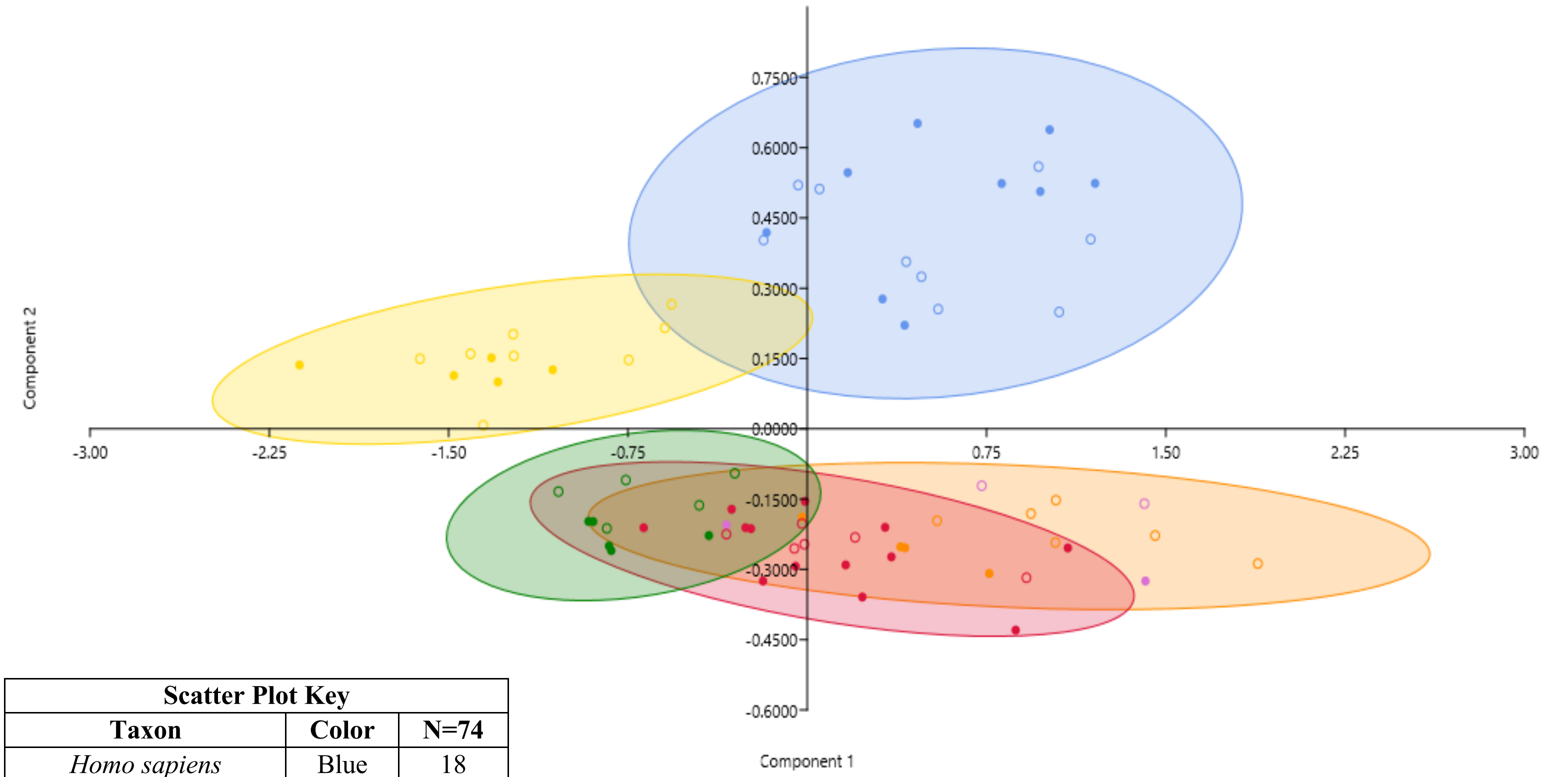
Scatter Plot Key		
Taxon	**Color**	**N=78**
Homo sapiens	Blue	18
Pan troglodytes	Yellow	14
Papio hamadryas	Red	21
Theropithecus gelada	Green	13
Macaca fascicularis	Orange	9
Macaca nemestrina	Purple	3

Figure 2: **Radius, Principal Components Analysis, Pooled-Sex**



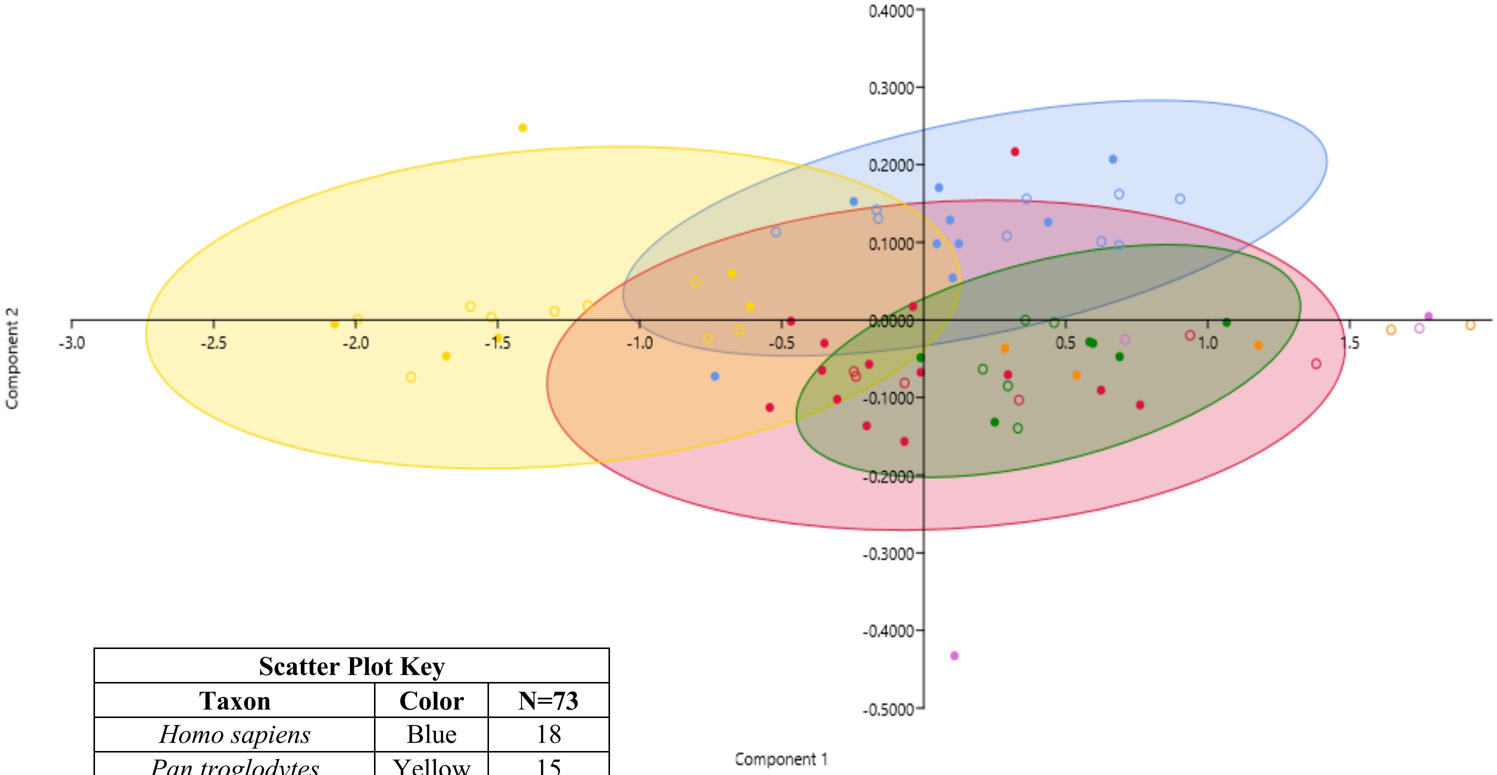
Scatter Plot Key		
Taxon	**Color**	**N=70**
Homo sapiens	Blue	18
Pan troglodytes	Yellow	15
Papio hamadryas	Red	18
Theropithecus gelada	Green	11
Macaca fascicularis	Orange	5
Macaca nemestrina	Purple	3

***Figure 3*: Femur, Principal Components Analysis, Pooled-Sex**



Scatter Plot Key		
Taxon	**Color**	**N=74**
Homo sapiens	Blue	18
Pan troglodytes	Yellow	13
Papio hamadryas	Red	19
Theropithecus gelada	Green	10
Macaca fascicularis	Orange	10
Macaca nemestrina	Purple	4

Figure 4: **Tibia, Principal Components Analysis, Pooled-Sex**



Scatter Plot Key		
Taxon	**Color**	**N=73**
Homo sapiens	Blue	18
Pan troglodytes	Yellow	15
Papio hamadryas	Red	20
Theropithecus gelada	Green	11
Macaca fascicularis	Orange	5
Macaca nemestrina	Purple	4

Small sample sizes, however, impact these analyses, even when it's only in a single group; this is because the data are scaled within the total sample, and therefore a relatively small group may appear widespread while a comparatively large group may appear reduced compared to its actual elliptical area. In these cases, it was prudent to display individual results yet not create an ellipse defining the area of largest variation around taxa with small sample sizes. This technique was applied most commonly to the macaques, so those results should be interpreted with caution. Although PCAs are not statistical tests, nonetheless, these analyses reveal the dimensions of the variation in the sample.

Measures of Variation

Table 3 includes the summations and averages of the measures of variation for each subsample and for each bony element. Measures of variation for each variable, organized by subsample (species/sex groups) and along with other relevant descriptive statistics are reported in their entirety in **Appendix F**. **Table 3** reports pooled sex values, on data adjusted by the geometric mean only. Single sex sample sizes are likely too small to detect meaningful differences in variance (see **Appendix F**). While sex is known among all individuals in this dataset, it is an unlikely scenario for a fossil assemblage to have all elements identified to sex; therefore, sexual dimorphism was not considered a factor in these analyses.

Table 3 reveals at least two patterns inherent in the data. First, it is notable that the individual bony elements do not return the same results. For example, more versatile species (*H. sapiens*, *P. hamadryas*, *M. fascicularis*) seem to have more variance than less

Table 3: Measures of Variation by taxon, from GM adjusted variables with sexes pooled[1]

	Variance		Standard Deviation		Coefficient of Variance	
	Sum	***Mean***	***Sum***	***Mean***	***Sum***	***Mean***
Humerus						
H. sapiens	0.191815	0.013701	1.19618	0.085441	83.16961	5.940687
P. troglodytes	0.110608	0.007901	0.889762	0.063554	62.29828	4.449877
P. hamadryas	0.136289	0.009735	1.041821	0.074416	82.6925	5.906607
T. gelada	0.064985	0.004642	0.73413	0.052438	61.69253	4.406609
M. fascicularis	0.597974	0.042712	1.785455	0.127533	91.91339	6.565242
M. nemestrina	0.293839	0.020989	1.249145	0.089225	67.58512	4.827509
Radius						
H. sapiens	0.256547	0.025655	1.093457	0.109346	76.8662	7.68662
P. troglodytes	0.110954	0.011095	0.789952	0.078995	66.62256	6.662256
P. hamadryas	0.303055	0.030305	1.167596	0.11676	81.28334	8.128334
T. gelada	0.066998	0.0067	0.655961	0.065596	66.52284	6.652284
M. fascicularis	0.944723	0.094472	1.844677	0.184468	99.50356	9.950356
M. nemestrina	0.448502	0.04485	1.340161	0.134016	85.96786	8.596786
Femur						
H. sapiens	0.271337	0.015961	1.491302	0.087724	139.294	8.193764
P. troglodytes	0.262125	0.015419	1.547375	0.091022	128.361	7.550646
P. hamadryas	0.242542	0.014267	1.274161	0.074951	93.60432	5.506137
T. gelada	0.096487	0.005676	0.971539	0.057149	88.29636	5.193904
M. fascicularis	0.375085	0.022064	1.614851	0.094991	120.1283	7.066372
M. nemestrina	0.73372	0.04316	1.967224	0.115719	129.263	7.603706
Tibia						
H. sapiens	0.228015	0.019001	1.021584	0.085132	70.06744	5.838953
P. troglodytes	0.28752	0.02396	1.134807	0.094567	71.50279	5.958566
P. hamadryas	0.286476	0.023873	1.102742	0.091895	69.32143	5.776786
T. gelada	0.103738	0.008645	0.810797	0.067566	72.3309	6.027575
M. fascicularis	0.510857	0.042571	1.415766	0.11798	81.1298	6.760817
M. nemestrina	0.713206	0.059434	1.655974	0.137998	92.80106	7.733422

[1] Reported from geomean-adjusted data.

versatile species in the forelimb (humerus and radius), but not necessarily the hindlimb (femur and tibia). Across taxa, the humerus displays the least amount of variation, whereas the radius displays the most. Second, no taxon is easily distinguishable as "most variable". While *H. sapiens*, for example, displays more variation than *P. troglodytes* on three of four elements (humerus, radius, and femur), *H. sapiens* does not display more variation than *M. nemestrina* across all elements. These statistics are informative, but comparison between them does not constitute a statistical test of the hypothesis and must be supplemented with further investigations.

Analyses of Variation

To determine if the patterns of variation observed from measures of variance and from the PCAs are significantly different among study taxa, analyses of variance (ANOVA) were performed in *SAS*. These ANOVAs test the hypothesis of equal variance among groups. If this hypothesis is rejected, then pairwise T-tests with Bonferroni adjusted alpha values were used to test for pairwise differences; this analysis produces more conservative determinations for between group differences.

In total, reported here are the results of forty-two ANOVAs performed on taxa with sexes pooled including four skeletal elements and three composite skeletal subsets, each with three measures of variation. The measures of variation are reported based on both unadjusted data, and data adjusted by the geometric mean. **Table 4** displays p-values from these analyses, where significant results are bolded with asterisks; highlighted significant results are available in **Figures 5-8**. Box plots and pairwise tables for all 42 ANOVAs are available in **Appendix H**.

Table 4: Skeletal Element Generalized Linear Models, p-values per measure of variance[1]

	Stan Dev	***Samp Var***	***Coef Var***	***Adj SD***	***Adj SV***	***Adj CV***
Humerus	0.5882	0.6265	**<.0001***	0.4522	0.1277	0.1475
Radius	0.9768	0.9535	**<.0001***	0.5725	0.3124	0.4795
Femur	0.6617	0.7101	**<.0001***	0.7469	0.4972	0.3362
Tibia	0.9246	0.8774	**<.0001***	0.8750	0.6163	0.7775
Skeletal, Total	0.4586	0.4123	**<.0001***	0.1417	**0.0169**	0.2922
Skeletal, Length	**0.0001***	**0.0002***	**<.0001***	**<.0001***	**<.0001***	**<.0001***
Skeletal, Width	**<.0001***	**<.0001***	**<.0001***	0.5905	0.7507	0.9112

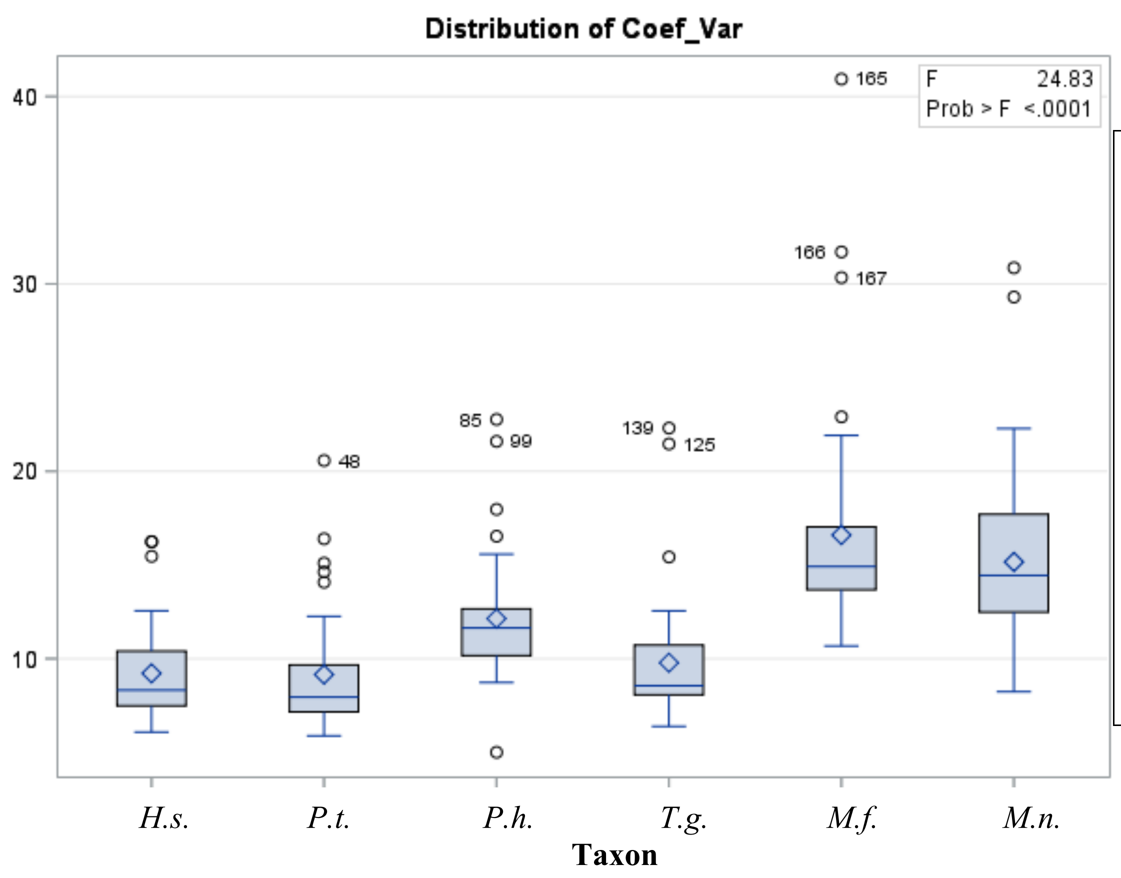
[1] Bold type marks significance at *a*=0.05; asterisks mark significance after Bon. corr.

Perhaps the most obvious pattern discernible in **Table 4** is that the only measure of variation that produces consistently significant results is the coefficient of variation based on unadjusted data. This is likely due to the nature of the statistic itself, because the coefficient of variation is a ratio of the standard deviation to the arithmetic mean, and therefore is more sensitive to variance due to absolute scale. Once data adjusted for absolute size is introduced, the statistical significance disappears. It is important to note that except for composite length, no element or measure of variance indicates a significant difference in variation among taxa.

Highlighted results of the generalized linear models are reported in **Figures 5-8**; all four figures feature a box plot on the left, and the pairwise rankings on the right. Here, all possible pairwise combinations between taxa are tested, and the rankings table indicates which taxa are significantly different from which, if any.

Figure 5

Coefficient of Variation in ‘Skeletal, Total’, Box Plot (left) and Bonferroni Groupings (right)



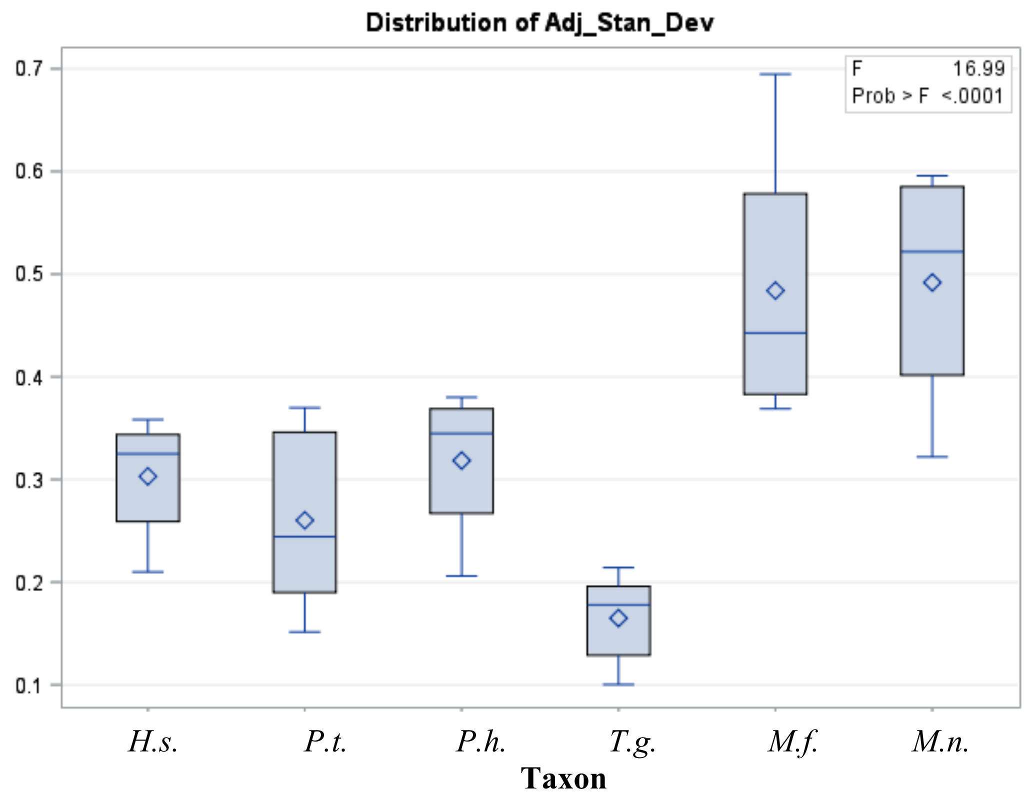
Means with the same letter are not significantly different.

Bon Grouping	Mean	Taxon
A	6.9603	*M.f.*
A	6.8391	*M.n.*
B	4.6775	*P.h.*
B	4.5709	*H.s.*
B	4.2675	*P.t.*
C	2.4278	*T.g.*

[1] Data was adjusted by the geometric mean per individual

Figure 6

Standard Deviation in ‘Skeletal, Lengths’, Box Plot (left) and Bonferroni Groupings (right)[1]



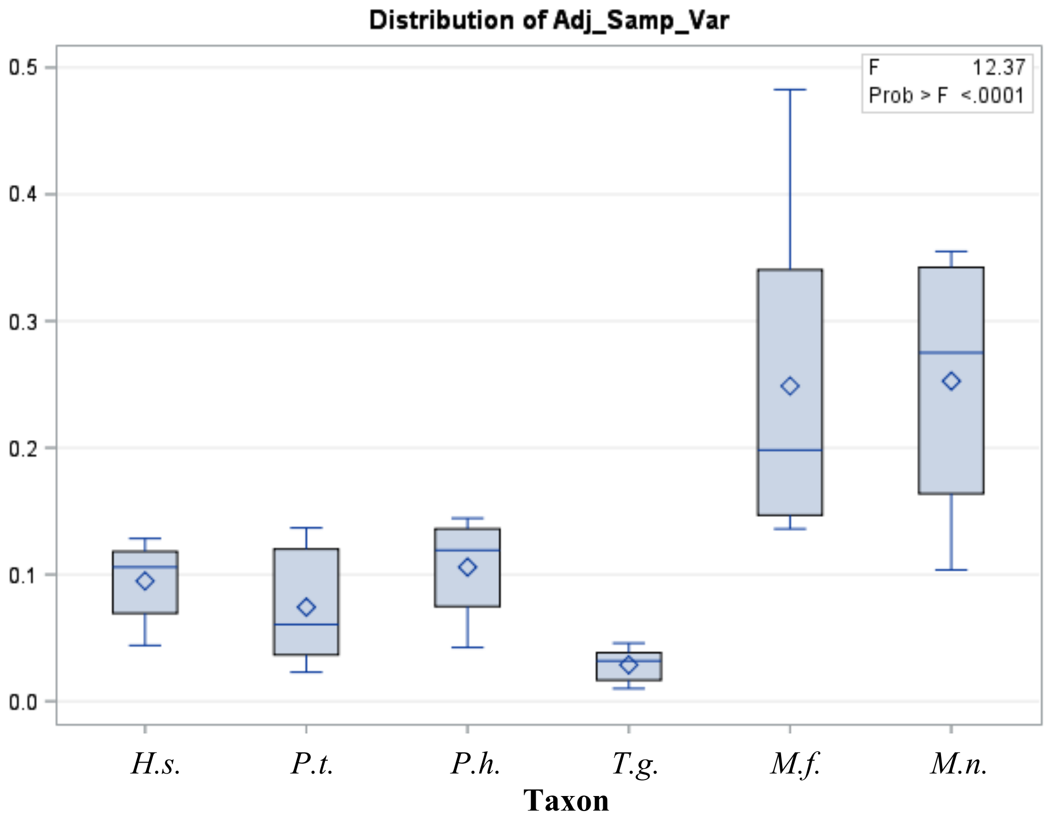
Means with the same letter are not significantly different.

Bon Grouping		**Mean**	**Taxon**
	A	0.49187	*M.n.*
	A	0.48399	*M.f.*
	B	0.31843	*P.h.*
	B	0.30302	*H.s.*
C	B	0.26022	*P.t.*
C		0.16500	*T.g.*

[1] Data was adjusted by the geometric mean per individual

Figure 7

Sample Variation in ‘Skeletal, Lengths’, Box Plot (left) and Bonferroni Groupings (right)[1]



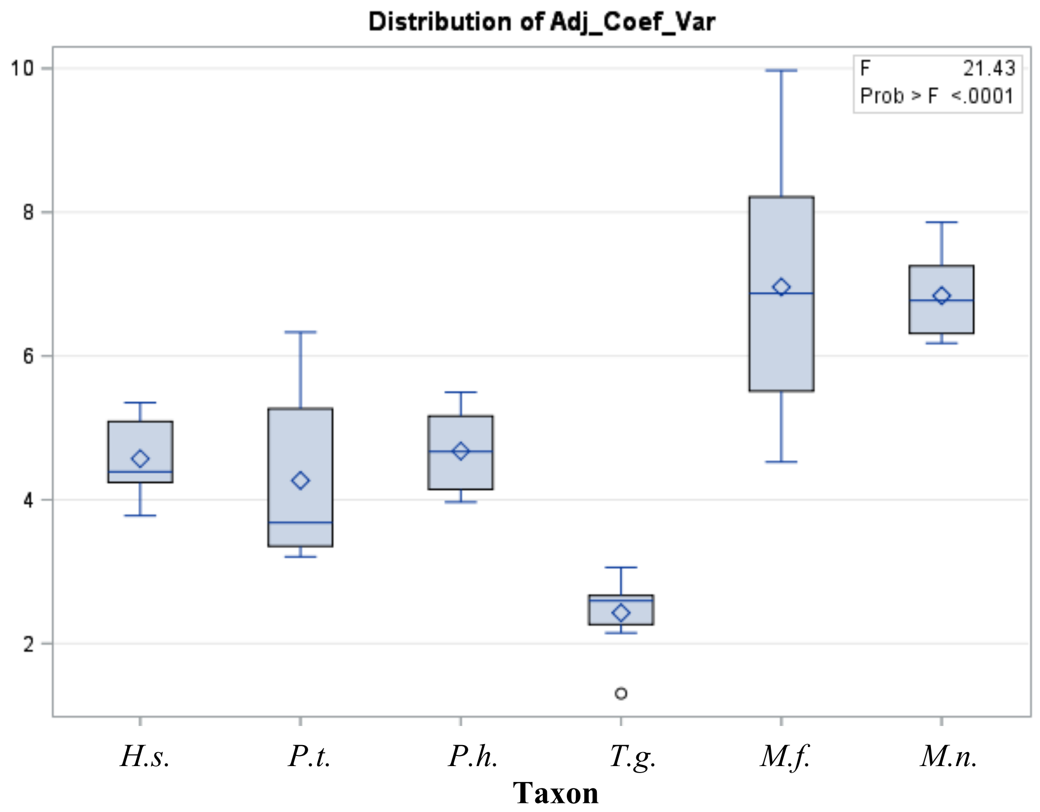
Means with the same letter are not significantly different.

Bon Grouping	Mean	Taxon
A	0.25263	*M.n.*
A	0.24873	*M.f.*
B	0.10584	*P.h.*
B	0.09494	*H.s.*
B	0.07430	*P.t.*
B	0.02871	*T.g.*

[1] Data was adjusted by the geometric mean per individual

Figure 8

Coefficient of Variation in 'Skeletal, Lengths', Box Plot (left) and Bonferroni Groupings (right)[1]



Means with the same letter are not significantly different.

Bon Grouping	Mean	Taxon
A	6.9603	*M.f.*
A	6.8391	*M.n.*
B	4.6775	*P.h.*
B	4.5709	*H.s.*
B	4.2675	*P.t.*
C	2.4278	*T.g.*

[1] Data was adjusted by the geometric mean per individual

The significant results on unadjusted data for the total skeletal composite variable, **Figure 5**, may indicate why the lengths variable is the only measure showing consistent differences. This figure shows that the macaques are significantly different from the other four species, but not from each other. Likewise, the apes are significantly different from the monkeys, but not from each other. However, in three of four bony elements the baboons do indicate significant differences from one another, where *Papio* is consistently more variable than *Theropithecus*. The box plot does not easily indicate the rankings visually, but one can observe the relative scatter among the pairs. Each plot also has a sizable number of outliers. These are the lengths, which vary more than the diameters, (e.g. distal width); this pattern is discernible among the measures of variance reported in **Appendix F**. These results are clear: the measurements which drive the majority of variation are those that capture the maximum lengths of the long bones.

Significant results for "skeletal, length" are reported in **Figures 6-8**. Again, we can observe that macaques are the most variable, but are not significantly different to each other. Humans and chimpanzees are also not significantly different to one another, but the baboon pair is significantly different where *P. hamadryas* is more variable. **Figures 6-8** show the patterns among taxa, which are also echoed by the total skeletal composite variable results (**Figure 5**). *Theropithecus gelada* scores lowest among all taxa, the macaque species score highest, and the ape pair occupy the middle rung. Within study pairs, only the baboons are significantly different from each other.

Discussion

These results on analyses of variation in postcranial elements revealed several consistent patterns. First, isolated skeletal elements display different patterns of variation from one another; for example, tibiae do not vary as femora do. While this result may seem somewhat obvious, it implies that documenting postcranial variation is heavily influenced by the choice of bony element, the number of elements, and the number of measures that are included in analyses.

Second, measures of variation and PCAs suggested that more versatile taxa (*H. sapiens*, *P. hamadryas*, and *M. fascicularis*) may display more postcranial variation, particularly in the forelimb. However, this effect was reduced to non-significance once the data was adjusted for absolute size using the geometric mean. The ANOVAs also initially indicate that forelimbs are more variable, but these results did not rise to the level of statistical significance in any single element once absolute scale was removed. The composite skeletal data sets revealed the source of most variation (within each bone and across the appendicular skeleton) to be the long bone lengths. These length measurements, analyzed alone, revealed the only significant results relevant to the hypothesis: among postcranial variation in long bone lengths, *Papio hamadryas* was more variable than *Theropithecus gelada*. The other pairs did not show differences between species. Taken together, these results reveal a number of interesting observations of both biological and methodological relevance.

Hypothesis assessment

As described in Chapter One, support for the overarching hypothesis of this dissertation (that ecological flexibility correlates with increased phenotypic variation) would feature 1) significant differences in measures of variation among taxa, 2) more ecologically versatile species (*H. sapiens*, *P. hamadryas*, *M. fascicularis*) showing greater variation than less ecologically versatile pair partners (*P. troglodytes*, *T. gelada*, *M. nemestrina*), and 3) modern humans would consistently have higher means of their measures of variance.

The central hypothesis of this chapter expects that ecologically flexible species are more postcranially variable than less ecologically flexible species of a similar size and phylogeny. However, the PCA plots suggest no consistent pattern between the taxa (**Figures 1-4**), with the exception of *Papio hamadryas* being more variable than *Theropithecus gelada*. Pooled-sex measures of variation (Sample Variance, Standard Deviation, and the Coefficient of Variance; **Table 3**) indicated that more versatile species (*H. sapiens*, *P. hamadryas*, *M. fascicularis*) were only more variable in the forelimb, and only when not adjusted for absolute scale. Thus, there was also no consistent pattern evidenced between taxa in the reported measures of variance, except, again, *P. hamadryas* does appear to display more variation than *T. gelada*. The composite skeletal ANOVAs reveal that these results are consistent across variables; while the other two species pairs do not consistently display any pattern of variation, the baboon pair does.

Interestingly, throughout this study *Papio hamadryas* is being used *sensu lato* (*e.g.* Gilbert *et al.* 2018; Frost *et al.* 2003; Szalay and Delson 1979; Jolly and Brett 1973) and therefore includes several subspecies. Two subspecies (*P.h. anubis* and *P.h. ursinus*) are represented in the postcranial analyses, while five are present in the craniodental material. Early in these investigations, I considered that the *Papio* sample would have to be reduced to a single subspecies in order to make an equivalent comparison with *Theropithecus gelada*. The gelada baboon is more geographically restricted and is the single remaining species from a genus which was much more diverse in the past

(Jablonski and Frost 2010; Szalay and Delson 1979). On the other hand, *Papio* as a genus is widely considered one of the most phenotypically and ecologically diverse extant old world monkeys (Strum 2001; Devore and Washburn 1963; *see* Harvati *et al* 2004). Therefore, if ecological flexibility were correlated with phenotypic variability, then we would expect the differences between these two taxa to be substantial. However, analyses of variance have revealed only moderate patterns of difference between the two taxa in all anatomical regions sampled in this dissertation. These results themselves are not the most notable aspect here, but rather why it is that *Papio hamadryas* (*sensu lato*) is not obviously and consistently more variable than *Theropithcus gelada*.

No line of analysis performed here returned results indicating that humans are the most variable taxon. In most analyses, the amount of postcranial variation within *H. sapiens* is moderate, greater than *T. gelada*, but less than *P. hamadryas*. The pairwise rankings showed that they were not greater than *Pan troglodytes* on any measure of variation, and this result is especially robust because as a pair, these taxa had roughly equivalent sample sizes and lacked missing data.

Neither macaque species was consistently more variable than the other. Although the macaques appear to have more variation overall, this result is quite likely due to small sample sizes and incomplete datasets. Thus, either these confounding factors obscured meaningful results, or there were no differences between these taxa. Unfortunately, this was especially problematic in this genus (see following subsection). Therefore, any comparisons involving *Macaca* from this data set should be approached with extreme caution.

Overall, this investigation finds little support for any of the central hypotheses. The single study pair with results indicating that a more ecologically versatile species displays more variation postcranially are the baboons. Given the test conditions, further exploration of phenotypic and genotypic variation between *Papio* and *Theropithecus* may be informative.

Confounding factors

The lack of consistent pattern between the taxa observable in the PCA plots (**Figures 1-4**) suggests that either the small samples, or the disparate number of variables per element, may be influencing patterns of variation, as variance is highly sensitive to differing sample sizes. As this study makes clear, the number and relative magnitudes of individual variables greatly influence sample variation.

These datasets include many variables per individual and are large enough to exceed the minimum of 20 data points per taxon, the threshold at which meaningful conclusions about variance can be derived according to Gilbert and Grine (2010). However, differences in number of individuals or variables can influence patterns of variance in samples above that dataset threshold. For example, the humerus may appear less variable than the radius only because the radial dataset contains ten linear measures while the humeral set has fourteen. These inequities were addressed in the composite variables utilized in the ANOVAs, where each skeletal variable had an equal number of measures selected from each bone. Here, reviewable in **Figure 5**, we learn that once equivalent measures are introduced, and absolute size is accounted for, differences among taxa are absent. This was also true for the composite variable "skeletal, widths" (Coefficient of Variation, adjusted, p=0.9112).

Sample sizes are the smallest among macaques (only 36 included in total for analyses reported here) and this may confound patterns of variation. Further, although missing data occurred minimally in some taxa, it was the most prominent in the macaques. Because these factors were true for both species, their results are still fairly comparable to each other, though we must be cautious when comparing them to other taxa. Thus, they were not able to be assessed well in the PCA analyses, and their overall variance was inflated in the pairwise rankings of the ANOVAs. While every effort was made to correct for these factors, some were unavoidable. *M. nemestrina*, for example, is infrequent among museum collections and frequently have soft tissue remnants, resulting in a higher rate of missing data. It has become obvious to me in the course of this investigation that variance is a statistic that is sensitive to sample size and in the case of the macaques these were significant confounding factors for obtaining meaningful results about postcranial variation.

Postcranial Features

This postcranial dataset poses some challenges to measuring phenotypic variation compared to the craniodental material considered in Chapter One. Namely, both crania and dentition are more spherical in shape, and, as measured, their linear dimensions do not vary as much between each other in magnitude. In other words, molar widths and molar breadths are roughly the same size. More elongated objects, like long bones, may have dimensions which do vary substantially from one (proximal width of the radius) to the other (length of the radius). In order to reflect true biological variation about postcranial elements, measurements were taken from all dimensions of the bones. From a statistical point of view, however, this technique poses some challenges for exploration of the hypotheses. Because so much variation in the samples was ultimately attributable to long bone lengths, that factor weighed heavily in all analyses. When long bone lengths are examined as a subset, they indicate a limited support for the overall hypothesis; that is, long bone lengths are consistent with the hypothesis that ecologically versatile catarrhines are more variable than less flexible sister taxa (see **Figure 8**). However, when that factor is removed, or scattered across all elements with other variables, evidence for differences in variation among taxon pairs diminishes.

While it is debatable whether long bone lengths qualify as sufficient indicators of postcranial skeletal variation, I argue they do. Certainly, there are other functionally informative aspects of the postcranium whose values will and do vary. However, limb bone lengths contribute a large component of overall body shape and proportions relevant to locomotion (such as human height, or the inter-membranal index). Further, limb lengths are known to vary within populations due to factors such as climate and nutritional status (Allen's rule; *see* Ruff 1993). These observations indicate that not only do long bones influence many body processes, but that they are also developmentally plastic in response to the external environment.

Developmental plasticity, that is the ability to incorporate environmental input into the adult phenotype during periods of growth to at least some degree, is likely a source of at least some variation for most every phenotypic trait (West-Eberhard 2003; Schlichting and Pigliucci 1998). Traits with long postnatal growth periods are more susceptible to environmental input than others, and these traits may reveal increased variation in the adult if juveniles are encountering varied habitats and substrates (Antón *et al* 2016; West-Eberhard 1989). Postcranial variation, particularly long bone lengths, may be the strongest indicator of ecological versatility in a population examined in this study. It is notable that Sanchez and Schoch (2013) found that bone histology, rather than bone morphology, revealed patterns of variation correlated to varied habitat use (and evolutionary success) in an extinct lineage of tetrapods.

Although long bone length may be a strong indicator, here, the trait remains a single composite variable among many others tested. All other variables tested among the postcranial samples, including 44 variables from bony elements and two other composite skeletal variables, did not indicate consistent differences between study taxa. Further, craniodental material does not support the hypothesis that phenotypic variation in these study taxa are discernible by ecological versatility. It is possible that long bone lengths are singularly informative traits, indicating the result of ecological versatility, but more research should be conducted. Specifically, comparisons of variation in long bone lengths among developmental stages, and across taxa of differing ecological versatility levels, should reveal if long bone lengths increase in variation within more versatile species.

Conclusion

In this chapter, support for ecological versatility increasing phenotypic variation is moderate at best, given the ambiguity of the results of most variables tested. In general, *Papio hamadryas* is more variable than *Theropithecus gelada*, but the macaques and the apes are less consistent. Furthermore, if ecological versatility does affect phenotypic variation, then I expect modern humans and *P. hamadryas* (*sensu lato*) to exhibit notably greater variation, perhaps by orders of magnitude. According to these results, human variation is modest compared to that of chimpanzees, and the increase in variation seen in hamadryas over gelada baboons is slight.

If ecological flexibility is correlated with increased phenotypic variation in catarrhines, then based on the sample used here that effect is smaller than the impact of sample size and missing data. In other words, the effect is slight enough to be overwhelmed by confounding factors which may be difficult to avoid in normal practice, and impossible to avoid under some conditions such as the fossil record. Obscured patterns and false positives may arise when variance can easily be swayed by a number of factors like sample size, absolute scale, and the anatomical region measured. Fossil assemblages, for example, where associated elements are rare and most are fragmented, may prove difficult to assess in terms of phenotypic variation in a biologically meaningful way. These factors may obscure the reliable detection of a correlation between ecological versatility and phenotypic variation or may instead indicate a pattern where none exists. These ideas will be explored further in the next chapter.

Although there are not consistent differences indicated among taxa for any measure of variance on adjusted data, long bone lengths as a single composite variable did reflect increased variation in more ecologically flexible taxa (**Table 4**). These results suggest that long bone growth may be a fruitful avenue for further investigation. Growth periods can be particularly sensitive to environmental perturbations, in the sense that activity and nutrition in early development likely has a larger impact on the adult phenotype than those same factors do in early adulthood (Antón and Snodgrass 2012; Kuzawa and Bragg 2012; West Eberhard 2003). These effects of developmental plasticity and accommodation may be strongest in the limb bones, relative to other anatomical regions, due to the functional integration of environmental impacts during growth periods (Turley and Frost 2018; Wang 2011). Therefore, long bone lengths may reflect the causal relationship (developmental plasticity) between ecological versatility and increased phenotypic variation, which Antón, Potts, and Aiello (2014) originally posed.

This study represents the second phase in a continuing investigation of a central hypothesis: does ecological versatility correspond with increased phenotypic variation in catarrhine primates? The first phase (Chapter 1) focused on craniodental variation. Here, I focused on postcranial variation including the humerus, radius, femur, and tibia. In both instances, similar analyses were conducted to explore the magnitude of variation within the study samples. For the third, and final phase of this investigation, I will take a different approach by modeling fossil assemblage conditions to further evaluate detectable patterns of variance in my samples.

CHAPTER IV:

MEASURING VARIATION IN FOSSIL HOMININS: HUMAN EVOLUTION, ECOLOGICAL VERSATILITY, AND THE VARIABILITY SELECTION HYPOTHESIS

Introduction

The variability selection hypothesis (VSH) proposes that the ecological strategy of diversifying resource and habitat use by a species, in response to fluctuating environments, has increased phenotypic variation in early *Homo* (Antón, Potts, and Aiello 2014). Simply, variability selection can be described as "adaptation to adaptability" (Potts 1998a); specifically, VS is based on paleoecological evidence that species which diversified their diets and the range of habitats that they could exploit in eastern Africa between 2.5-1.5 ma persisted, while more specialized species went extinct (Potts 2012, 2002). VS hypothesizes that the increase in diversity of anatomical and behavioral traits within early eastern African *Homo spp.*, relative to contemporaneous australopiths, is a result of adapting to ecological fluctuations (Potts and Faith 2015; Potts 2013, 2002, 1998a).

The hypothesis that a more ecologically versatile primate species may display more phenotypic variation than less ecologically versatile species is a directly testable prediction of VSH, provided adequate samples. Antón, Potts, and Aiello (2014) report the variation in several morphological features to argue that early *Homo spp.* tend to be more variable than australopith species, but one potential concern with their analysis is that available early hominin sample sizes are too limited. In this chapter, I will evaluate the sample sizes necessary to test for differences in variance between populations using the several of the anatomic characters of Antón, Potts, and Aiello (2014; see Table 1) where I have equivalent skeletal data.

Using extant taxa (*Homo sapiens* and *Pan troglodytes*) alongside published extinct hominin data (australopiths and early *Homo spp*.), I compare patterns of skeletal variation within dental and postcranial measures. Directly comparable measures across taxa allow a determination on the sample size threshold for reliably measuring variance among specific skeletal measures; here, molar areas and femoral lengths. Chapters 1 and 2 revealed the contours of standing phenotypic variation between these and other extant taxa in three separate anatomic regions: cranial, dental, and postcranial variation. Factors, such as sexual dimorphism, body size, and phylogeny, which may impact sample variation and obscure comparisons, were minimized or controlled for; not all of these factors are avoidable in fossil samples.

Here, permuted samples of increasing size are used to empirically determine sample sizes necessary to estimate phenotypic variation present in these populations using specific measures from of Antón, Potts, and Aiello (2014). The focus of this chapter is not to necessarily evaluate the biological hypotheses offered by VSH, but rather to evaluate the necessary conditions for being able to test the hypothesis in the first place.

Background

<u>*Variability Selection Hypothesis*</u>

Among hominin evolutionary studies, the relationship between fluctuating environments and phenotype is described in the variability selection (VS) hypothesis, first proposed by Potts in 1996 and refined through a series of papers (Potts and Faith 2015; Antón, Potts, and Aiello 2014; Potts 2013, 2012, 2002, 1998a, 1998b). It is offered as an adaptive framework to explain the origin and subsequent success of *Homo*, relative to an increasingly variable climate. Paleoecological evidence suggests that early *Homo spp.* regularly encountered environments in flux, and as such had to diversify its diet, habitat occupation, and social behaviors to cope with novel environmental factors (Antón *et al* 2016; Potts and Faith 2015; Grove *et al* 2015; Stewart and Stringer 2012). The result of this selection for environmental versatility is that early *Homo* spp. display "versatilist" traits, like generalized dentition, larger brain, and more complex material structures such as tools (Potts 1998a; see Borg and Channon 2012 for operationalization of this in social learning modelling). Another proposed outcome of VS is an increase in the range of adult phenotypic variability, facilitated by developmental adjustments to environmental flux during growth periods (Antón *et al* 2016; Potts and Faith 2015; Antón, Potts, and Aiello 2014; but see Zichello *et al* 2018).

The variability selection hypothesis (VSH) states that *Homo* is under selection for adaptability, as an evolved response to a variable and unpredictable environment (Potts and Faith 2015; Antón, Potts, and Aiello 2014; Potts 1996, 1998a, 1998b, 2012). Fossil evidence from early *Homo* and *H. erectus* in eastern Africa is argued to show increases through time in both phenotypic variation and ecological versatility as compared to contemporaneous australopiths (Antón, Potts, and Aiello 2014; Potts 2012; but see Schroeder *et al* 2014). Potts (2012,1998a,b) hypothesizes that the increases in body size, brain size, geographic range, and niche diversification are features of *Homo* that evolved in response to extreme fluctuations in food availability and seasonal predictability. Especially between 2.5 and 1.5 Ma there are an increasing number of oscillating climatic periods, during which time phenotypic variation among early *Homo spp.* also increases (Potts and Faith 2015; Antón, Potts, and Aiello 2014; Ash and Gallop 2007).

Decreasing environmental predictability was likely a pressure, asserts Potts, for hominin populations in eastern Africa throughout the later Miocene through Plio-Pleistocene and would have been an impetus for the use of a wide range of habitats (Antón *et al* 2016; Antón, Potts, and Aiello 2014; Potts and Faith 2015; Stewart and Stringer 2012). Paleoecological data indicates that seasonal duration, temperature, rainfall, and food availability become increasingly variable and unpredictable from the late Miocene to the recent (*see* Levin 2015; Stewart and Stringer 2012). Climatic conditions are well documented from multiple lines of evidence such as marine oxygen isotope analysis, oceanic dust records, sedimentology, palynology, paleosol and loess patterning, fossil pollen, and carbon isotope analyses in soils, plant wax, and tooth enamel (e.g. Winder *et al* 2015; Cerling *et al.* 2011; Jolly 2009; Bobe 2006; Delson, Tattersall, and Van Couvering 2004; de Menocal 2004; Wynne *et al.* 2004; Zachos *et al.* 2001; Reed 1997; see Potts 2012, 1998b and references therein; de Menocal and Bloemendal 1995).

When an environment varies so unpredictably that habitats cannot support a particular species, that species can respond in three ways: migrate, broaden the range of responses to the environment, or go extinct (Grove *et al* 2015; Grove 2011; Potts 1998a; Vrba 1992). In eastern Africa, fossils of early *Homo* are found in more diverse habitats, were of larger and more varied body sizes, and had a more generalized diet compared to contemporary australopiths (Antón, Potts, and Aiello 2014; Potts 2002, 1998a and references therein). Potts (1998a) proposes that broadening environmental response can be achieved through "versatilist" traits, i.e. ones that support diverse ecological occupation, such as a generalized locomotor strategy, a dietary structure or behavior which could readily allow a shift to newly available foods, a large brain, and mutable social structures (Potts 1998a). Another feasible outcome when responding to environmental fluctuations is to maintain large amounts of phenotypic variation, as Potts and coauthors have argued (Potts and Faith 2015; Antón, Potts, and Aiello 2014; Potts 2012; *see* Lande 2014, 2009; Davidson, Jennions, and Nicotra 2011; Pfenning *et al* 2010; Kussell and Leiber 2005). Evidence put forth in support of this idea includes increasing amounts of intrataxon phenotypic variance from early *Homo*, through *H. erectus*, peaking at the diversity and large population numbers of anatomically modern humans (for early *Homo* phenotypic variation, see Pontzer 2012; also Will and Stock 2015 and Schroeder *et al* 2014).

VSH is rarely advanced in concert with anatomical evidence (but see Potts 2002). However, one of the most specific phenotypic predictions of VSH appears in *Science* (Antón, Potts, and Aiello 2014). Data summarized in their Table 1 presents cranial volumes, body mass estimates, and skeletal metrics which appear to indicate an increase in within-population variation through time, especially for early *Homo spp*. relative to contemporaneous australopiths. In addition to morphological and paleoclimatic evidence, the authors suggest that versatility on multiple biological levels was favored in the dynamic habitats of our ancestors', evidenced in part by an increase in phenotypic variation among *Homo spp*. They further propose these changes were probably not achieved at the genetic level alone, but at least partially through phenotypic and developmental plasticity (Antón et al 2016; Antón, Potts, and Aiello 2014). Phenotypic plasticity as a proposed mechanism for integrating environmental input, therefore correlating environmental flux with increased phenotypic variation, aligns with many other broader hypotheses from across evolutionary biology (Lande 2009; Kussell and Leiber 2005; West Eberhard 2003, 1989; Pigliucci 2001; Schlichting and Pigliucci 1998; Lande and Shannon 1996).

Measuring Fossil Variation

Measures of variance are highly sensitive to sample size (Sokal and Rolfe 2012; Simpson, Roe, and Lewontin 1960). As this dissertation and other studies have shown, detecting patterns of variance reliably across taxa can require large and robust datasets, which are often lacking in the fossil record (*see* Gilbert and Grine 2010). Small sample sizes tend to overestimate the variation actually present in the larger population, in the sense that the larger a sample of individuals becomes, the more reliably we can trust statistical inferences drawn from that sample. However, the precise value at which this threshold is reached does not objectively exist, but it is instead a trait of the sample itself (Sokal and Rolfe 2012). Given a known sample, minimal sample size which will reliably return a result can be rather precisely determined; that is, we can describe the error intervals of our statistical estimates, and gauge how large a sample must be as to exceed the threshold at which the estimates of variance converge with the true sample variance value.

To determine the sample size threshold at which reliable measures of variation can be detected, permutations are conducted on randomized and increasingly large subsamples until convergence on the true sample variance value is reached. By directly comparing skeletal dimensions (here, femoral length and occlusal surface area of molars) between extinct hominin taxa reported by Antón, Potts, and Aiello (2014), and extant hominoids *Pan troglodytes* and *Homo sapiens*, we are able to get a sense of the sample sizes required to reliably measure variance for these anatomic traits.

Materials and Methods

To assess the sample sizes necessary to detect an increase in phenotypic variation between extinct hominin populations, I use skeletal molar areas and femoral lengths from extant *Pan troglodytes* and modern *Homo sapiens* to compare with equivalent measures in fossil hominin samples provided by Antón, Potts, and Aiello (2014). These extant hominoids provide a reasonable comparison to australopith and early *Homo* spp. populations for the purposes of determining necessary sample sizes for measuring variance in these skeletal traits. **Table 1** provides a summary of these samples, while the next subsections provide details on the populations, measurements, and analyses included in this chapter.

Sample Populations

Table 1 offers a summation of the sample data utilized here, including comparisons of australopiths and early *Homo spp.* to a similar extant pair of hominoids, modern humans and chimpanzees. Two columns represent the australopith sample

(South African *Australopithecus africanus* and eastern African *Australopithecus afarensis*) and two represent the early *Homo spp.* sample (eastern African non-erectus *Homo* and eastern African early *H. erectus*); all four columns are derived from Antón, Potts, and Aiello (2014).

Table 1: Study Samples of Fossil and Extant Hominoids

	South Africa *A. africanus*[1]	East Africa *A. afarensis*[1]	East Africa non-erectus *Homo*[1]	East Africa early *H. erectus*[1]	Extant *P. troglodytes*	Modern *H. sapiens*
M^1 area (mm^2)						
N	6	6	8	2	85	42
Range	41	73	53	28	56	77
Mean	179.5	164.1	179.8	163.0	119.6	118.7
Total Samp.Var.	231.50	689.01	327.55	392.00	154.95	248.22
M$_1$ area (mm^2)						
N	7	16	16	7	75	41
Range	60	73	54	46	47	50
Mean	173.1	164.0	163.1	153.4	108.3	118.4
Total Samp.Var.	425.48	401.31	349.60	397.95	116.34	148.47
M^2 area (mm^2)						
N	6	8	10	3	81	41
Range	74	61	93	36	77	81
Mean	221.8	192.4	193.3	164.0	120.8	121.1
Total Samp.Var.	672.17	399.30	642.68	372.00	233.02	236.71
M$_2$ area (mm^2)						
N	0	19	13	4	79	42
Range	–	97	108	28	73	72
Mean	–	188.1	204.3	166.0	118.5	117.7
Total Samp.Var.	–	956.93	1049.42	516.00	194.60	186.68
Femur length (mm)						
N	2	3	3	4	13	18
Range	158	101	86	56	62	97
Mean	355.0	346.0	398.0	450.5	289.0	436.2
Total Samp.Var.	12482.00	3181.00	2330.33	675.00	288.98	703.47

[1] Fossil hominin data reprinted from Anton, Potts, and Aiello 2014; Supplementary materials from this source include original publishing references. Mean area values for *A. africanus* and all *Homo spp.* were originally published incorrectly, where molar area means and ranges were inflated by a factor of 10; these values have been adjusted from the original linear measures, with means and sample variation recalculated here. Molar area values have been added for *A. afarensis* from Kimbel *et al* 2004; means and sample variance for these values was recalculated by the author.

The extinct hominin data is presented as found in from Table 1 in Antón, Potts, and Aiello (2014); individual data points included in these species' means, and their original published sources, can be found in their Supplementary Materials (Table S2). Major sources of data in (especially for the dental measurements) include Wood's *Fossil Remains of Koobi Fora* (1994) with newer *Homo* data contributed from other sources (Leakey *et al* 2012, Spoor *et al* 2007, Rightmire *et al* 2006); *Australopithecus afarensis* data is derived from Kimbel *et al* (2004). These data are based on the most complete members of the labeled taxa and skews some groups to larger or smaller sizes (1470 and 1813 groups, respectively).

Extant populations sampled here are original data derived from populations first reported in Chapters 1 and 2 for *Pan troglodytes* and extant *Homo* sapiens. This pair of closely related taxa approximate fossil hominin differences in body size, and ecological distinctions between the two have been paralleled to proposed distinctions between Australopiths and early Homo *sensu lato* (e.g. Grine and Kay 1988; but see Sponheimer *et al* 2006; Jolly 2001). All specimens included here are adults, with known sex and age; see **Table 1** for sample information used in this chapter, see **Appendix A** for specimen sources.

Skeletal Data

Skeletal data included in this analysis are taken from two regions sampled in the previous chapters: dental and postcranial. Following Antón, Potts, and Aiello (2014), molar area data is derived from linear caliper measures of the buccolingual and mediolateral maximum distances in millimeters, as described in **Appendix B**. Molar width dimensions were multiplied together, and the product is presented in millimeters squared. These data include the occlusal molar areas of M^1, M^2, M_1, and M_2. Also following Antón, Potts, and Aiello (2014), femoral length data is also caliper derived and is represented by a single linear measure; this measure is defined in protocols listed in **Appendix E**, as *Femur Length 2, #26*.

Table 1 presents the ranges, means, and the total sample variance on these measures of dental and postcranial material, including the occlusal molar areas of M^1, M^2, M_1, and M_2, along with femoral lengths. To match extant data with published fossil hominin data, these data have not been adjusted to compensate for differences in absolute size and are presented, and analyzed, as pooled-sex groups. Ranges are reported as whole numbers, means rounded to the nearest tenth of a millimeter, and total sample variance rounded to the nearest hundredth.

Analyses of Sample Size

To determine the sample size necessary to reliably estimate population variance within these taxa for these measurements, permutation analyses of increasingly large sample sizes should illustrate the maximal limit for sample variance accuracy within a population (*see* Gilbert and Grine 2010). Beginning with a sample size of two, a random subsample of n=2 is selected and their sample variance recorded; subsampling variance is repeated 1000 times at each sample size, without replacement. As the sample size is increased (n=3,4,5,etc…), sample variance estimates begin to converge at the total sample variance which is defined per sample. The results will display approximate thresholds in the sample size at which measures of variance become reliable; reliability is determined, here, when 90% of permutation variance estimates fall within 20% of the total sample variation. In other words, these analyses indicate how large a sample must be to reliably return a reasonably accurate measure of variance.

Permutations were performed using *SAS v9.4* software, using analyses designed to illuminate the relationship between sample size and sample variance (*SAS* code written by K. McNulty and S. Frost, and was used here with permission). Each trait was analyzed separately, per taxon. These analyses were performed on pooled sex groups and have not been adjusted for absolute body size, to reflect data published by Anton, Potts, and Aiello (2014).

From these permutation analyses, **Table 2** provides a summary of sample size thresholds where the 95th and 5th percentiles are within 50%, 25%, 20%, and 10% of TSV for any given measure. It should be noted that this author discerns a reasonably reliable estimate of variance at 'within 20%' of TSV; **Table 2** provides both an illustration of the effects of sample size on variance and a general guide for more (or less) stringent estimate accuracy standards. The permutation analyses presented here do not center on biological expectations, as was the case in the previous two chapters, but rather are aimed at determining the necessary sample size for assessing questions involving variation in these taxa.

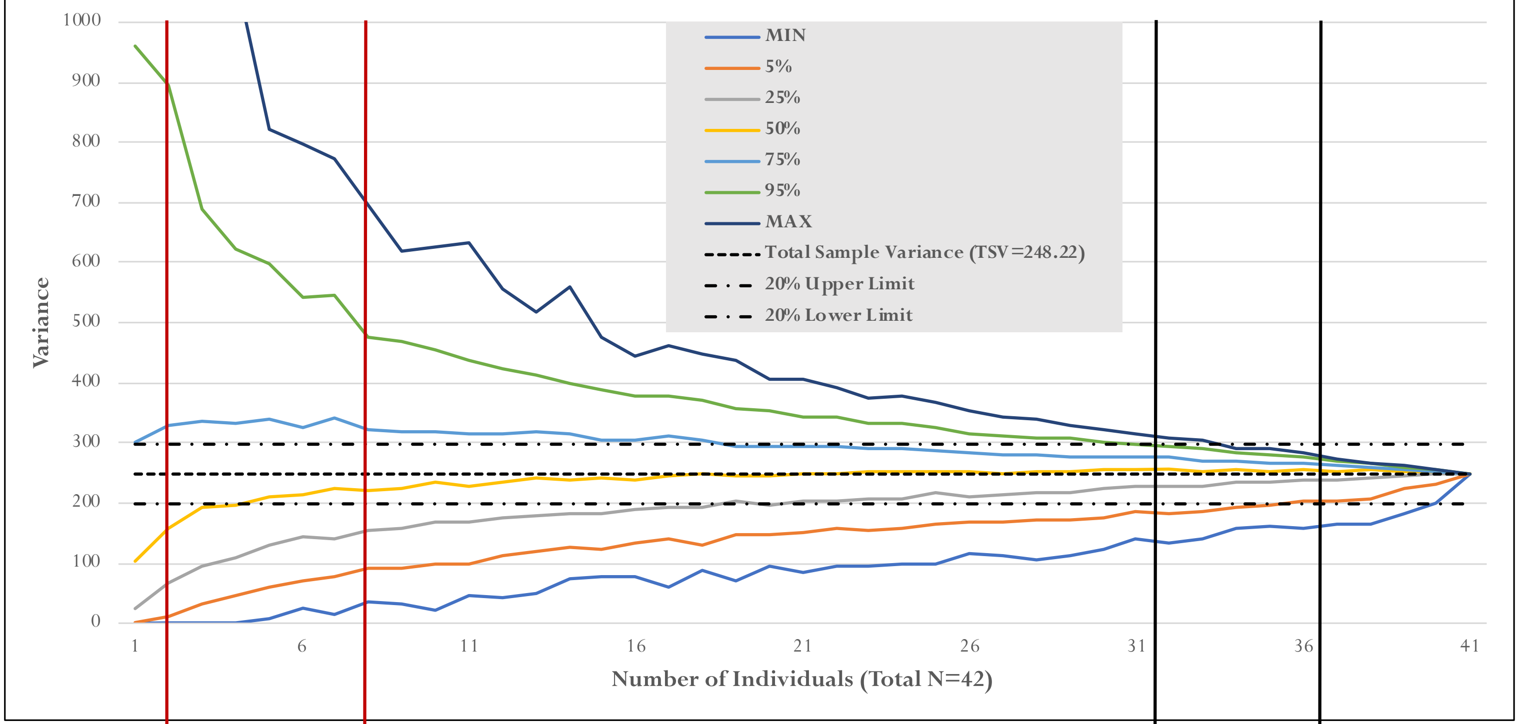
Results

This section begins with a brief discussion of the sample variance reported in **Table 1**, for all hominoid species. Following, **Figures 1-10** present line plots of variance permutations on four different molar areas and femoral length, for both *Pan troglodytes* and modern *Homo sapiens.* Sample sizes for study species, and reliable sample size ranges for detecting variance (established as within 20% of the total sample variation), are reported for each measure. Finally, **Table 2** reports the reliability of sample variance at various sample sizes across skeletal measures. The reliability of an estimate of variance is defined within 50%, 25%, 20%, and 10% accuracy of the total sample variance for that dataset.

Sample Variance

Total sample variance is reported for each taxon per trait in **Table 1**; this measure is equivalent to total sample variance (TSV) reported in variance permutations (**Figs. 1-10**), as representing the total variation measured for that sample. Across all four teeth and sampled species, TSVs range from 116.34 to 1049.42. The low end of variation (TSV=116.34) is occupied by *P. troglodytes* in M_1, the high end is East African non-erectus *Homo spp.*, M_2 (TSV=1049.42). Though both extant taxa have generally lower TSVs than the extinct samples overall, where the highest TSV values are all among early *Homo* samples, there is significant overlap. The lower second molars exhibit the widest range of variation among dentition (TSV range=186.89-1049.29), displaying a range which looks more like the femoral data than the other molars.

Figure 1: Modern *Homo sapiens* M^1 Area, Sample Variance Permutations

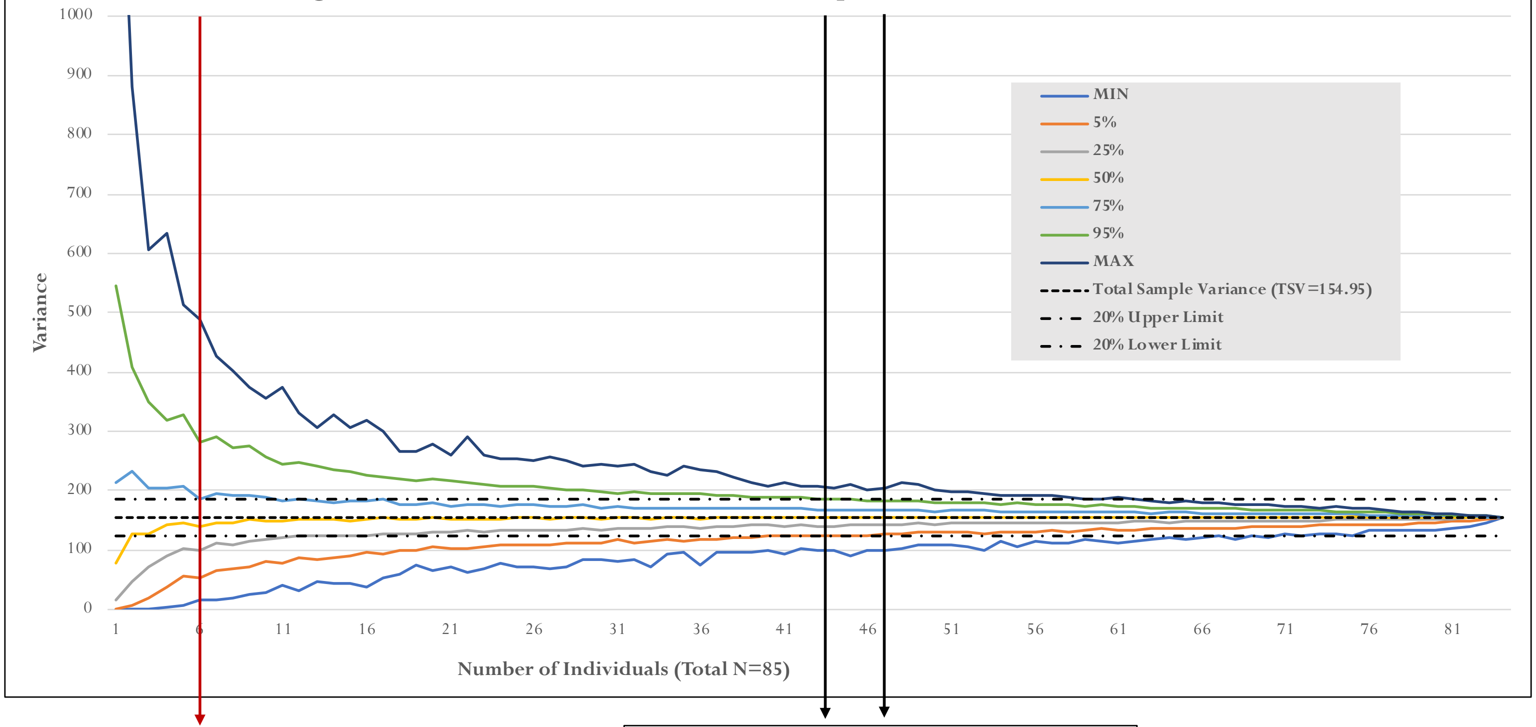


East Africa early *Homo erectus* (N=2)

East Africa all non-erectus Homo (N=8)

Within 20% of true Sample Variance, in 90% of 1000 randomizations (n range=32-37).

Figure 2: Extant *Pan troglodytes* M^1 Area, Sample Variance Permutations

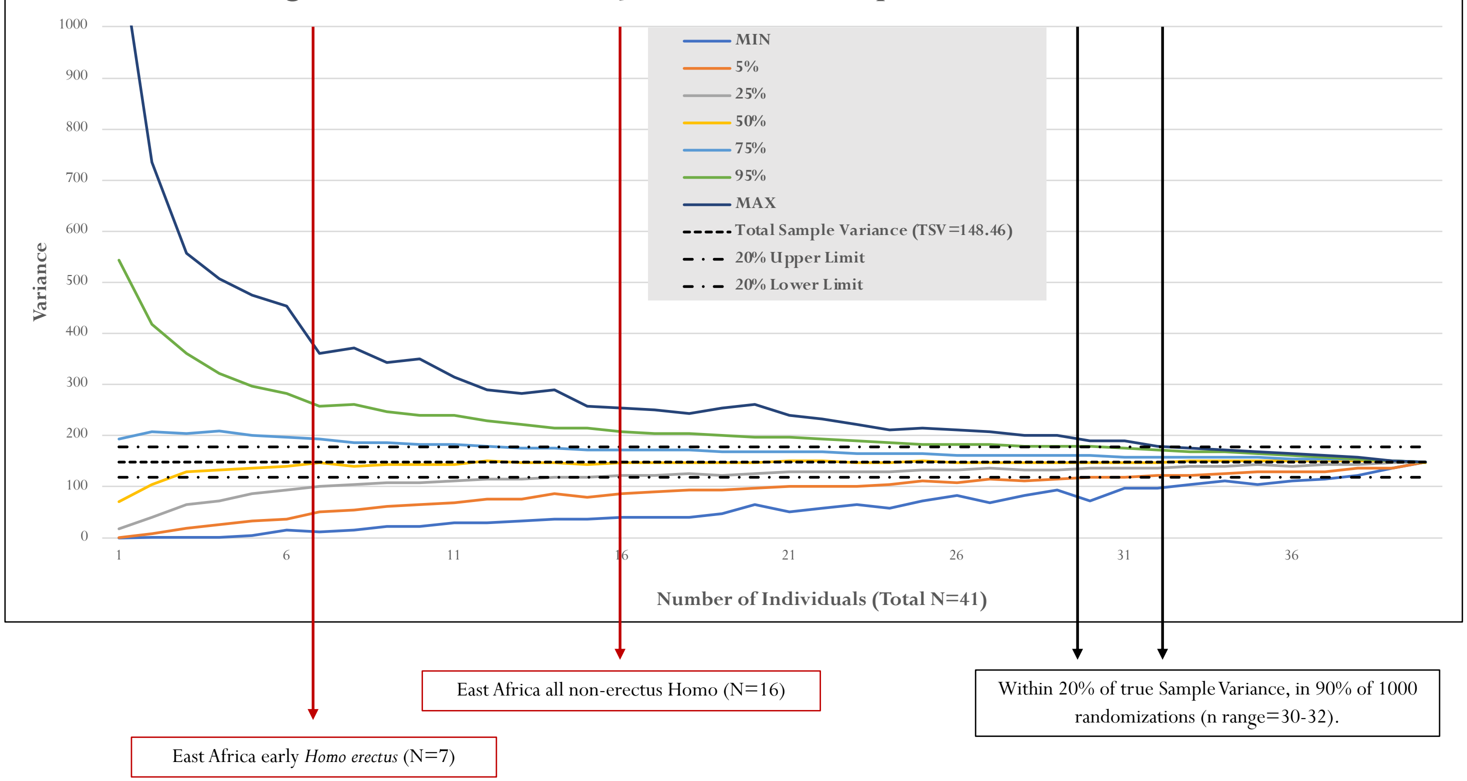


South Africa *Australopithecus africanus* (N=6)

East Africa *Australopithecus afarensis* (N=6)

Within 20% of true Sample Variance, in 90% of 1000 randomizations (n range=44-47).

Figure 3: Modern *Homo sapiens* M_1 Area, Sample Variance Permutations

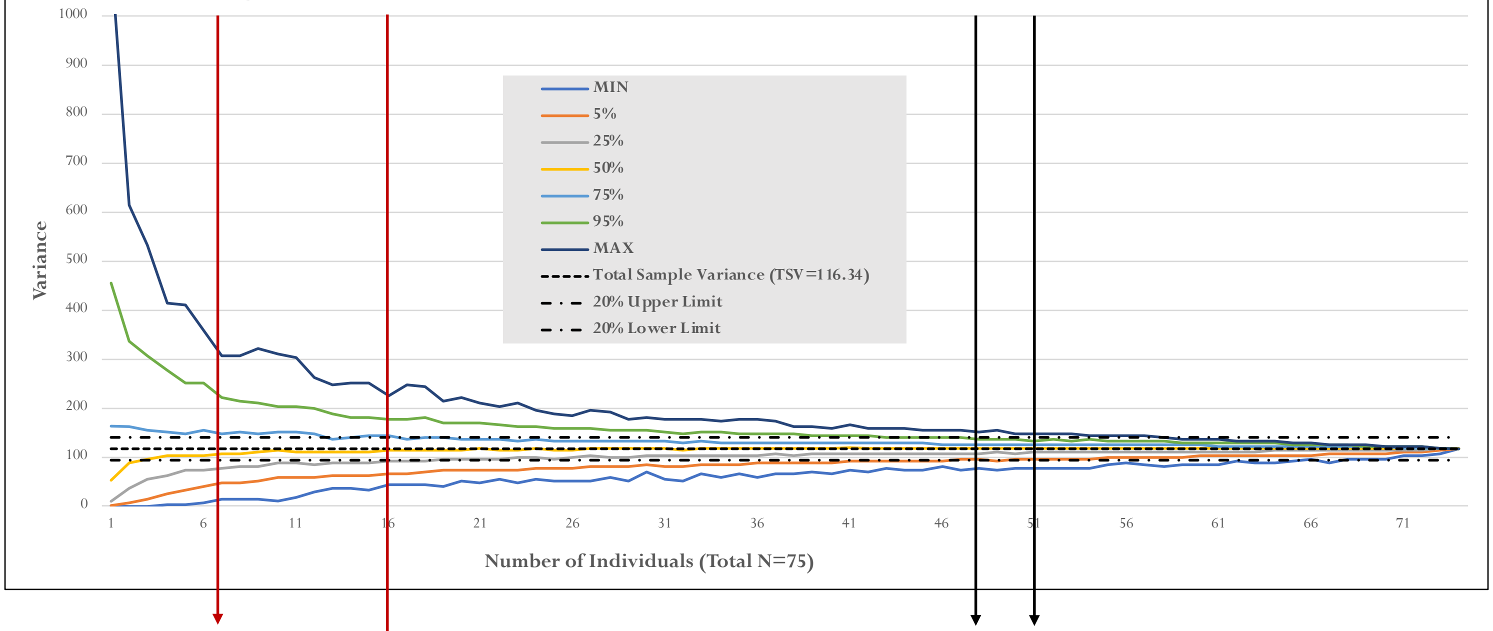


East Africa all non-erectus Homo (N=16)

Within 20% of true Sample Variance, in 90% of 1000 randomizations (n range=30-32).

East Africa early *Homo erectus* (N=7)

Figure 4: Extant *Pan troglodytes* M$_1$ Area, Sample Variance Permutations

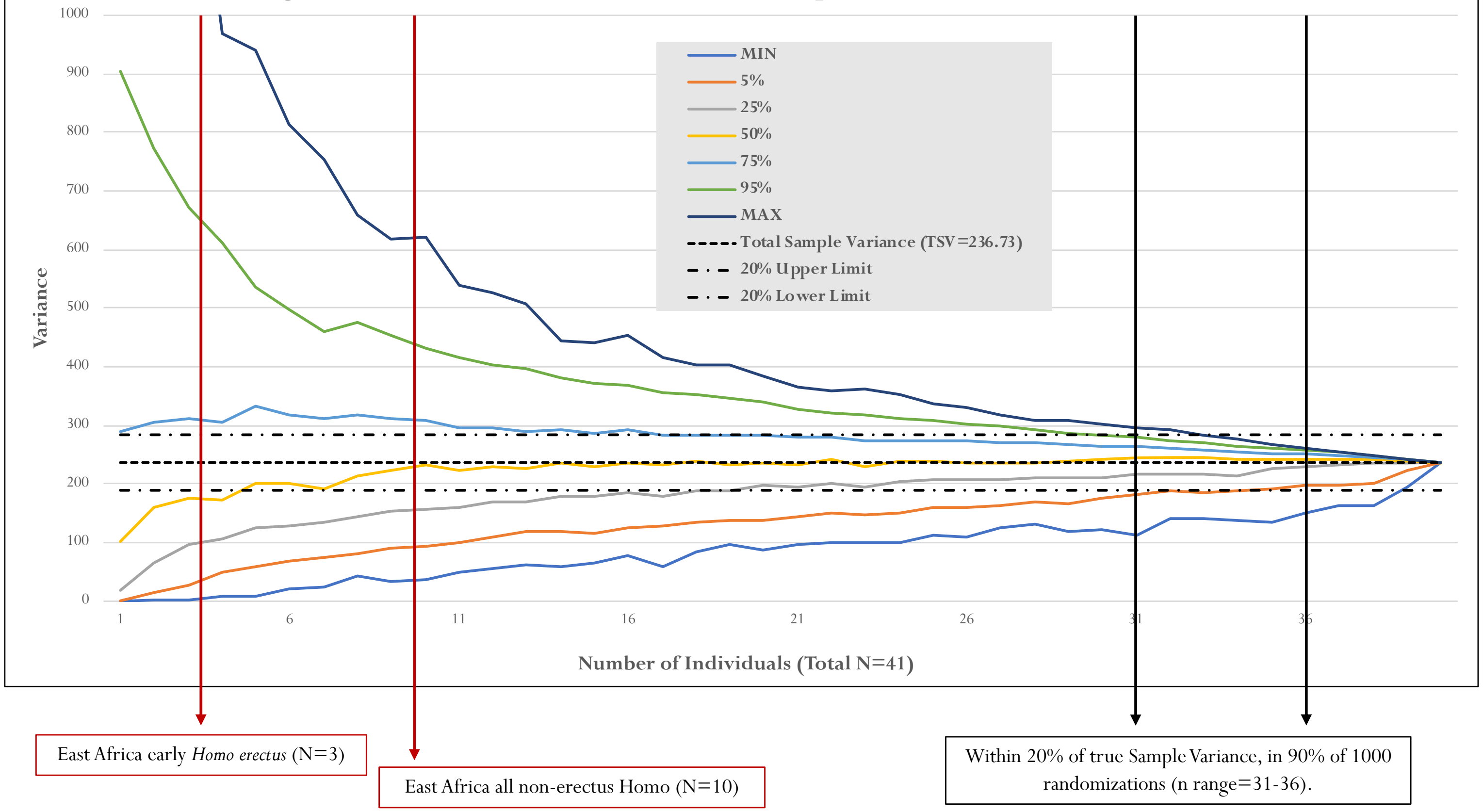


South Africa *Australopithecus africanus* (N=7)

East Africa *Australopithecus afarensis* (N=16)

Within 20% of true Sample Variance, in 90% of 1000 randomizations (n range=48-51).

Figure 5: Modern *Homo sapiens* M^2 Area, Sample Variance Permutations



East Africa early *Homo erectus* (N=3)

East Africa all non-erectus Homo (N=10)

Within 20% of true Sample Variance, in 90% of 1000 randomizations (n range=31-36).

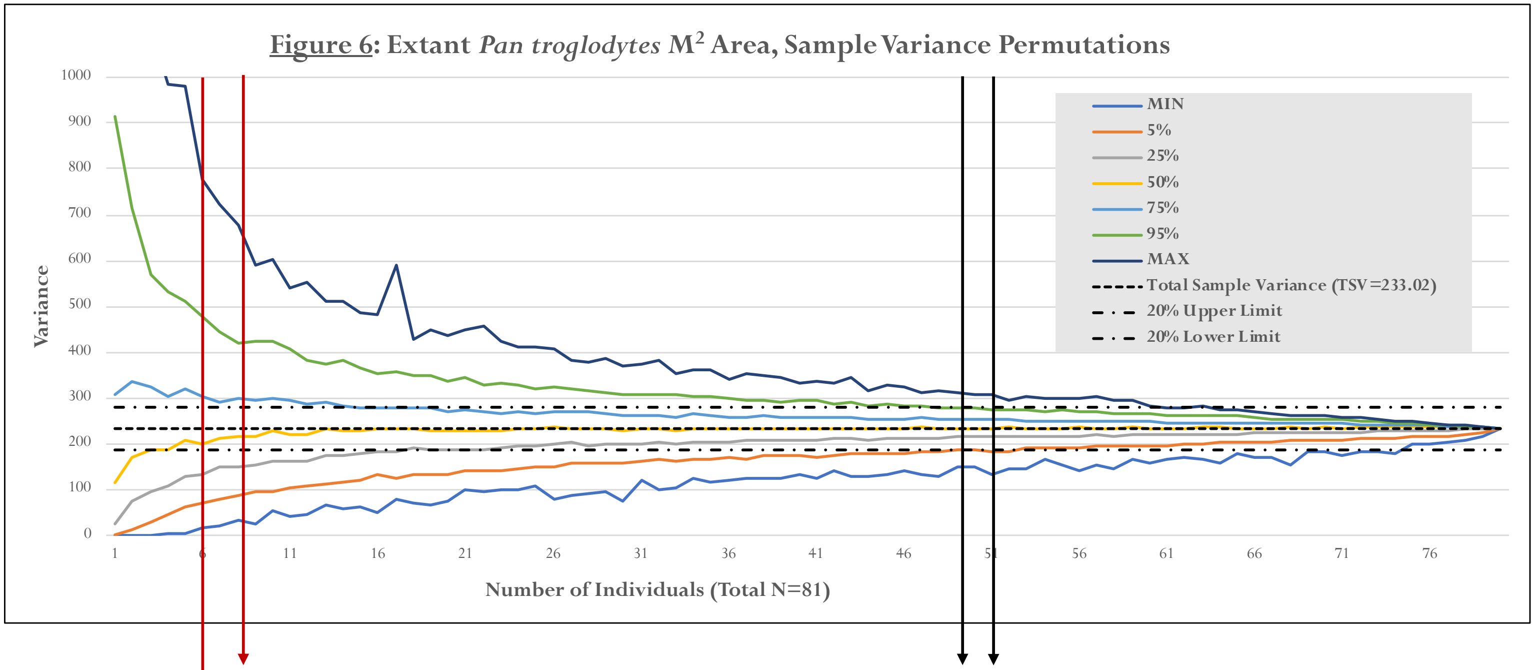


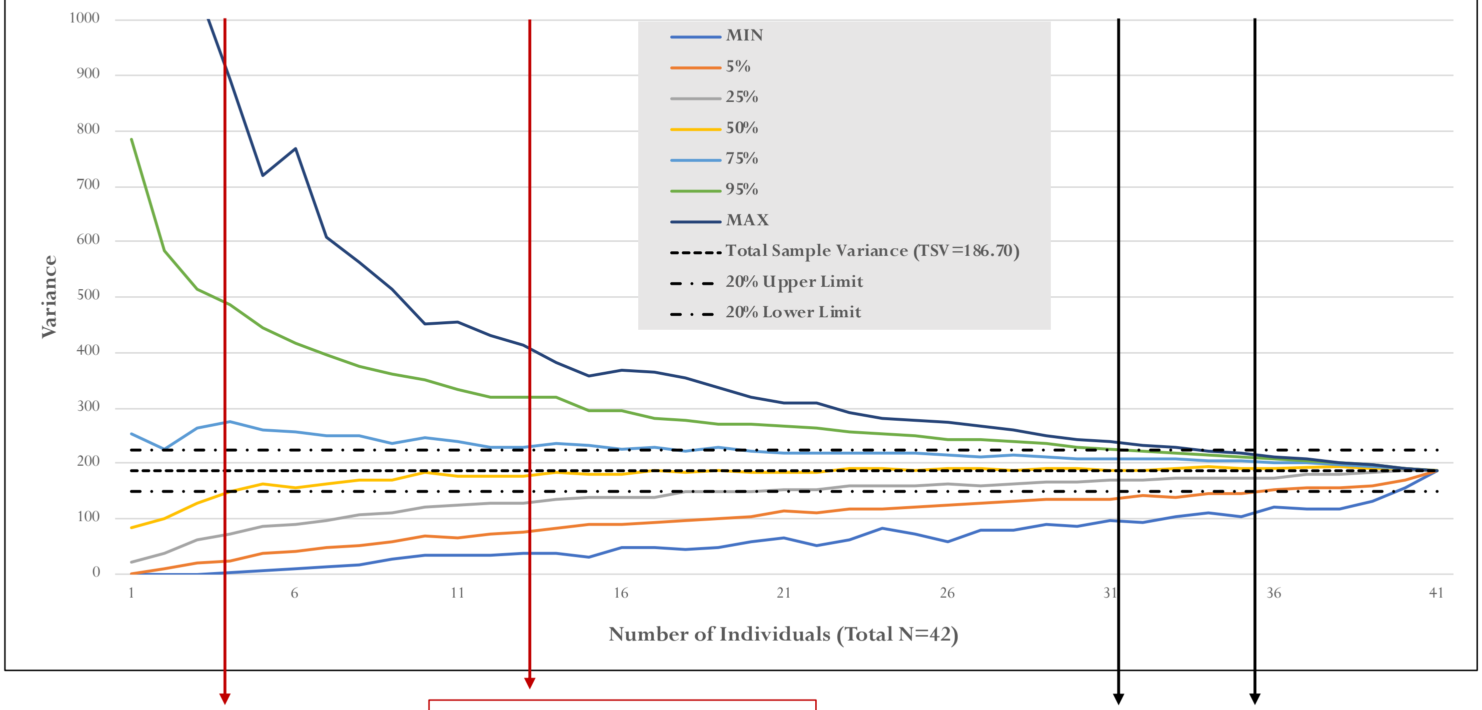
Figure 6: Extant *Pan troglodytes* M^2 Area, Sample Variance Permutations

East Africa *Australopithecus afarensis* (N=8)

Within 20% of true Sample Variance, in 90% of 1000 randomizations (n range=50-51).

South Africa *Australopithecus africanus* (N=6)

Figure 7: Modern *Homo sapiens* M_2 Area, Sample Variance Permutations



East Africa early *Homo erectus* (N=4)

East Africa all non-erectus Homo (N=13)

Within 20% of true Sample Variance, in 90% of 1000 randomizations (n range=33-37).

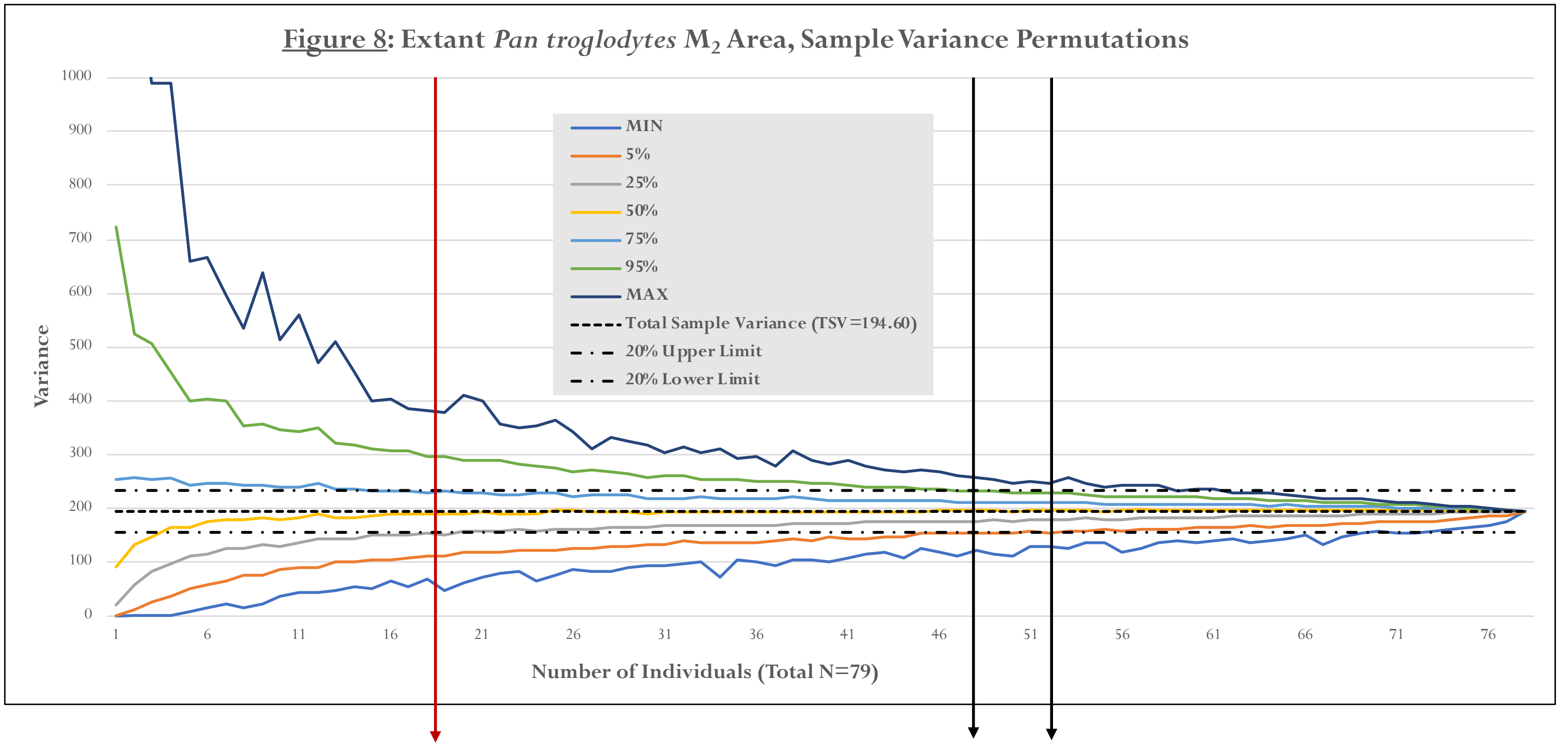


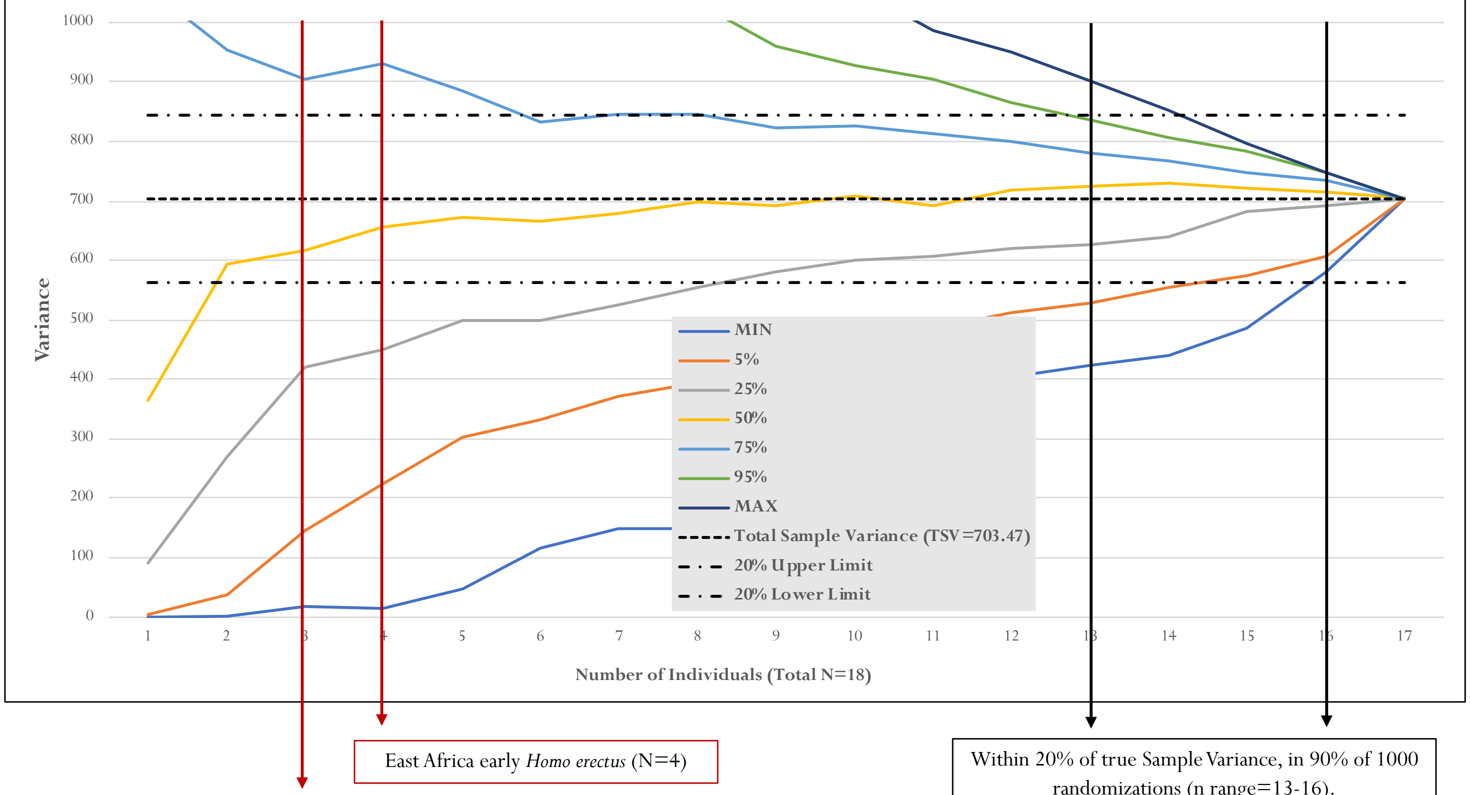
Figure 8: Extant *Pan troglodytes* M_2 Area, Sample Variance Permutations

East Africa *Australopithecus afarensis* (N=19)

Within 20% of true Sample Variance, in 90% of 1000 randomizations (n range=48-52).

South Africa *Australopithecus africanus* (N=0)

Figure 9: Modern *Homo sapiens* Femoral Length, Sample Variance Permutations

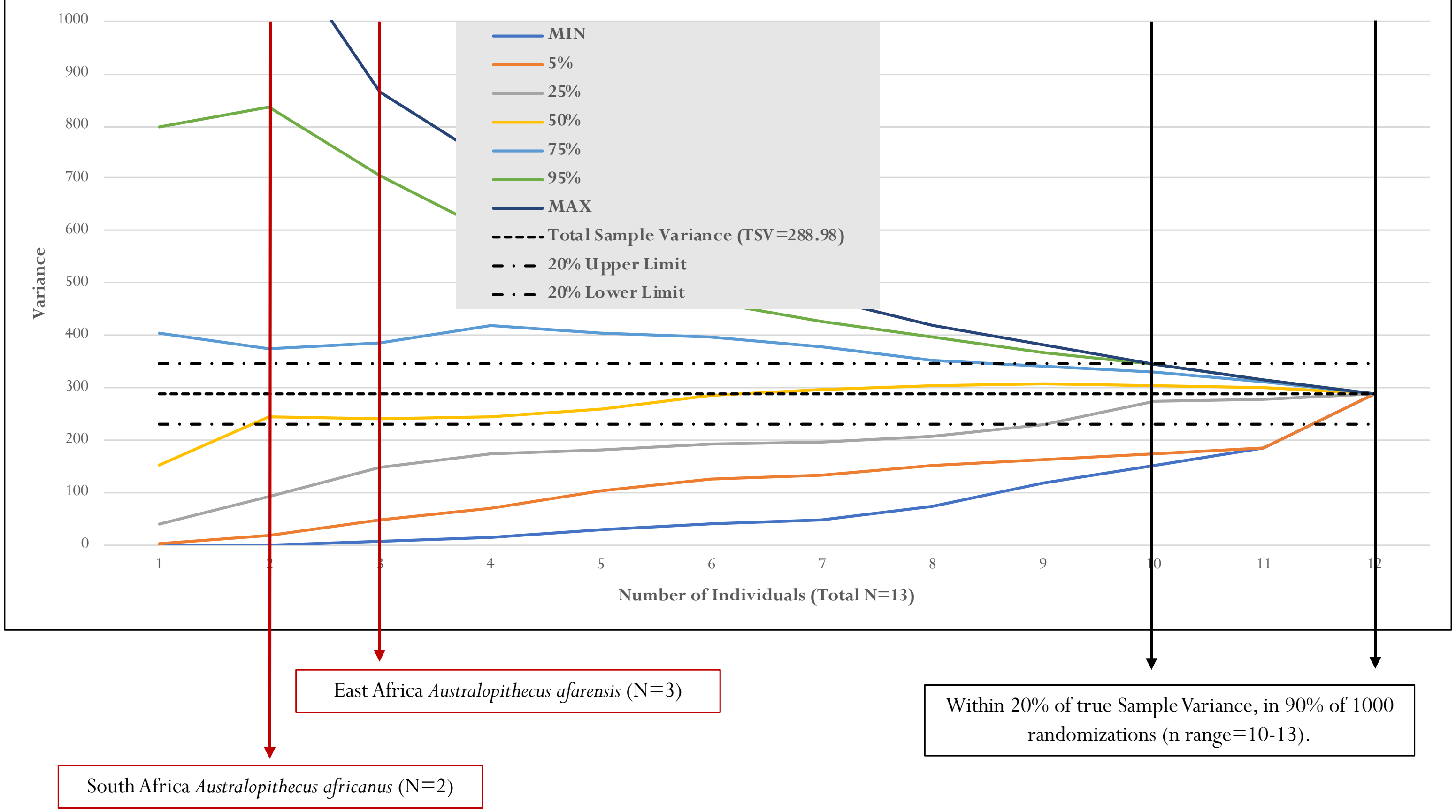


East Africa early *Homo erectus* (N=4)

Within 20% of true Sample Variance, in 90% of 1000 randomizations (n range=13-16).

East Africa all non-erectus Homo (N=3)

Figure 10: Extant *Pan troglodytes* Femoral Length, Sample Variance Permutations



East Africa *Australopithecus afarensis* (N=3)

Within 20% of true Sample Variance, in 90% of 1000 randomizations (n range=10-13).

South Africa *Australopithecus africanus* (N=2)

Femoral data displays a wider range of both actual size (mean length range=289-450.5mm) and range of sample variation than does the molar data. Among femoral lengths, TSVs are high for both australopith samples (South African *A. africanus*, TSV=12482.00; East African *A. afarensis*, TSV=3181.00) relative to modern samples (*P. troglodytes*, TSV=288.98; *H. sapiens*, TSV=703.47). Among early Homo samples there is a significant difference between species (non erectus *Homo spp.*, TSV=2330.33; *H. erectus,* TSV=675.00) where values overlap with both australopiths and extant forms.

Sample Sizes for Reliably Measuring Variation

Permutation analyses were performed separately on extant *P. troglodytes* and *H. sapiens* samples for each anatomic trait. Results are presented in **Figures 1-10**, which display trends in the dispersion of variances calculated for each permutation as subsample size increases. Colored trendlines indicate percentiles of the subsampled variance estimates. These lines converge on TSV as permutation sample size approaches the total sample size. Convergence of percentiles of variance estimates to within 20% of the TSV are denoted, along with sample sizes in comparable hominin samples of the same anatomic trait. **Table 2** provides a summary of sample size thresholds where the 95th and 5th percentiles are within 50%, 25%, 20%, and 10% of TSV. It should be noted that this author discerns a reasonably reliable estimate of variance at 'within 20%' of TSV; **Table 2** provides both an illustration of the effects of sample size on variance and a general guide for more (or less) stringent accuracy standards.

In **Figure 1**, which depicts variance permutations for *H. sapiens* M^1 occlusal area, we can see that convergence between 95% and 5% trendlines reaches 20% of the total sample variance (TSV=248.22) in sample sizes around 32-37 individuals (black arrows and text inset highlight this threshold). This indicates that among this population, a sample size of approximately 35 individuals should reliably estimate TSV. Note that red arrows and text insets within figures indicate sample sizes of comparable hominin samples, early *Homo spp.* and East African *H. erectus*. At these sample sizes, n=2 and n=8 respectively, variance estimates are returning results within about 400% of the total sample variance. In **Figure 2**, a larger sample size (n=85) on the same trait on *Pan troglodytes* displays a similar pattern to **Figure 1**. Most variance estimates (90% of randomized subsamples) converge within 20% of total sample variance by about 45 individuals and converge within 10% of total sample variance at a sample size of about 70 individuals (see **Table 2**). As in these first two analyses, the other three molar area results (**Figs. 3-8; Table 2**) display a similar pattern, where convergence within 20% of total sample variance among modern humans occurs around a sample size of about 30 individuals, and among chimpanzees at around 40 individuals.

Table 2: Estimate Error by Sample Size, in Sample Variance Permutations

			Sample Size Ranges at Percentile Variance Estimate			
	Total Sample Size	Total Sample Variance (TSV)	Within 50% of TSV	Within 25% of TSV	Within 20% of TSV	Within 10% of TSV
H. sapiens M^1	42	248.22	15-19	29-32	32-37	38-40
P. troglodytes M^1	85	154.95	11-17	37-38	44-47	68-74
H. sapiens M_1	41	148.46	13-15	26-28	30-32	37-39
P. troglodytes M_1	75	116.34	14-20	39-40	48-51	64-68
H. sapiens M^2	41	236.73	17-19	29-32	31-36	37-40
P. troglodytes M^2	81	233.02	16-19	42-43	50-51	68-73
H. sapiens M_2	42	186.70	18-19	31-35	33-37	38-41
P. troglodytes M_2	79	194.60	13-21	41-42	48-52	66-73
H. sapiens FEML	18	703.48	7-9	12-15	13-16	16-18
P. troglodytes FEML	13	288.98	7-9	10-13	10-13	11-13

Femoral length study samples have significantly smaller sample sizes compared to those for molars, and the variances from permutations reflect this in **Figs. 9 and 10**. As also visible in **Table 2**, modern human femoral lengths vary substantially more than any other extant study sample (FEML, TSV=703.48), and the chimpanzee femoral sample has the next highest variance estimate, albeit significantly lower than the modern human sample (*P. troglodytes* FEML, TSV=288.98). In both species, percentile estimate trendlines converge dramatically at the end of the sample as the degrees of freedom for permutations become more constrained, suggesting these samples may not be large enough to properly estimate the sample size needed for this trait. Extant sample sizes used here (n=18 *H. sapiens*, n=13 *P. troglodytes* femora) are significantly larger than the sample sizes for extinct hominoids (n range=2-4; see **Figs. 9-10**); fossil femoral data are highly unlikely to return reliable estimates of sample variance.

Discussion

Robust sample sizes are necessary to reliably assess statistical variance (Sokal and Rolfe 2012; Gilbert and Grine 2010). Among extinct hominin molar samples used here, none of the sample sizes are large enough to confidently surpass the 'within 25%' threshold of reliability. Even the largest fossil sample size reported (n=19, *Australopithecus afarensis* M_2) will only provide sample variance estimates that are probabilistically within 50% of the TSV of that population, returning an estimate of sample variance likely within 200% of the actual sample variance (see **Figure 8**). For example, in **Table 2** we can see that in *Pan troglodytes* M_2 variance estimates are within 50% at 13-21 individuals, but 48-52 individuals are needed to achieve the 'within 20%

TSV' threshold. This illustrates the likelihood that the range of estimate error among published fossil hominins reported here exceeds the perceivable differences which may or may not be inherent the broader populations.

Differences in variation of this magnitude could be due to differing coping strategies with between australopiths and *Homo* spp., as Anton, Potts, and Aiello (2014) asserted; however, observed differences may also be due to the unreliability of measuring variance in small sample sizes. Identifiable fossil remains (identifiable to taxon and individual) are required by the VSH, to determine for example whether early *Homo spp.* are more variable than australopiths, a requirement which limits available samples. That sample is reduced again to include only complete elements, as Antón, Potts, and Aiello (2014) determined to only include the most complete elements in their analysis (see their Table 1) in effort to reduce the variation due to fragmentation or unassignable individual elements. This decision significantly reduced the overall number of testable variables within the study populations. Complete elements, particularly of the post crania, are rare, as the fossil hominin sample sizes used in this study indicate.

Among molar areas, variation does not appear dramatically different among the extant pair than among the extinct pairings. Across all four teeth and all samples, TSVs range from 116.34 to 1049.42. This is a limited range of variation given that *a*) we know from Chapter One that the extant hominoid pair are not significantly different to each other in molar variation, and *b*) sample size can greatly affect CV reliability. Further, these values have not been adjusted for differences in absolute body size, a transformation which can reduce variation due only to size. Absolute body size differences may also be contributing to the generally high variance observed in the femoral data, where mean femoral lengths span 289-450.5mm. This degree of absolute size variation should be accounted for before a reliable determination of variation can be made.

Conclusion

In previous chapters of this dissertation, I discuss patterns of variation as quite specific to the anatomic region from which the measures were obtained; for example, differences in variation were negligible among study taxa in molar dimensions, yet differences in postcranial bone lengths were detectable among those same taxa. In addition to sample size, measures of variance were also found to be highly influenced by factors such as anatomic region, sexual dimorphism, and absolute body size. Given these factors, I would expect that comparisons among fossil samples across anatomic regions and across taxa would require robust sample sizes to accurately detect population-level variation.

Measuring variance from past populations, reliably and accurately, is difficult to accomplish because fossils are simply not as abundant as extant materials and likely never will be. The maximal limits of sample variation in any specific population are frequently not knowable given current fossil availability. Some studies, on the other hand, have attempted to determine just how large sample sizes must be in order to reliably record population differences in the past, as in the case of sexual dimorphism and species recognition (Plavcan and Cope 2001). The authors determined that most currently available fossil sample sizes were not sufficiently large as to reliably detect a consistent difference in species identification due in part to confounding factors like sexual dimorphism. Due to these factors, constraint must be exercised when abstracting larger theoretical import of the apparent patterns of variation in the fossil record. While sample size may not be a serious limitation for many studies, e.g. reporting novel morphological descriptions or pathologies, but certain types of inquiries are likely to be constrained by fossil remains.

Fossil assemblages allow an unparalleled view into the past. Skeletal remains can reveal information about the lifestyle, diet, and time period in which an individual lived. Intra-taxon morphological variation of extinct forms shows phenotypic changes over time among lineages, which can relate to adaptational patterns of environmental use (see Sanchez and Schoch 2013 for a relevant review in tetrapods). Combined with paleoecological evidence, fossil assemblages offer powerful insights into environments and populations that help us understand our modern world. However, preservational biases can obscure our ability to discern some of these patterns reliably, and this may be particularly true in the case of phenotypic signatures of VSH. The ability to detect the hypothesized signature of VSH (that is, increasing phenotypic variation as ecological versatility increases) is directly dependent on the ability to reliably detect sample variation at all.

CHAPTER V: CONCLUSION,
MEASURING SKELETAL VARIATION IN VERSATILE PRIMATES

Variation is the raw material on which selective pressures act (Darwin 1859). Therefore, variability, a measure of population variation can be indictive of selective pressures; these two characteristics (population variability and selective pressure) are related (Yablokov 1974). Some scholars argue variability itself is a characteristic that can be altered as part of an adaptive strategy, allowing populations to display a narrow or wide range of phenotypic (or genotypic) traits simultaneously (Grove 2014; Pfenning *et al* 2010; Potts 1998a; Vrba 1992). There may be an advantage for a diverse population in the face of environmental diversity or change (Turley and Frost 2018; Antón, Potts, and Aiello 2014; Kuzawa and Bragg 2012; Davidson, Jennions, and Nicotra 2011; Ash and Gallop 2007).

In this dissertation, I assessed phenotypic variation in six selected catarrhine primate species. In total, 81 skeletal traits were analyzed across cranial, dental, and postcranial anatomic regions, using a total sample of 4084 extant individuals. The main hypothesis of this dissertation, that ecological versatility positively correlates with phenotypic variation, was not supported among the vast majority of craniodental or postcranial features researched here.

Chapter One findings do not support the hypothesis of a correlative relationship between more ecologically versatile primates and in increase in variation among craniodental materials. The coefficient of variation, a robust measure of variance, was only significantly different among any study pairs on three cranial or dental traits: pooled sex dentition, male dentition (likely the driver of the first result), and male crania. Among these, patterns between taxa are not apparent: *P. troglodytes* (a putative specialist) is most cranially variable, while *Papio hamadryas* (a putative versatilist) is more dentally variable. Further, modern humans are the least variable of all study species and are significantly less variable than *P. troglodytes* specifically among male crania. Although more apparent patterns of variation were observed in data which had not been adjusted to correct for absolute body size, these differences in variation disappeared once transformed data (by the geometric mean for that individual) was analyzed.

Chapter Two results indicate that while different postcranial elements may reveal different profiles of variation, when taken together these measures do not show significant differences in variation among study taxa. Among the 53 linear measures analyzed, the majority of traits, and elements taken as whole regions, were not significantly different in terms of variation. As an exception, the length measurement of each long bone did display significant differences even after adjusted for absolute size. This result was driven by one major difference, among the baboon study pair (*Papio hamadryas* and *Theropithecus gelada*). Long bone lengths are a developmentally plastic characteristic (Stoessel, Kilbourne, and Fischer 2013; Cunnnigham, Schuer, and Black 2016), and this difference may reflect that plasticity in the sense that *Papio hamadryas* (sensu lato) occupies a broader range of habits and substrates than does *Theropithecus gelada*, which is restricted to grassy highlands (Rowe and Myers 2016). Among all skeletal traits examined in this dissertation, long bone lengths are perhaps the worthiest of further investigation for the relationship between ecological versatility and phenotypic variation.

Chapter Three results indicate that sample sizes required for accurately detecting patterns of phenotypic variation occupy a range of 30-52 individuals for molar areas, and 10-16 individuals for femoral lengths. These sample sizes are substantially larger than those offered by Antón, Potts, and Aiello (2014), and may be beyond currently available fossil sample sizes more generally. This result illustrates the limitations of assessing potentially adaptive signatures of variation; fossil sample size limits are so constrained that other factors of known variation (e.g. body size, sexual dimorphism, anatomic region) cannot be accounted for. These factors most certainly should provide caution for biological interpretation.

Detecting differences in variation across species requires careful data preparation and study design. False positives, where associating an increase in variation with an exigent trait such ecological versatility, can occur in a number of reasonable scenarios if not specifically considered. Throughout this dissertation, I encountered various factors which confounded my ability to assess my central hypotheses. Although study species were carefully selected for availability in large number, and comparability on body size and phylogeny, results were often affected by sample size disparities, differing sexual dimorphism rates and magnitudes of skeletal measurements. In most cases, it was possible to reduce these factors through data transformations and cleaning techniques to arrive at reliable results. However, these techniques did reduce overall sample sizes, and similar limitations would be faced by like-minded studies. Where significant results did occur in this study, such as cranial differences between male *P. troglodytes* and *H.*

sapiens, or long bone length differences in *Papio* and *Theropithecus*, the patterns were subtle. Further investigation of these relationships, among extinct or extant populations would benefit from more postcranial data and specimen availability, and an increase in juvenile materials.

Extant nonhuman primates exhibit a range of ecological versatility, providing an opportunity to study the potential advantages of ecological versatility in our close relatives. Almost 70% of primates today are determined to be “Near Threatened with Extinction” in the wild, or a more dire level of extinction threat (IUCN 2018). However, a few species have widespread populations, occurring in both arboreal and terrestrial environments and consuming variable diets that are often supplemented with human cultivated, manufactured, or distributed foods (IUCN 2018; Rowe and Myers 2016). The relative success of these species may reflect enhanced tolerance to environmental fluctuation (see Hill and Winder 2019 for operationalizing this in the study of baboons). The aim of this project was to test the hypothesis that more ecologically versatile species will exhibit greater phenotypic variation, measured as skeletal variation. Although these results cannot support that hypothesis to a great extent, I remain committed to understanding why some primates are thriving in our modern, fluctuating world. Detecting a signature of such adaptability has potential for increasing our understanding of biodiversity more generally, and perhaps predicting which species are likely to thrive into the next century.

APPENDIX A

CRANIODENTAL MEASUREMENT PROTOCOL

The focus of this protocol is on homologous anatomical landmarks between adult catarrhine taxa. Equivalent measures are provided where data was collected from other sources; complete references for equivalent measurements are located at end of measurement list and numbered in brackets throughout. Final analyses were conducted on variables 1-28 only, because 29-40 apply only Old World monkeys and were collapsed into variables 23-28. However, their inclusion here reflects a desire to be transparent in methodology.

Cranial Measures, 1-16.

All linear distances were collected by either spreading calipers (human specimens, oriented along the Frankfort horizon) or by deriving a linear distance from digitized 3D landmarks collected using a Microscribe 3DX (nonhuman primate specimens).

1. **INBR.** *Parietal Length*. Linear distance from inion (opisthicranion) to bregma, superior view. Inion and opisthocranion are equivalent between old world monkeys, chimpanzees, and humans. Equivalent to variables INBR (PRIMO [1]), PAC (Howells [2] and FDB [3]); equivalent to the linear distance between 3D landmarks F1,F2 (Frost [4]) and M1,M20 (McNulty [5]).
2. **NAIN.** *Nasio-Occipital Length*. Linear distance from nasion to inion, lateral view. Equivalent to variables NAIN [1] and NOL [2]; equivalent to the linear distance between 3D landmarks F1,F4 [4] and M1,M23 [5].

3. **NABR.** *Frontal Length*. Linear distance from nasion to bregma, anterior view. Equivalent to variables NABR [1], FRC [2,3]; equivalent to the linear distance between 3D landmarks F2,F4 [4] and M20,M23 [5].

4. **BABR.** *Basion-Bregma Length*. Linear distance from basion to bregma, lateral view. Equivalent to variables BABR [1], BBH [2,3]; equivalent to the linear distance between 3D landmarks F2,F31 [4] and M20,M60 [5].

5. **NAPR.** *Nasion-Prosthion Length*. Linear distance from nasion to prosthion, anterior view. Howells' NPH [2] is not quite equivalent, but very close: "Length of isosceles triangle rather than the bisector (ns)". This distinction does not matter for most studies, unless it is used in a proportional study. Also equivalent to NAPR [1]; equivalent to the linear distance between 3D landmarks F4,F7 [4] and M23,M35 [5].

6. **NABA.** *Nasion-Basion Length*. Linear distance from nasion to basion, lateral view. Equivalent to variables NABA [1], BNL [2,3]; equivalent to the linear distance between 3D landmarks F4,F31 [4] and M23,M60 [5].

7. **PRBA**. *Prosthion-Basion Length*. Linear distance from prosthion to basion, lateral view. Equivalent to variables BAPR [1], BPL [2,3]; equivalent to the linear distance between 3D landmarks F7,F31 [4] and M37,M60 [5].

8. **IORB**. *Interorbital Breadth*. Linear distance from dacryon to dacryon, anterior view. For cercopithecoids, this measure is close to bi-dacryon; but often not taken as deep into orbit [1]. Equivalent for this study to variables INOR [1], DKB [2,3]; equivalent to the linear distance between 3D landmarks F12,F23 [4] and M12,M51 [5].

9. **BORB**. *Bi-Orbital Breadth*. Linear distance from ectoconchion to ectoconchion, anterior view. For cercopithecoids, this measure is taken at the points on lateral margin of

frontal/zygoma; it is also known as the landmark FMO, near FMT [1]. Equivalent to variables BIOR [1], EKB [2,3]; equivalent to the linear distance between 3D landmarks F15,F26 [4] and M7,M46 [5].

10. **BIPO**. *Neurocranial Breadth*. Linear distance from porion to porion, anterior view. Equivalent to variables MAXW [1], XCB [2,3]; equivalent to the linear distance between 3D landmarks F17,F28 [4] and M2,M41 [5].

11. **BIZY**. *Bi-Zygomatic Breadth*. Maximum transverse breadth across zygomatics, anterior view. Equivalent to variables BIZY [1], ZYB [2,3]; equivalent to the linear distance between 3D landmarks F18,F29 [4] and M16,M55 [5].

12. **ORBH**. *Orbital Height*. Measured at orbital rim along the midline, on the frontal at the superior point and on the maxilla at the inferior point. Anterior view, measured on the left orbit if possible. Equivalent to variables ORBH [1], OBH [2,3]; equivalent to the linear distance between 3D landmarks F22,F24 [4] and M48,M52 [5].

13. **ORBB**. *Orbital Breadth*. Left if possible. Linear distance from dacryon to ectoconchion, anterior view. Measured on the left orbit if possible. Equivalent to variables ORBW [1], OBB [2,3]; equivalent to the linear distance between 3D landmarks F23,F26 [4] and M47,M51 [5].

14. **OPBA**. *Foramen Magnum Length*. Linear distance from opisthion to basion, inferior view. Equivalent to variables FORL [1], FOL [2,3]; equivalent to the linear distance between 3D landmarks F30,F31 [4] and M59,M60 [5].

15. **BIPG**. *Bi-Auricular Breadth*. Linear distance from postglenoid to postglenoid, inferior view; measured from the center of the inferiormost point of the process.

Equivalent to variables BIPG [1], AUB [2,3]; equivalent to the linear distance between 3D landmarks F34,F40 [4] and M61,M62 [5].

16. **BUME**. *External Palate Breadth*. Linear distance from ectomolare to ectomolare, inferior view. This is the lateral point on the maxillary alveolar margin where M1 and M2 contact; ectomolare to ectomolare is usually the widest distance across the palate. Equivalent to variables BMEU [1], MAB [2,3]; equivalent to the linear distance between 3D landmarks F37,F43 [4] and M72,M81 [5].

Molar Measures, 17-40.

All measures were collected using sliding calipers. Permanent molars are the most directly similar across taxa among all dentition and are not remodeled after eruption. Where significant distortion of the tooth was evident, such as exhibiting pathological conditions (enamel wear or breakage, caries), that tooth was not processed.

17. **UM1MD**. *Upper Molar 1 Mesiodistal*. Maximum mesiodistal length of the first upper molar, with external sliding caliper jaws perpendicular to tooth row. Equivalent to the variables UM1L [1] and M1 MD (Plavcan [6]).

18. **UM2MD**. *Upper Molar 2 Mesiodistal*. Maximum mesiodistal length of the second upper molar, with external sliding caliper jaws perpendicular to tooth row. Equivalent to the variables UM2L [1] and M2 MD [6].

19. **UM3MD**. *Upper Molar 3 Mesiodistal*. Maximum mesiodistal length of the third upper molar, with external sliding caliper jaws perpendicular to tooth row. Equivalent to the variables UM3L [1] and M3 MD [6].

20. **LM1MD**. *Lower Molar 1 Mesiodistal*. M Maximum mesiodistal length of the first lower molar, with external sliding caliper jaws perpendicular to tooth row. Equivalent to the variables LM1L [1] and m1 md [6].

21. **LM2MD**. *Lower Molar 2 Mesiodistal*. Maximum mesiodistal length of the second lower molar, with external sliding caliper jaws perpendicular to tooth row. Equivalent to the variables LM2L [1] and m2 md [6].

22. **LM3MD**. *Lower Molar 3 Mesiodistal*. Maximum mesiodistal length of the third lower molar, with external sliding caliper jaws perpendicular to tooth row. Equivalent to the variables LM3L [1] and m3 md [6].

23. **UM1BLX**. *Upper Molar 1 Buccolingual*. Maximum buccolingual distance of the permanent first upper molar, with caliper arms parallel to the tooth row. Measured using internal jaws of sliding calipers; in old world monkeys, this measure is an average of the maximum buccolingual length of the mesial loph **UM1MBL** (29) and the maximum buccolingual length of the distal loph **UM1DBL** (30). Equivalent to the variable M1 BL [6].

24. **UM2BLX.** *Upper Molar 2 Buccolingual.* Maximum buccolingual distance of the permanent second upper molar, with caliper arms parallel to the tooth row. Measured using internal jaws of sliding calipers; in old world monkeys, this measure is an average of the maximum buccolingual length of the mesial loph **UM2MBL** (31) and the maximum buccolingual length of the distal loph **UM2DBL** (32). Equivalent to the variable M2 BL [6].

25. **UM3BLX**. *Upper Molar 3 Buccolingual*. Maximum buccolingual distance of the permanent third upper molar, with caliper arms parallel to the tooth row. Measured using

internal jaws of sliding calipers; in old world monkeys, this measure is an average of the maximum buccolingual length of the mesial loph **UM3MBL** (33) and the maximum buccolingual length of the distal loph **UM3DBL** (34). Equivalent to the variable M3 BL [6].

26. **LM1BLX**. *Lower Molar 1 Buccolingual.* Maximum buccolingual distance of the permanent first lower molar, with caliper arms parallel to the tooth row. Measured using internal jaws of sliding calipers; in old world monkeys, this measure is an average of the maximum buccolingual length of the mesial loph **LM1MBL** (35) and the maximum buccolingual length of the distal loph **LM1DBL** (36).

27. **LM2BLX**. *Lower Molar 2 Buccolingual.* Maximum buccolingual distance of the permanent second lower molar, with caliper arms parallel to the tooth row. Measured using internal jaws of sliding calipers; in old world monkeys, this measure is an average of the maximum buccolingual length of the mesial loph **LM2MBL** (37) and the maximum buccolingual length of the distal loph **LM2DBL** (38).

28. **LM3BLX**. *Lower Molar 3 Buccolingual.* Maximum buccolingual distance of the permanent third lower molar, with caliper arms parallel to the tooth row. Measured using internal jaws of sliding calipers; in old world monkeys, this measure is an average of the maximum buccolingual length of the mesial loph **LM3MBL** (39) and the maximum buccolingual length of the distal loph **LM3DBL** (40).

29. **UM1MBL**. *Upper Molar 1 Mesial Loph Buccolingual.* Maximum buccolingual distance of the mesial loph of the first upper molar. Taken only in old world monkeys, it is measured using external jaws of sliding calipers. Equivalent to the variable UM1AW [1].

30. **UM1DBL**. *Upper Molar 1 Distal Loph Buccolingual*. Maximum buccolingual distance of the distal loph of the first upper molar. Taken only in old world monkeys, it is measured using external jaws of sliding calipers. Equivalent to the variable UM1PW [1].

31. **UM2MBL**. *Upper Molar 2 Mesial Loph Buccolingual*. Maximum buccolingual distance of the mesial loph of the second upper molar. Taken only in old world monkeys, it is measured using external jaws of sliding calipers. Equivalent to the variable UM2AW [1].

32. **UM2DBL**. *Upper Molar 2 Distal Loph Buccolingual*. Maximum buccolingual distance of the distal loph of the second upper molar. Taken only in old world monkeys, it is measured using external jaws of sliding calipers. Equivalent to the variable UM2PW [1].

33. **UM3MBL**. *Upper Molar 3 Mesial Loph Buccolingual*. Maximum buccolingual distance of the mesial loph of the third upper molar. Taken only in old world monkeys, it is measured using external jaws of sliding calipers. Equivalent to the variable UM3AW [1].

34. **UM3DBL**. *Upper Molar 3 Distal Loph Buccolingual*. Maximum buccolingual distance of the distal loph of the third upper molar. Taken only in old world monkeys, it is measured using external jaws of sliding calipers. Equivalent to the variable UM3PW [1].

35. **LM1MBL**. *Lower Molar 1 Mesial Loph Buccolingual*. Maximum buccolingual distance of the mesial loph of the first lower molar. Taken only in old world monkeys, it is measured using external jaws of sliding calipers. Equivalent to the variables LM1AW [1] and m1 bl tal [6].

36. **LM1DBL**. *Lower Molar 1 Distal Loph Buccolingual*. Maximum buccolingual distance of the distal loph of the first lower molar. Taken only in old world monkeys, it is measured using external jaws of sliding calipers. Equivalent to the variables LM1PW [1] and m1 bl tri [6].

37. **LM2MBL**. *Lower Molar 2 Mesial Loph Buccolingual*. Maximum buccolingual distance of the mesial loph of the second lower molar. Taken only in old world monkeys, it is measured using external jaws of sliding calipers. Equivalent to the variables LM2AW [1] and m2 bl tal [6].

38. **LM2DBL**. *Lower Molar 2 Distal Loph Buccolingual*. Maximum buccolingual distance of the distal loph of the second lower molar. Taken only in old world monkeys, it is measured using external jaws of sliding calipers. Equivalent to the variables LM2PW [1] and m2 bl tri [6].

39. **LM3MBL**. *Lower Molar 3 Mesial Loph Buccolingual*. Maximum buccolingual distance of the mesial loph of the third lower molar. Taken only in old world monkeys, it is measured using external jaws of sliding calipers. Equivalent to the variables LM3AW [1] and m3 bl tal [6].

40. **LM3DBL**. *Lower Molar 3 Distal Loph Buccolingual*. Maximum buccolingual distance of the distal loph of the third lower molar. Taken only in old world monkeys, it is measured using external jaws of sliding calipers. Equivalent to the variables LM3PW [1] and m3 bl tri [6].

References and Acknowledgements

[1] PRIMO (Primate Morphometrics Online), the NYCEP Primate Morphometric database, is a resource for researchers who use metrical (including 3D) data to study aspects of primate morphology and evolution. Some data for this project were downloaded from PRIMO, the NYCEP Primate Morphology Online database (http://primo.nycep.org). I thank Dr. Eric Delson and colleagues for access to these data.

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APPENDIX B

CRANIODENTAL MEASURES OF VARIANCE

Table A. Unscaled Cranial Variation in *Homo sapiens*, by trait[1]

	INBR	*NAIN*	*NABR*	*BABR*	*NAPR*	*NABA*	*PRBA*	*IORB*	*BORB*	*BIPO*	*BIZY*	*ORBH*	*ORBB*	*OPBA*	*BIPG*
Pooled Sex															
N	2524	2524	2524	2524	2524	2524	2524	2524	2524	2524	2524	2524	2524	2524	2524
Range (mm)	46	49	35	48	34	37	43	19	30	51	53	15	13	23	51
Min (mm)	89	151	93	107	48	83	80	13	83	116	105	26	33	27	98
Max (mm)	135	200	128	155	82	120	123	32	113	167	158	41	46	50	149
Mean (mm)	110.58	176.89	109.539	131.644	65.976	99.120	97.782	21.382	97.339	136.848	130.766	33.668	39.487	35.785	120.591
Standard Err.	0.13	0.16	0.109	0.144	0.110	0.116	0.127	0.048	0.084	0.145	0.155	0.044	0.040	0.053	0.147
Standard Dev.	6.63	7.92	5.469	7.239	5.535	5.809	6.378	2.411	4.239	7.288	7.789	2.228	2.024	2.643	7.390
Sample Var.	43.95	62.69	29.914	52.407	30.635	33.739	40.684	5.813	17.970	53.118	60.664	4.965	4.095	6.983	54.616
Coeff. of Var.	6.00	4.48	4.993	5.499	8.389	5.860	6.523	11.276	4.355	5.326	5.956	6.619	5.125	7.385	6.128
Females Only															
N	1156	1156	1156	1156	1156	1156	1156	1156	1156	1156	1156	1156	1156	1156	1156
Range (mm)	38	43	32	42	32	30	33	19	22	45	41	12	11	17	41
Min (mm)	89	151	93	107	48	83	80	13	83	116	105	27	33	27	98
Max (mm)	127	194	125	149	80	113	113	32	105	161	146	39	44	44	139
Mean (mm)	107.973	172.728	106.967	128.178	63.542	96.247	95.448	20.791	95.165	134.151	125.582	33.353	38.681	34.815	116.922
Standard Err.	0.183	0.198	0.142	0.181	0.145	0.144	0.169	0.070	0.105	0.194	0.170	0.063	0.054	0.071	0.187
Standard Dev.	6.231	6.747	4.818	6.148	4.933	4.911	5.733	2.370	3.576	6.587	5.793	2.128	1.825	2.429	6.353
Sample Var.	38.830	45.523	23.216	37.800	24.330	24.117	32.873	5.618	12.789	43.383	33.554	4.526	3.329	5.898	40.363
Coeff. of Var.	5.771	3.906	4.504	4.797	7.763	5.102	6.007	11.401	3.758	4.910	4.613	6.379	4.717	6.976	5.434

Males Only															
N	1368	1368	1368	1368	1368	1368	1368	1368	1368	1368	1368	1368	1368	1368	1368
Range (mm)	45	41	32	41	33	35	42	19	28	48	43	15	12	20	46
Min (mm)	90	159	96	114	49	85	81	13	85	119	115	26	34	30	103
Max (mm)	135	200	128	155	82	120	123	32	113	167	158	41	46	50	149
Mean (mm)	112.779	180.401	111.712	134.573	68.033	101.548	99.755	21.881	99.175	139.127	135.147	33.934	40.167	36.605	123.692
Standard Err.	0.166	0.192	0.136	0.183	0.140	0.146	0.168	0.063	0.105	0.191	0.175	0.062	0.052	0.069	0.183
Standard Dev.	6.142	7.088	5.028	6.785	5.171	5.387	6.230	2.332	3.872	7.073	6.456	2.277	1.932	2.537	6.760
Sample Var.	37.724	50.245	25.276	46.043	26.738	29.019	38.811	5.436	14.989	50.031	41.684	5.185	3.733	6.437	45.696
Coeff. of Var.	5.446	3.929	4.500	5.042	7.601	5.305	6.245	10.656	3.904	5.084	4.777	6.710	4.810	6.931	5.465

[1] Cranial traits are defined in Appendix 1A.

Table B. Scaled Cranial Variation in *Homo sapiens*, by trait[1]

	INBR	***NAIN***	***NABR***	***BABR***	***NAPR***	***NABA***	***PRBA***	***IORB***	***BORB***	***BIPO***	***BIZY***	***ORBH***	***ORBB***	***OPBA***	***BIPG***
Pooled Sex															
N	2524	2524	2524	2524	2524	2524	2524	2524	2524	2524	2524	2524	2524	2524	2524
Range	0.524	0.470	0.418	0.437	0.363	0.364	0.441	0.247	0.226	0.507	0.396	0.174	0.138	0.239	0.383
Min	1.110	2.003	1.168	1.438	0.634	1.070	1.013	0.161	1.125	1.496	1.442	0.324	0.426	0.358	1.344
Max	1.634	2.472	1.585	1.875	0.996	1.434	1.454	0.408	1.352	2.003	1.838	0.497	0.564	0.597	1.727
Mean	1.397	2.234	1.383	1.662	0.832	1.251	1.235	0.270	1.229	1.729	1.650	0.425	0.499	0.452	1.522
Standard Err.	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.002	0.001	0.001	0.000	0.001	0.001
Standard Dev.	0.075	0.066	0.052	0.066	0.052	0.046	0.064	0.029	0.033	0.079	0.054	0.025	0.019	0.029	0.061
Sample Var.	0.006	0.004	0.003	0.004	0.003	0.002	0.004	0.001	0.001	0.006	0.003	0.001	0.000	0.001	0.004

Coeff. of Var.	5.378	2.963	3.745	3.960	6.227	3.670	5.164	10.600	2.655	4.596	3.297	5.943	3.854	6.366	4.039
Females Only															
N	1156	1156	1156	1156	1156	1156	1156	1156	1156	1156	1156	1156	1156	1156	1156
Range	0.461	0.402	0.317	0.395	0.332	0.348	0.377	0.244	0.211	0.497	0.359	0.137	0.136	0.195	0.383
Min	1.174	2.019	1.232	1.455	0.634	1.070	1.044	0.164	1.137	1.506	1.442	0.359	0.426	0.370	1.344
Max	1.634	2.420	1.549	1.850	0.965	1.417	1.421	0.408	1.348	2.003	1.801	0.497	0.562	0.565	1.727
Mean	1.400	2.239	1.387	1.662	0.823	1.247	1.237	0.270	1.234	1.740	1.628	0.432	0.501	0.451	1.515
Standard Err.	0.002	0.002	0.001	0.002	0.002	0.001	0.002	0.001	0.001	0.002	0.001	0.001	0.001	0.001	0.002
Standard Dev.	0.077	0.066	0.050	0.064	0.051	0.045	0.062	0.030	0.032	0.078	0.050	0.024	0.019	0.028	0.062
Sample Var.	0.006	0.004	0.003	0.004	0.003	0.002	0.004	0.001	0.001	0.006	0.002	0.001	0.000	0.001	0.004
Coeff. of Var.	5.530	2.940	3.639	3.830	6.196	3.607	5.027	11.106	2.627	4.491	3.054	5.580	3.780	6.290	4.076
Males Only															
N	1368	1368	1368	1368	1368	1368	1368	1368	1368	1368	1368	1368	1368	1368	1368
Range	0.524	0.470	0.418	0.437	0.344	0.330	0.441	0.226	0.226	0.479	0.348	0.174	0.120	0.239	0.368
Min	1.110	2.003	1.168	1.438	0.652	1.104	1.013	0.161	1.125	1.496	1.490	0.324	0.444	0.358	1.347
Max	1.634	2.472	1.585	1.875	0.996	1.434	1.454	0.388	1.352	1.975	1.838	0.497	0.564	0.597	1.715
Mean	1.394	2.229	1.380	1.663	0.840	1.254	1.232	0.270	1.225	1.719	1.669	0.419	0.496	0.452	1.528
Standard Err.	0.002	0.002	0.001	0.002	0.001	0.001	0.002	0.001	0.001	0.002	0.001	0.001	0.001	0.001	0.002
Standard Dev.	0.073	0.066	0.053	0.068	0.051	0.046	0.065	0.027	0.032	0.079	0.051	0.025	0.019	0.029	0.061
Sample Var.	0.005	0.004	0.003	0.005	0.003	0.002	0.004	0.001	0.001	0.006	0.003	0.001	0.000	0.001	0.004
Coeff. of Var.	5.239	2.967	3.822	4.067	6.104	3.706	5.272	10.156	2.638	4.618	3.045	5.882	3.853	6.430	3.972

[1] Scaled data has been adjusted to correct for body size, where adjusted data is "trait/geometric mean of individual=scaled trait".

Table C. Unscaled Cranial Variation in *Pan troglodytes*, by trait[1]

	INBR	***NAIN***	***NABR***	***BABR***	***NAPR***	***NABA***	***PRBA***	***IORB***	***BORB***	***BIPO***	***BIZY***	***ORBH***	***ORBB***	***OPBA***	***BIPG***
Pooled Sex															
N	193	193	193	192	193	192	192	193	192	193	193	193	193	187	193
Range (mm)	32.626	62.547	36.843	33.273	79.763	57.789	105.585	24.364	64.070	64.371	60.972	22.623	17.028	12.669	49.140
Min (mm)	63.308	90.184	55.590	67.912	33.733	54.532	55.351	5.679	57.749	49.674	51.454	20.001	23.892	21.332	56.349
Max (mm)	95.934	152.730	92.432	101.185	113.496	112.321	160.936	30.043	121.820	114.045	112.426	42.624	40.920	34.001	105.489
Mean (mm)	79.190	126.790	71.700	86.836	77.398	93.259	120.180	16.526	93.560	93.628	87.456	32.861	32.954	27.799	84.839
Standard Err.	0.353	0.655	0.420	0.360	0.963	0.779	1.543	0.377	0.896	0.923	0.911	0.213	0.207	0.170	0.684
Standard Dev.	4.909	9.101	5.831	4.989	13.383	10.793	21.376	5.231	12.409	12.822	12.658	2.954	2.876	2.322	9.502
Sample Var.	24.095	82.836	33.996	24.888	179.108	116.499	456.928	27.363	153.978	164.405	160.237	8.729	8.271	5.391	90.297
Coeff. of Var.	6.199	7.178	8.132	5.745	17.291	11.574	17.787	31.652	13.263	13.695	14.474	8.991	8.727	8.353	11.201
Females Only															
N	103	103	103	103	103	103	103	103	102	103	103	103	103	101	103
Range (mm)	27.165	41.217	27.071	26.380	58.379	48.206	83.666	24.364	49.342	58.492	52.940	18.416	15.510	12.039	42.352
Min (mm)	68.769	102.862	60.310	74.805	40.915	61.603	65.094	5.679	65.836	50.881	55.890	24.208	23.892	21.963	56.693
Max (mm)	95.934	144.078	87.381	101.185	99.294	109.809	148.761	30.043	115.177	109.374	108.830	42.624	39.403	34.001	99.045
Mean (mm)	78.664	126.049	70.893	86.161	77.142	92.533	119.194	16.618	92.750	92.863	86.761	32.855	32.771	27.646	84.329
Standard Err.	0.454	0.768	0.532	0.469	1.150	0.976	1.898	0.465	1.050	1.135	1.070	0.301	0.265	0.244	0.831
Standard Dev.	4.603	7.797	5.400	4.764	11.671	9.902	19.259	4.718	10.608	11.519	10.855	3.056	2.692	2.457	8.429
Sample Var.	21.191	60.792	29.158	22.700	136.203	98.059	370.923	22.256	112.526	132.683	117.841	9.341	7.245	6.035	71.048
Coeff. of Var.	5.852	6.186	7.617	5.530	15.129	10.702	16.158	28.388	11.437	12.404	12.512	9.302	8.213	8.886	9.995

Males Only															
N	90	90	90	89	90	89	89	90	90	90	90	90	90	86	90
Range (mm)	27.006	62.547	36.843	29.148	79.763	57.789	105.585	21.490	64.070	64.371	60.972	19.841	16.675	11.030	49.140
Min (mm)	63.308	90.184	55.590	67.912	33.733	54.532	55.351	5.975	57.749	49.674	51.454	20.001	24.245	21.332	56.349
Max (mm)	90.314	152.730	92.432	97.060	113.496	112.321	160.936	27.466	121.820	114.045	112.426	39.842	40.920	32.362	105.489
Mean (mm)	79.792	127.637	72.622	87.618	77.690	94.099	121.320	16.421	94.479	94.504	88.251	32.868	33.163	27.978	85.424
Standard Err.	0.548	1.094	0.652	0.546	1.599	1.245	2.507	0.610	1.495	1.495	1.525	0.300	0.324	0.232	1.119
Standard Dev.	5.197	10.376	6.189	5.153	15.170	11.742	23.651	5.788	14.183	14.183	14.472	2.850	3.075	2.154	10.617
Sample Var.	27.006	107.670	38.309	26.555	230.130	137.866	559.354	33.503	201.144	201.155	209.429	8.125	9.457	4.638	112.726
Coeff. of Var.	6.513	8.130	8.523	5.881	19.526	12.478	19.494	35.249	15.011	15.008	16.398	8.672	9.273	7.697	12.429

[1] Cranial traits are defined in Appendix 1A.

Table D. Scaled Cranial Variation in *Pan troglodytes*, by trait[1]

	INBR	***NAIN***	***NABR***	***BABR***	***NAPR***	***NABA***	***PRBA***	***IORB***	***BORB***	***BIPO***	***BIZY***	***ORBH***	***ORBB***	***OPBA***	***BIPG***
Pooled Sex															
N	193	193	193	192	193	192	192	193	192	193	193	193	193	187	193
Range	0.833	0.684	0.574	0.556	0.639	0.334	0.799	0.294	0.357	0.538	0.340	0.272	0.172	0.283	0.353
Min	0.960	1.623	0.854	1.133	0.828	1.249	1.359	0.112	1.286	1.087	1.174	0.419	0.449	0.324	1.128
Max	1.793	2.308	1.427	1.689	1.467	1.583	2.158	0.406	1.643	1.625	1.514	0.691	0.621	0.607	1.482
Mean	1.242	1.974	1.117	1.353	1.191	1.441	1.843	0.251	1.446	1.446	1.349	0.512	0.513	0.436	1.315
Standard Err.	0.012	0.008	0.006	0.008	0.008	0.004	0.012	0.004	0.004	0.006	0.005	0.003	0.002	0.004	0.004
Standard Dev.	0.166	0.114	0.090	0.115	0.105	0.053	0.167	0.061	0.057	0.082	0.067	0.044	0.032	0.056	0.059
Sample Var.	0.027	0.013	0.008	0.013	0.011	0.003	0.028	0.004	0.003	0.007	0.005	0.002	0.001	0.003	0.003

Coeff. of Var.	13.327	5.777	8.017	8.521	8.800	3.712	9.078	24.252	3.952	5.704	4.998	8.625	6.198	12.779	4.456
Females Only															
N	103	103	103	103	103	103	103	103	102	103	103	103	103	101	103
Range	0.778	0.647	0.459	0.518	0.540	0.295	0.693	0.294	0.261	0.524	0.297	0.186	0.137	0.279	0.332
Min	1.015	1.623	0.854	1.171	0.874	1.280	1.378	0.112	1.286	1.087	1.174	0.419	0.450	0.328	1.128
Max	1.793	2.270	1.313	1.689	1.415	1.575	2.071	0.406	1.547	1.611	1.472	0.605	0.587	0.607	1.461
Mean	1.236	1.969	1.108	1.349	1.194	1.438	1.842	0.254	1.440	1.441	1.346	0.513	0.511	0.435	1.312
Standard Err.	0.015	0.011	0.008	0.011	0.009	0.005	0.015	0.006	0.005	0.008	0.006	0.004	0.003	0.006	0.006
Standard Dev.	0.154	0.109	0.084	0.107	0.096	0.055	0.157	0.056	0.048	0.086	0.060	0.038	0.029	0.057	0.059
Sample Var.	0.024	0.012	0.007	0.011	0.009	0.003	0.025	0.003	0.002	0.007	0.004	0.001	0.001	0.003	0.004
Coeff. of Var.	12.474	5.533	7.588	7.904	8.041	3.795	8.537	21.996	3.341	5.982	4.446	7.370	5.585	13.007	4.509
Males Only															
N	90	90	90	89	90	89	89	90	90	90	90	90	90	86	90
Range	0.770	0.594	0.451	0.535	0.639	0.334	0.799	0.266	0.354	0.416	0.329	0.266	0.172	0.274	0.297
Min	0.960	1.714	0.977	1.133	0.828	1.249	1.359	0.120	1.289	1.209	1.185	0.425	0.449	0.324	1.185
Max	1.730	2.308	1.427	1.667	1.467	1.583	2.158	0.386	1.643	1.625	1.514	0.691	0.621	0.599	1.482
Mean	1.249	1.980	1.128	1.358	1.187	1.444	1.845	0.246	1.452	1.452	1.353	0.511	0.514	0.437	1.318
Standard Err.	0.019	0.013	0.010	0.013	0.012	0.006	0.019	0.007	0.007	0.008	0.008	0.005	0.004	0.006	0.006
Standard Dev.	0.178	0.120	0.095	0.125	0.114	0.052	0.179	0.066	0.066	0.078	0.075	0.051	0.035	0.055	0.058
Sample Var.	0.032	0.014	0.009	0.016	0.013	0.003	0.032	0.004	0.004	0.006	0.006	0.003	0.001	0.003	0.003
Coeff. of Var.	14.273	6.060	8.407	9.205	9.641	3.625	9.712	26.768	4.521	5.380	5.568	9.917	6.844	12.582	4.412

[1] Scaled data has been adjusted to correct for body size, where adjusted data is “trait/geometric mean of individual=scaled trait”.

Table E. Unscaled Cranial Variation in *Papio hamadryas*, by trait[1]

	INBR	***NAIN***	***NABR***	***BABR***	***NAPR***	***NABA***	***PRBA***	***IORB***	***BORB***	***BIPO***	***BIZY***	***ORBH***	***ORBB***	***OPBA***	***BIPG***
Pooled Sex															
N	485	487	503	463	510	471	470	511	511	511	506	511	511	455	510
Range (mm)	26.566	44.635	31.861	22.701	105.803	36.552	97.812	10.501	26.424	44.822	64.565	12.342	12.513	11.673	42.329
Min (mm)	43.455	86.252	51.156	58.255	53.038	63.923	82.617	3.468	54.473	68.171	68.476	20.048	25.078	16.322	59.219
Max (mm)	70.021	130.886	83.017	80.956	158.841	100.475	180.429	13.969	80.897	112.993	133.042	32.390	37.590	27.995	101.548
Mean (mm)	56.731	109.240	64.046	68.397	111.720	81.818	137.655	8.145	67.946	91.040	100.260	24.707	31.199	21.887	80.998
Standard Err.	0.187	0.363	0.207	0.189	1.008	0.343	1.002	0.081	0.251	0.386	0.608	0.087	0.109	0.094	0.339
Standard Dev.	4.119	8.017	4.636	4.060	22.766	7.435	21.724	1.838	5.666	8.720	13.674	1.972	2.475	2.007	7.651
Sample Var.	16.968	64.280	21.495	16.487	518.269	55.276	471.913	3.379	32.103	76.038	186.982	3.889	6.125	4.029	58.532
Coeff. of Var.	7.261	7.339	7.239	5.936	20.377	9.087	15.781	22.570	8.339	9.578	13.639	7.981	7.933	9.171	9.445
Females Only															
N	165	166	172	156	175	159	159	175	175	175	173	175	175	154	174
Range (mm)	17.481	27.701	20.759	14.534	65.397	25.074	68.777	7.775	20.257	32.893	42.832	9.897	10.132	10.038	28.204
Min (mm)	46.853	86.252	51.156	58.255	53.038	63.923	82.617	3.468	54.473	68.171	68.476	20.205	25.078	16.563	59.219
Max (mm)	64.334	113.953	71.914	72.789	118.434	88.997	151.394	11.242	74.729	101.065	111.308	30.102	35.210	26.602	87.423
Mean (mm)	55.913	102.367	61.214	65.313	91.484	74.747	115.836	6.821	62.781	83.712	87.074	24.305	29.169	21.229	74.573
Standard Err.	0.270	0.441	0.284	0.225	1.090	0.359	0.945	0.085	0.256	0.467	0.610	0.138	0.133	0.148	0.422
Standard Dev.	3.463	5.688	3.730	2.809	14.425	4.521	11.919	1.122	3.389	6.183	8.023	1.826	1.755	1.841	5.569
Sample Var.	11.995	32.355	13.910	7.889	208.085	20.435	142.056	1.259	11.484	38.230	64.362	3.336	3.080	3.391	31.017
Coeff. of Var.	6.194	5.557	6.093	4.300	15.768	6.048	10.289	16.453	5.398	7.386	9.213	7.515	6.017	8.674	7.468

Males Only															
N	320	321	331	307	335	312	311	336	336	336	333	336	336	301	336
Range (mm)	26.566	36.167	30.063	22.567	94.607	31.848	90.343	10.315	23.064	41.859	58.871	12.342	11.843	11.673	38.494
Min (mm)	43.455	94.720	52.954	58.389	64.233	68.628	90.086	3.654	57.833	71.134	74.171	20.048	25.747	16.322	63.054
Max (mm)	70.021	130.886	83.017	80.956	158.841	100.475	180.429	13.969	80.897	112.993	133.042	32.390	37.590	27.995	101.548
Mean (mm)	57.153	112.795	65.517	69.964	122.291	85.421	148.810	8.834	70.636	94.856	107.110	24.917	32.257	22.224	84.326
Standard Err.	0.244	0.369	0.240	0.210	1.029	0.333	0.936	0.096	0.254	0.398	0.584	0.110	0.115	0.116	0.347
Standard Dev.	4.365	6.615	4.375	3.685	18.835	5.880	16.509	1.760	4.660	7.297	10.649	2.015	2.109	2.008	6.354
Sample Var.	19.052	43.763	19.139	13.581	354.774	34.574	272.531	3.097	21.715	53.245	113.405	4.059	4.449	4.033	40.369
Coeff. of Var.	7.637	5.865	6.677	5.267	15.402	6.883	11.094	19.922	6.597	7.693	9.942	8.085	6.539	9.036	7.535

[1] Cranial traits are defined in Appendix 1A.

Table F. Scaled Cranial Variation in *Papio hamadryas*, by trait[1]

	INBR	***NAIN***	***NABR***	***BABR***	***NAPR***	***NABA***	***PRBA***	***IORB***	***BORB***	***BIPO***	***BIZY***	***ORBH***	***ORBB***	***OPBA***	***BIPG***
Pooled Sex															
N	485	487	503	463	510	471	470	511	511	511	506	511	511	455	510
Range	0.593	0.616	0.509	0.457	1.409	0.419	1.086	0.156	0.374	0.627	0.665	0.278	0.199	0.212	0.458
Min	0.725	1.698	0.959	1.021	1.146	1.258	1.770	0.073	1.084	1.375	1.522	0.338	0.487	0.287	1.238
Max	1.318	2.314	1.468	1.478	2.555	1.676	2.856	0.229	1.458	2.002	2.187	0.616	0.686	0.499	1.695
Mean	1.009	1.934	1.142	1.207	1.965	1.440	2.407	0.144	1.209	1.619	1.775	0.441	0.556	0.387	1.440
Standard Err.	0.005	0.003	0.004	0.003	0.011	0.002	0.009	0.001	0.002	0.004	0.006	0.002	0.001	0.001	0.003
Standard Dev.	0.101	0.074	0.079	0.073	0.248	0.054	0.201	0.025	0.054	0.080	0.134	0.042	0.030	0.031	0.064
Sample Var.	0.010	0.005	0.006	0.005	0.061	0.003	0.040	0.001	0.003	0.006	0.018	0.002	0.001	0.001	0.004

Coeff. of Var.	10.011	3.817	6.914	6.007	12.601	3.720	8.335	17.491	4.440	4.918	7.559	9.473	5.312	8.010	4.457
Females Only															
N	165	166	172	156	175	159	159	175	175	175	173	175	175	154	174
Range	0.446	0.556	0.424	0.354	1.010	0.387	1.008	0.133	0.354	0.565	0.430	0.250	0.198	0.181	0.390
Min	0.872	1.758	1.044	1.123	1.146	1.289	1.770	0.075	1.092	1.436	1.522	0.366	0.488	0.318	1.306
Max	1.318	2.314	1.468	1.478	2.156	1.676	2.779	0.208	1.446	2.002	1.952	0.616	0.686	0.499	1.695
Mean	1.082	1.975	1.190	1.255	1.765	1.434	2.217	0.132	1.221	1.625	1.687	0.473	0.567	0.408	1.447
Standard Err.	0.007	0.005	0.005	0.005	0.014	0.004	0.011	0.002	0.004	0.006	0.007	0.003	0.002	0.002	0.004
Standard Dev.	0.087	0.063	0.069	0.065	0.186	0.051	0.134	0.020	0.056	0.075	0.094	0.035	0.030	0.027	0.058
Sample Var.	0.007	0.004	0.005	0.004	0.035	0.003	0.018	0.000	0.003	0.006	0.009	0.001	0.001	0.001	0.003
Coeff. of Var.	8.003	3.177	5.771	5.190	10.549	3.573	6.056	15.324	4.551	4.622	5.600	7.348	5.205	6.536	4.012
Males Only															
N	320	321	331	307	335	312	311	336	336	336	333	336	336	301	336
Range	0.546	0.555	0.486	0.366	1.193	0.406	0.992	0.156	0.374	0.581	0.648	0.195	0.180	0.162	0.425
Min	0.725	1.698	0.959	1.021	1.362	1.258	1.864	0.073	1.084	1.375	1.539	0.338	0.487	0.287	1.238
Max	1.272	2.253	1.445	1.386	2.555	1.664	2.856	0.229	1.458	1.956	2.187	0.533	0.667	0.449	1.662
Mean	0.971	1.913	1.117	1.183	2.069	1.443	2.504	0.150	1.203	1.615	1.820	0.425	0.550	0.376	1.436
Standard Err.	0.005	0.004	0.004	0.004	0.011	0.003	0.009	0.001	0.003	0.004	0.007	0.002	0.002	0.002	0.004
Standard Dev.	0.086	0.070	0.072	0.064	0.209	0.055	0.154	0.025	0.052	0.082	0.129	0.036	0.028	0.027	0.067
Sample Var.	0.007	0.005	0.005	0.004	0.043	0.003	0.024	0.001	0.003	0.007	0.017	0.001	0.001	0.001	0.004
Coeff. of Var.	8.893	3.660	6.466	5.389	10.079	3.782	6.139	16.971	4.306	5.061	7.080	8.353	5.052	7.280	4.658

[1] Scaled data has been adjusted to correct for body size, where adjusted data is “trait/geometric mean of individual=scaled trait”.

Table G. Unscaled Cranial Variation in *Theropithecus gelada*, by trait[1]

	INBR	***NAIN***	***NABR***	***BABR***	***NAPR***	***NABA***	***PRBA***	***IORB***	***BORB***	***BIPO***	***BIZY***	***ORBH***	***ORBB***	***OPBA***	***BIPG***
Pooled Sex															
N	42	42	42	42	42	42	42	42	41	41	42	40	41	41	42
Range (mm)	13.772	21.665	19.800	11.999	38.626	21.793	53.221	5.226	13.973	21.192	31.953	5.700	6.209	5.573	20.288
Min (mm)	41.357	86.863	54.502	58.844	64.414	65.448	87.257	4.716	49.202	70.935	78.882	17.682	23.014	16.749	61.507
Max (mm)	55.130	108.528	74.301	70.843	103.040	87.241	140.478	9.942	63.175	92.127	110.835	23.382	29.223	22.323	81.795
Mean (mm)	48.200	99.269	63.429	65.291	85.475	78.482	116.986	7.027	57.115	82.614	95.428	20.608	26.502	19.622	73.783
Standard Err.	0.541	0.810	0.746	0.558	1.722	0.926	2.001	0.163	0.590	0.931	1.316	0.232	0.262	0.211	0.845
Standard Dev.	3.504	5.252	4.835	3.615	11.159	6.004	12.969	1.057	3.779	5.961	8.526	1.470	1.679	1.351	5.476
Sample Var.	12.281	27.587	23.376	13.068	124.530	36.042	168.208	1.116	14.279	35.534	72.686	2.161	2.817	1.826	29.991
Coeff. of Var.	7.271	5.291	7.623	5.537	13.056	7.650	11.086	15.036	6.616	7.216	8.934	7.134	6.334	6.886	7.422
Females Only															
N	13	13	13	13	13	13	13	13	13	13	13	13	13	13	13
Range (mm)	10.362	12.217	13.098	4.737	14.086	11.125	25.633	2.953	10.486	12.268	11.141	3.325	5.007	3.062	11.837
Min (mm)	42.623	86.863	54.502	58.844	64.414	65.448	87.257	4.716	49.202	70.935	78.882	17.748	23.014	16.749	61.507
Max (mm)	52.985	99.080	67.600	63.581	78.500	76.573	112.890	7.670	59.688	83.203	90.023	21.072	28.021	19.812	73.344
Mean (mm)	48.138	93.597	59.626	60.805	71.283	70.871	100.597	6.362	53.203	75.307	84.691	19.263	24.865	18.623	67.255
Standard Err.	0.852	0.934	1.088	0.399	1.317	0.898	1.735	0.249	0.815	0.972	0.867	0.253	0.400	0.259	0.948
Standard Dev.	3.071	3.369	3.924	1.438	4.749	3.239	6.254	0.898	2.939	3.503	3.127	0.913	1.442	0.934	3.419
Sample Var.	9.430	11.352	15.396	2.068	22.555	10.491	39.111	0.807	8.640	12.272	9.780	0.833	2.078	0.872	11.689
Coeff. of Var.	6.379	3.600	6.581	2.365	6.662	4.570	6.217	14.121	5.525	4.652	3.693	4.739	5.798	5.014	5.083
Males Only															
N	29	29	29	29	29	29	29	29	28	28	29	27	28	28	29
Range (mm)	13.772	14.019	16.283	7.947	26.357	11.161	29.144	4.933	9.981	11.883	20.776	5.700	4.905	5.379	10.643
Min (mm)	41.357	94.509	58.018	62.896	76.683	76.081	111.335	5.009	53.193	80.244	90.059	17.682	24.317	16.943	71.152
Max (mm)	55.130	108.528	74.301	70.843	103.040	87.241	140.478	9.942	63.175	92.127	110.835	23.382	29.223	22.323	81.795
Mean (mm)	48.228	101.811	65.134	67.302	91.837	81.894	124.332	7.325	58.932	86.006	100.241	21.256	27.261	20.086	76.710
Standard Err.	0.693	0.692	0.786	0.403	1.133	0.567	1.299	0.185	0.483	0.584	0.923	0.237	0.221	0.240	0.595
Standard Dev.	3.733	3.728	4.232	2.172	6.103	3.055	6.995	0.996	2.554	3.091	4.973	1.232	1.167	1.270	3.202
Sample Var.	13.939	13.897	17.906	4.716	37.243	9.331	48.937	0.991	6.522	9.553	24.727	1.517	1.362	1.613	10.250
Coeff. of Var.	7.741	3.662	6.497	3.227	6.645	3.730	5.626	13.590	4.334	3.594	4.961	5.795	4.282	6.323	4.174

[1] Cranial traits are defined in Appendix 1A.

Table H. Scaled Cranial Variation in *Theropithecus gelada*, by trait[1]

	INBR	***NAIN***	***NABR***	***BABR***	***NAPR***	***NABA***	***PRBA***	***IORB***	***BORB***	***BIPO***	***BIZY***	***ORBH***	***ORBB***	***OPBA***	***BIPG***
Pooled Sex															
N	42	42	42	42	42	42	42	42	41	41	42	40	41	41	42
Range	0.331	0.264	0.330	0.209	0.501	0.150	0.512	0.083	0.178	0.277	0.347	0.103	0.100	0.105	0.223
Min	0.808	1.831	1.122	1.205	1.428	1.457	2.037	0.102	1.039	1.489	1.675	0.346	0.471	0.336	1.318
Max	1.139	2.095	1.451	1.414	1.930	1.608	2.549	0.185	1.217	1.767	2.022	0.449	0.571	0.441	1.541
Mean	0.958	1.968	1.257	1.294	1.686	1.553	2.310	0.139	1.134	1.640	1.887	0.410	0.527	0.390	1.460
Standard Err.	0.014	0.010	0.012	0.007	0.020	0.006	0.019	0.003	0.006	0.009	0.012	0.003	0.003	0.004	0.007
Standard Dev.	0.094	0.065	0.075	0.044	0.131	0.041	0.123	0.018	0.040	0.058	0.080	0.021	0.021	0.024	0.044
Sample Var.	0.009	0.004	0.006	0.002	0.017	0.002	0.015	0.000	0.002	0.003	0.006	0.000	0.000	0.001	0.002
Coeff. of Var.	9.783	3.297	5.984	3.384	7.746	2.612	5.330	12.625	3.550	3.548	4.236	5.203	3.950	6.060	3.009
Females Only															
N	13	13	13	13	13	13	13	13	13	13	13	13	13	13	13
Range	0.270	0.156	0.258	0.164	0.235	0.126	0.301	0.056	0.123	0.264	0.238	0.056	0.063	0.051	0.108
Min	0.869	1.939	1.193	1.250	1.428	1.471	2.037	0.105	1.094	1.503	1.675	0.393	0.508	0.374	1.394
Max	1.139	2.095	1.451	1.414	1.663	1.597	2.338	0.161	1.217	1.767	1.913	0.449	0.571	0.425	1.503
Mean	1.044	2.028	1.292	1.318	1.543	1.535	2.178	0.138	1.152	1.632	1.836	0.417	0.538	0.404	1.457
Standard Err.	0.022	0.013	0.020	0.013	0.018	0.011	0.020	0.005	0.009	0.020	0.020	0.004	0.005	0.005	0.010
Standard Dev.	0.080	0.046	0.071	0.046	0.065	0.041	0.072	0.016	0.032	0.073	0.072	0.016	0.019	0.017	0.036
Sample Var.	0.006	0.002	0.005	0.002	0.004	0.002	0.005	0.000	0.001	0.005	0.005	0.000	0.000	0.000	0.001
Coeff. of Var.	7.704	2.255	5.467	3.475	4.190	2.661	3.303	11.824	2.800	4.457	3.938	3.787	3.477	4.300	2.486
Males Only															
N	29	29	29	29	29	29	29	29	28	28	29	27	28	28	29
Range	0.262	0.204	0.275	0.142	0.444	0.150	0.375	0.083	0.157	0.229	0.251	0.090	0.083	0.105	0.223
Min	0.808	1.831	1.122	1.205	1.486	1.457	2.174	0.102	1.039	1.489	1.771	0.346	0.471	0.336	1.318
Max	1.069	2.035	1.397	1.347	1.930	1.608	2.549	0.185	1.196	1.718	2.022	0.436	0.554	0.441	1.541
Mean	0.920	1.941	1.242	1.283	1.750	1.561	2.369	0.140	1.126	1.644	1.910	0.406	0.521	0.383	1.462
Standard Err.	0.013	0.010	0.014	0.007	0.018	0.007	0.017	0.003	0.008	0.010	0.014	0.004	0.004	0.004	0.009

Standard Dev.	0.071	0.053	0.073	0.039	0.097	0.039	0.091	0.018	0.041	0.051	0.073	0.023	0.020	0.024	0.047
Sample Var.	0.005	0.003	0.005	0.002	0.009	0.001	0.008	0.000	0.002	0.003	0.005	0.001	0.000	0.001	0.002
Coeff. of Var.	7.763	2.736	5.887	3.030	5.566	2.468	3.840	13.130	3.681	3.115	3.827	5.631	3.762	6.169	3.248

[1] Scaled data has been adjusted to correct for body size, where adjusted data is "trait/geometric mean of individual=scaled trait".

Table I. Unscaled Cranial Variation in *Macaca fascicularis*, by trait[1]

	INBR	***NAIN***	***NABR***	***BABR***	***NAPR***	***NABA***	***PRBA***	***IORB***	***BORB***	***BIPO***	***BIZY***	***ORBH***	***ORBB***	***OPBA***	***BIPG***
Pooled Sex															
N	243	243	243	242	243	242	242	243	243	243	243	243	243	242	243
Range (mm)	17.143	23.367	21.076	11.918	39.790	23.611	41.610	7.062	15.490	26.588	31.961	10.098	6.918	6.400	20.032
Min (mm)	31.138	66.134	38.982	42.073	34.324	46.796	60.988	0.921	40.328	49.929	52.926	18.071	19.490	12.260	41.890
Max (mm)	48.281	89.501	60.058	53.991	74.114	70.407	102.598	7.983	55.818	76.517	84.887	28.169	26.408	18.660	61.922
Mean (mm)	39.420	76.690	46.916	47.312	53.338	58.952	79.012	4.321	47.863	63.596	67.208	22.998	22.776	15.083	51.244
Standard Err.	0.206	0.276	0.198	0.156	0.494	0.264	0.582	0.069	0.178	0.327	0.430	0.128	0.085	0.076	0.250
Standard Dev.	3.206	4.302	3.089	2.431	7.705	4.111	9.051	1.081	2.776	5.097	6.710	1.989	1.319	1.175	3.889
Sample Var.	10.281	18.510	9.545	5.910	59.367	16.904	81.921	1.169	7.704	25.981	45.021	3.957	1.740	1.382	15.127
Coeff. of Var.	8.134	5.610	6.585	5.138	14.446	6.974	11.455	25.025	5.799	8.015	9.984	8.649	5.791	7.793	7.590
Females Only															
N	96	96	96	95	96	95	95	96	96	96	96	96	96	95	96
Range (mm)	16.589	13.767	12.726	9.026	26.342	15.237	23.875	6.907	12.096	20.171	20.249	9.466	5.856	5.516	12.418
Min (mm)	31.138	66.134	40.366	42.073	34.324	46.796	60.988	0.921	40.328	49.929	52.926	18.211	19.490	12.622	41.890
Max (mm)	47.726	79.901	53.092	51.099	60.666	62.032	84.863	7.828	52.423	70.100	73.175	27.677	25.346	18.138	54.308
Mean (mm)	38.565	73.499	45.519	45.743	47.769	55.619	70.970	3.980	45.953	60.057	60.908	22.543	21.911	14.787	47.836
Standard Err.	0.336	0.296	0.257	0.175	0.566	0.284	0.548	0.109	0.218	0.440	0.388	0.189	0.111	0.113	0.260
Standard Dev.	3.294	2.903	2.517	1.709	5.544	2.770	5.337	1.069	2.135	4.309	3.803	1.854	1.084	1.102	2.548
Sample Var.	10.848	8.427	6.336	2.920	30.735	7.673	28.483	1.143	4.558	18.567	14.465	3.437	1.175	1.215	6.491
Coeff. of Var.	8.541	3.950	5.530	3.736	11.606	4.980	7.520	26.865	4.646	7.175	6.244	8.224	4.947	7.453	5.326
Males Only															
N	147	147	147	147	147	147	147	147	147	147	147	147	147	147	147
Range (mm)	15.594	20.347	21.076	11.424	34.552	18.005	34.608	5.901	11.804	19.750	27.827	10.098	5.380	6.400	16.637
Min (mm)	32.686	69.153	38.982	42.567	39.561	52.402	67.990	2.083	44.014	56.767	57.060	18.071	21.028	12.260	45.285
Max (mm)	48.281	89.501	60.058	53.991	74.114	70.407	102.598	7.983	55.818	76.517	84.887	28.169	26.408	18.660	61.922

Mean (mm)	39.978	78.774	47.828	48.326	56.976	61.106	84.209	4.544	49.111	65.907	71.323	23.295	23.341	15.274	53.469
Standard Err.	0.250	0.310	0.255	0.189	0.551	0.274	0.569	0.085	0.199	0.344	0.387	0.167	0.094	0.098	0.237
Standard Dev.	3.031	3.759	3.095	2.289	6.685	3.326	6.900	1.033	2.416	4.168	4.697	2.024	1.142	1.185	2.869
Sample Var.	9.188	14.131	9.578	5.239	44.687	11.064	47.610	1.068	5.837	17.369	22.061	4.097	1.305	1.405	8.231
Coeff. of Var.	7.582	4.772	6.471	4.736	11.733	5.443	8.194	22.741	4.920	6.323	6.585	8.689	4.893	7.759	5.366

[1] Cranial traits are defined in Appendix 1A.

Table J. Scaled Cranial Variation in *Macaca fascicularis*, by trait[1]

	INBR	***NAIN***	***NABR***	***BABR***	***NAPR***	***NABA***	***PRBA***	***IORB***	***BORB***	***BIPO***	***BIZY***	***ORBH***	***ORBB***	***OPBA***	***BIPG***
Pooled Sex															
N	243	243	243	242	243	242	242	243	243	243	243	243	243	242	243
Range	0.450	0.387	0.504	0.334	0.758	0.311	0.630	0.175	0.252	0.374	0.462	0.301	0.154	0.211	0.320
Min	0.860	1.864	1.033	1.090	1.063	1.363	1.773	0.028	1.166	1.471	1.558	0.456	0.531	0.304	1.181
Max	1.310	2.251	1.536	1.424	1.820	1.674	2.403	0.202	1.418	1.845	2.020	0.757	0.685	0.515	1.501
Mean	1.043	2.027	1.241	1.251	1.404	1.556	2.080	0.114	1.265	1.679	1.772	0.608	0.602	0.399	1.353
Standard Err.	0.006	0.004	0.005	0.004	0.009	0.003	0.008	0.002	0.003	0.005	0.006	0.003	0.002	0.002	0.004
Standard Dev.	0.089	0.063	0.075	0.060	0.142	0.043	0.128	0.025	0.042	0.071	0.093	0.046	0.025	0.035	0.056
Sample Var.	0.008	0.004	0.006	0.004	0.020	0.002	0.016	0.001	0.002	0.005	0.009	0.002	0.001	0.001	0.003
Coeff. of Var.	8.505	3.085	6.062	4.809	10.086	2.741	6.131	22.045	3.346	4.245	5.227	7.554	4.200	8.742	4.109
Females Only															
N	96	96	96	95	96	95	95	96	96	96	96	96	96	95	96
Range	0.438	0.329	0.410	0.264	0.758	0.300	0.452	0.175	0.252	0.329	0.361	0.216	0.128	0.176	0.233
Min	0.871	1.922	1.036	1.160	1.063	1.363	1.773	0.028	1.166	1.498	1.558	0.541	0.557	0.340	1.210
Max	1.310	2.251	1.446	1.424	1.820	1.663	2.225	0.202	1.418	1.827	1.918	0.757	0.685	0.515	1.443
Mean	1.078	2.053	1.272	1.277	1.332	1.552	1.978	0.111	1.283	1.675	1.700	0.629	0.612	0.413	1.336
Standard Err.	0.010	0.006	0.008	0.006	0.013	0.004	0.010	0.003	0.004	0.008	0.007	0.004	0.003	0.004	0.005
Standard Dev.	0.096	0.061	0.074	0.055	0.127	0.044	0.095	0.027	0.042	0.074	0.068	0.039	0.026	0.035	0.047
Sample Var.	0.009	0.004	0.005	0.003	0.016	0.002	0.009	0.001	0.002	0.005	0.005	0.002	0.001	0.001	0.002

Coeff. of Var.	8.883	2.990	5.808	4.297	9.549	2.817	4.822	24.304	3.262	4.403	3.973	6.168	4.303	8.511	3.547
Males Only															
N	147	147	147	147	147	147	147	147	147	147	147	147	147	147	147
Range	0.383	0.296	0.504	0.285	0.695	0.250	0.502	0.138	0.188	0.374	0.429	0.266	0.128	0.167	0.320
Min	0.860	1.864	1.033	1.090	1.099	1.423	1.900	0.054	1.178	1.471	1.590	0.456	0.531	0.304	1.181
Max	1.242	2.161	1.536	1.375	1.794	1.674	2.403	0.192	1.366	1.845	2.020	0.722	0.659	0.471	1.501
Mean	1.021	2.010	1.221	1.234	1.451	1.559	2.145	0.116	1.253	1.681	1.819	0.594	0.596	0.390	1.365
Standard Err.	0.006	0.005	0.006	0.005	0.011	0.003	0.008	0.002	0.003	0.006	0.006	0.004	0.002	0.003	0.005
Standard Dev.	0.076	0.057	0.069	0.057	0.131	0.042	0.100	0.024	0.038	0.070	0.075	0.045	0.022	0.032	0.058
Sample Var.	0.006	0.003	0.005	0.003	0.017	0.002	0.010	0.001	0.001	0.005	0.006	0.002	0.001	0.001	0.003
Coeff. of Var.	7.448	2.855	5.662	4.645	9.006	2.685	4.648	20.470	3.056	4.148	4.126	7.600	3.765	8.121	4.229

[1] Scaled data has been adjusted to correct for body size, where adjusted data is “trait/geometric mean of individual=scaled trait”.

Table K. Unscaled Cranial Variation in *Macaca nemestrina*, by trait[1]

	INBR	***NAIN***	***NABR***	***BABR***	***NAPR***	***NABA***	***PRBA***	***IORB***	***BORB***	***BIPO***	***BIZY***	***ORBH***	***ORBB***	***OPBA***	***BIPG***
Pooled Sex															
N	18	18	18	18	18	18	18	18	18	18	18	18	18	18	18
Range (mm)	13.246	31.554	20.725	9.829	44.072	20.635	50.184	4.425	17.185	27.896	31.454	6.634	6.755	5.350	20.887
Min (mm)	38.508	78.086	48.627	48.564	49.366	57.078	73.321	3.336	46.898	59.421	64.248	21.661	22.865	14.053	53.349
Max (mm)	51.754	109.640	69.352	58.393	93.438	77.714	123.505	7.761	64.083	87.317	95.703	28.295	29.619	19.403	74.236
Mean (mm)	45.973	90.657	55.822	52.650	65.661	65.283	94.465	6.053	56.184	72.218	78.982	25.106	26.186	16.407	62.090
Standard Err.	0.971	1.773	1.050	0.493	3.050	1.543	3.421	0.289	1.158	1.865	2.320	0.469	0.475	0.337	1.389
Standard Dev.	4.120	7.520	4.456	2.090	12.939	6.547	14.515	1.225	4.912	7.911	9.843	1.989	2.015	1.431	5.895
Sample Var.	16.976	56.557	19.859	4.368	167.422	42.867	210.677	1.501	24.127	62.588	96.887	3.957	4.059	2.049	34.745
Coeff. of Var.	8.962	8.295	7.983	3.969	19.706	10.029	15.365	20.241	8.743	10.955	12.462	7.924	7.694	8.724	9.493
Females Only															
N	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8
Range (mm)	13.246	12.974	9.131	5.790	17.758	7.682	17.286	4.425	11.656	12.007	13.484	6.569	3.630	4.281	10.517
Min (mm)	38.508	78.086	51.746	48.564	49.366	57.078	73.321	3.336	46.898	59.421	64.248	21.661	22.865	14.053	53.349
Max (mm)	51.754	91.060	60.877	54.355	67.124	64.761	90.606	7.761	58.555	71.428	77.733	28.230	26.495	18.333	63.866
Mean (mm)	43.929	85.656	55.252	51.563	56.146	60.760	83.396	5.792	52.965	65.927	71.071	24.667	24.826	15.616	57.641
Standard Err.	1.678	1.770	1.051	0.595	2.091	1.062	2.276	0.490	1.415	1.555	1.797	0.713	0.493	0.462	1.158
Standard Dev.	4.747	5.005	2.973	1.684	5.913	3.003	6.436	1.386	4.003	4.399	5.082	2.016	1.395	1.306	3.276
Sample Var.	22.537	25.051	8.839	2.836	34.968	9.016	41.425	1.922	16.021	19.349	25.826	4.063	1.946	1.707	10.733
Coeff. of Var.	10.807	5.843	5.381	3.266	10.532	4.942	7.718	23.935	7.557	6.672	7.150	8.171	5.619	8.366	5.684
Males Only															
N	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10
Range (mm)	9.939	21.974	20.725	7.114	39.675	18.299	39.611	3.110	11.656	21.021	21.437	5.690	4.314	4.632	14.951
Min (mm)	41.285	87.666	48.627	51.279	53.763	59.415	83.894	4.616	52.427	66.295	74.266	22.605	25.305	14.771	59.285
Max (mm)	51.223	109.640	69.352	58.393	93.438	77.714	123.505	7.725	64.083	87.317	95.703	28.295	29.619	19.403	74.236
Mean (mm)	47.609	94.658	56.277	53.520	73.274	68.902	103.320	6.263	58.758	77.250	85.311	25.457	27.273	17.040	65.650
Standard Err.	0.886	2.176	1.735	0.644	3.797	2.030	4.119	0.351	1.286	1.997	2.506	0.633	0.565	0.392	1.600
Standard Dev.	2.802	6.880	5.488	2.038	12.008	6.421	13.027	1.110	4.067	6.314	7.924	2.002	1.788	1.241	5.060
Sample Var.	7.849	47.330	30.119	4.154	144.180	41.226	169.690	1.231	16.543	39.862	62.793	4.007	3.197	1.540	25.606
Coeff. of Var.	5.885	7.268	9.752	3.808	16.387	9.319	12.608	17.719	6.922	8.173	9.289	7.864	6.557	7.283	7.708

[1] Cranial traits are defined in Appendix 1A.

Table L. Scaled Cranial Variation in *Macaca nemestrina*, by trait[1]

	INBR	*NAIN*	*NABR*	*BABR*	*NAPR*	*NABA*	*PRBA*	*IORB*	*BORB*	*BIPO*	*BIZY*	*ORBH*	*ORBB*	*OPBA*	*BIPG*
Pooled Sex															
N	18	18	18	18	18	18	18	18	18	18	18	18	18	18	18
Range	0.280	0.264	0.358	0.272	0.611	0.291	0.507	0.083	0.103	0.191	0.281	0.165	0.060	0.096	0.134
Min	0.908	1.858	1.050	1.021	1.234	1.344	1.883	0.087	1.206	1.527	1.644	0.503	0.549	0.323	1.324
Max	1.188	2.122	1.408	1.292	1.845	1.634	2.390	0.171	1.310	1.718	1.925	0.668	0.610	0.419	1.458
Mean	1.029	2.027	1.252	1.182	1.457	1.458	2.100	0.135	1.255	1.611	1.760	0.563	0.586	0.368	1.387
Standard Err.	0.018	0.014	0.025	0.018	0.045	0.016	0.035	0.005	0.007	0.015	0.019	0.011	0.004	0.007	0.009
Standard Dev.	0.078	0.060	0.106	0.076	0.189	0.069	0.150	0.021	0.029	0.063	0.080	0.046	0.015	0.030	0.037
Sample Var.	0.006	0.004	0.011	0.006	0.036	0.005	0.023	0.000	0.001	0.004	0.006	0.002	0.000	0.001	0.001
Coeff. of Var.	7.569	2.978	8.449	6.424	12.985	4.740	7.143	15.940	2.288	3.940	4.554	8.132	2.611	8.282	2.646
Females Only															
N	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8
Range	0.218	0.110	0.194	0.141	0.243	0.166	0.148	0.083	0.058	0.105	0.128	0.156	0.031	0.096	0.134
Min	0.970	1.980	1.214	1.152	1.234	1.344	1.883	0.087	1.230	1.528	1.644	0.512	0.579	0.323	1.324
Max	1.188	2.090	1.408	1.292	1.476	1.510	2.031	0.171	1.288	1.633	1.772	0.668	0.610	0.419	1.458
Mean	1.046	2.042	1.320	1.231	1.337	1.450	1.986	0.137	1.261	1.571	1.693	0.589	0.592	0.373	1.375
Standard Err.	0.025	0.014	0.029	0.019	0.035	0.022	0.018	0.009	0.007	0.014	0.014	0.019	0.003	0.011	0.015
Standard Dev.	0.072	0.039	0.083	0.053	0.100	0.063	0.050	0.027	0.021	0.039	0.039	0.053	0.010	0.032	0.043
Sample Var.	0.005	0.002	0.007	0.003	0.010	0.004	0.002	0.001	0.000	0.001	0.002	0.003	0.000	0.001	0.002
Coeff. of Var.	6.898	1.902	6.276	4.327	7.467	4.342	2.497	19.428	1.655	2.459	2.325	9.021	1.625	8.657	3.141
Males Only															
N	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10
Range	0.233	0.264	0.292	0.211	0.589	0.269	0.427	0.054	0.103	0.191	0.187	0.098	0.050	0.077	0.095
Min	0.908	1.858	1.050	1.021	1.255	1.366	1.963	0.098	1.206	1.527	1.738	0.503	0.549	0.328	1.360
Max	1.141	2.122	1.342	1.232	1.845	1.634	2.390	0.153	1.310	1.718	1.925	0.601	0.599	0.405	1.454
Mean	1.016	2.015	1.198	1.142	1.553	1.465	2.191	0.133	1.250	1.643	1.813	0.542	0.581	0.364	1.396
Standard Err.	0.026	0.023	0.029	0.022	0.061	0.024	0.045	0.006	0.011	0.020	0.020	0.008	0.006	0.009	0.009
Standard Dev.	0.084	0.073	0.092	0.069	0.192	0.076	0.141	0.018	0.034	0.062	0.062	0.025	0.018	0.030	0.029
Sample Var.	0.007	0.005	0.009	0.005	0.037	0.006	0.020	0.000	0.001	0.004	0.004	0.001	0.000	0.001	0.001
Coeff. of Var.	8.234	3.628	7.716	6.041	12.354	5.214	6.428	13.278	2.726	3.795	3.431	4.699	3.016	8.243	2.102

[1] Scaled data has been adjusted to correct for body size, where adjusted data is "trait/geometric mean of individual=scaled trait".

Table M. Unscaled Molar Variation in *Homo sapiens*, by trait[1]

	UM1md	*UM2md*	*UM3md*	*UM1bl*	*UM2bl*	*UM3bl*	*LM1md*	*LM2md*	*LM3md*	*LM1bl*	*LM2bl*	*LM3bl*
Homo sapiens												
Pooled Sex												
N	42	41	38	41	42	40	42	41	37	40	42	40
Range (mm)	5.25	3.62	4.78	2.67	4.03	4.79	3.29	3.88	4.25	2.25	2.965	3.94
Min (mm)	6.62	8	6.87	9.95	8.69	9.08	9.58	9.87	9.5	9.185	8.935	8.245
Max (mm)	11.87	11.62	11.65	12.62	12.72	13.87	12.87	13.75	13.75	11.435	11.9	12.185
Mean (mm)	10.448	10.271	9.331	11.309	11.179	11.351	11.324	11.757	11.436	10.456	10.497	10.329
Standard Error	0.133	0.119	0.167	0.104	0.127	0.173	0.125	0.131	0.181	0.092	0.087	0.128
Standard Deviation	0.862	0.761	1.027	0.665	0.825	1.094	0.807	0.838	1.102	0.579	0.565	0.809
Sample Variance	0.744	0.579	1.054	0.442	0.681	1.197	0.651	0.701	1.214	0.336	0.319	0.654
Coefficient of V	8.253	7.410	11.004	5.876	7.381	9.638	7.126	7.124	9.633	5.540	5.382	7.828
Females Only												
N	20	19	18	20	20	20	20	19	17	20	20	20
Range (mm)	4.5	3.58	4.78	1.92	3.36	3.2	2.67	3.13	4	2	2.425	3.44
Min (mm)	6.62	8	6.87	9.95	8.69	9.17	9.58	9.87	9.5	9.185	8.935	8.245
Max (mm)	11.12	11.58	11.65	11.87	12.05	12.37	12.25	13	13.5	11.185	11.36	11.685
Mean (mm)	10.141	10.141	9.192	11.034	10.747	11.152	10.979	11.379	11.035	10.254	10.305	10.183
Standard Error	0.215	0.183	0.265	0.137	0.168	0.199	0.175	0.182	0.229	0.125	0.133	0.204
Standard Deviation	0.964	0.798	1.124	0.613	0.752	0.888	0.782	0.791	0.943	0.558	0.597	0.914
Sample Variance	0.929	0.637	1.264	0.376	0.566	0.789	0.611	0.626	0.889	0.311	0.356	0.835
Coefficient of V	9.502	7.871	12.231	5.555	7.000	7.966	7.120	6.953	8.543	5.439	5.789	8.975
Males Only												
N	22	22	20	21	22	20	22	22	20	21	22	20
Range (mm)	2.92	2.62	3.15	2.6	2.61	4.79	2.71	2.9	4.15	1.925	2	2.755
Min (mm)	8.95	9	7.6	10.02	10.11	9.08	10.16	10.85	9.6	9.51	9.9	9.43
Max (mm)	11.87	11.62	10.75	12.62	12.72	13.87	12.87	13.75	13.75	11.435	11.9	12.185
Mean (mm)	10.727	10.384	9.457	11.571	11.572	11.550	11.637	12.083	11.778	10.632	10.672	10.475
Standard Error	0.141	0.155	0.211	0.134	0.147	0.281	0.151	0.159	0.253	0.118	0.103	0.152
Standard Deviation	0.663	0.727	0.942	0.615	0.691	1.259	0.709	0.748	1.133	0.540	0.484	0.680
Sample Variance	0.440	0.528	0.887	0.378	0.478	1.584	0.503	0.559	1.285	0.291	0.234	0.462
Coefficient of V	6.185	7.001	9.961	5.314	5.974	10.897	6.092	6.186	9.623	5.076	4.533	6.489

[1] Molar traits are defined in Appendix 1A.

Table N. Scaled Molar Variation in *Homo sapiens*, by trait[1]

	UM1md	*UM2md*	*UM3md*	*UM1bl*	*UM2bl*	*UM3bl*	*LM1md*	*LM2md*	*LM3md*	*LM1bl*	*LM2bl*	*LM3bl*
Homo sapiens												
Pooled Sex												
N	42	41	38	41	42	40	42	41	37	41	42	40
Range	0.439	0.167	0.296	0.276	0.189	0.283	0.210	0.165	0.301	0.189	0.156	0.160
Min	0.652	0.863	0.745	0.886	0.924	0.890	0.950	1.009	0.903	0.870	0.891	0.875
Max	1.091	1.030	1.042	1.162	1.113	1.173	1.160	1.174	1.204	1.059	1.047	1.035
Mean	0.970	0.950	0.865	1.051	1.037	1.055	1.051	1.087	1.060	0.971	0.975	0.961
Standard Error	0.010	0.007	0.010	0.008	0.007	0.010	0.006	0.006	0.010	0.005	0.005	0.006
Standard Deviation	0.066	0.046	0.064	0.052	0.044	0.061	0.042	0.042	0.058	0.033	0.032	0.041
Sample Variance	0.004	0.002	0.004	0.003	0.002	0.004	0.002	0.002	0.003	0.001	0.001	0.002
Coefficient of V	6.821	4.853	7.409	4.943	4.200	5.781	3.997	3.827	5.452	3.418	3.271	4.248
Females Only												
N	20	19	18	20	20	20	20	19	17	20	20	20
Range	0.439	0.166	0.282	0.230	0.189	0.181	0.128	0.150	0.258	0.092	0.084	0.160
Min	0.652	0.864	0.760	0.932	0.924	0.964	0.975	1.009	0.947	0.930	0.937	0.875
Max	1.091	1.030	1.042	1.162	1.113	1.145	1.103	1.160	1.204	1.022	1.020	1.035
Mean	0.966	0.960	0.871	1.052	1.024	1.061	1.045	1.077	1.049	0.977	0.981	0.968
Standard Error	0.020	0.011	0.018	0.012	0.012	0.011	0.010	0.010	0.013	0.006	0.004	0.010
Standard Deviation	0.088	0.046	0.077	0.053	0.054	0.048	0.043	0.042	0.055	0.028	0.019	0.045
Sample Variance	0.008	0.002	0.006	0.003	0.003	0.002	0.002	0.002	0.003	0.001	0.000	0.002
Coefficient of V	9.104	4.817	8.852	4.995	5.253	4.538	4.069	3.938	5.201	2.860	1.938	4.618
Males Only												
N	22	22	20	21	22	20	22	22	20	21	22	20
Range	0.159	0.159	0.202	0.233	0.099	0.283	0.210	0.161	0.262	0.189	0.156	0.142
Min	0.889	0.863	0.745	0.886	1.004	0.890	0.950	1.014	0.903	0.870	0.891	0.878
Max	1.048	1.022	0.947	1.118	1.102	1.173	1.160	1.174	1.164	1.059	1.047	1.020
Mean	0.973	0.942	0.859	1.051	1.049	1.049	1.056	1.096	1.070	0.965	0.969	0.953
Standard Error	0.008	0.010	0.011	0.012	0.006	0.016	0.009	0.008	0.013	0.008	0.008	0.008
Standard Deviation	0.039	0.045	0.051	0.053	0.028	0.072	0.042	0.040	0.060	0.037	0.040	0.036
Sample Variance	0.002	0.002	0.003	0.003	0.001	0.005	0.002	0.002	0.004	0.001	0.002	0.001
Coefficient of V	4.006	4.823	5.929	5.016	2.623	6.901	3.966	3.631	5.622	3.869	4.106	3.788

[1] Scaled data has been adjusted to correct for body size, where adjusted data is “trait/geometric mean of individual=scaled trait”.

Table O. Unscaled Molar Variation in *Pan troglodytes*, by trait[1]

	UM1md	*UM2md*	*UM3md*	*UM1bl*	*UM2bl*	*UM3bl*	*LM1md*	*LM2md*	*LM3md*	*LM1bl*	*LM2bl*	*LM3bl*
Pan troglodytes												
Pooled Sex												
N	85	83	82	81	81	78	86	85	81	77	80	80
Range (mm)	3.47	4.77	4.53	3.15	4.43	4.58	2.97	3.18	3.68	1.955	2.64	2.875
Min (mm)	8.41	7.86	7.6	9.1	8.7	8.42	9.78	9.95	9.45	8.61	8.8	8.565
Max (mm)	11.88	12.63	12.13	12.25	13.13	13	12.75	13.13	13.13	10.565	11.44	11.44
Mean (mm)	10.390	10.340	9.555	11.063	11.404	10.770	11.503	11.621	10.959	9.765	10.338	9.887
Standard Error	0.077	0.094	0.095	0.073	0.096	0.111	0.066	0.072	0.079	0.056	0.062	0.071
Standard Deviation	0.709	0.852	0.858	0.657	0.860	0.977	0.614	0.666	0.710	0.494	0.551	0.636
Sample Variance	0.503	0.727	0.737	0.431	0.740	0.954	0.377	0.444	0.504	0.244	0.304	0.405
Coefficient of V	6.828	8.244	8.985	5.935	7.541	9.068	5.336	5.734	6.478	5.056	5.329	6.433
Females Only												
N	50	50	46	48	46	44	50	49	45	45	45	45
Range (mm)	2.76	3.89	3.22	3.15	3.45	4.22	2.97	3.18	3	1.735	1.815	2.055
Min (mm)	8.62	7.86	7.6	9.1	9.55	8.78	9.78	9.95	9.55	8.77	9.31	8.565
Max (mm)	11.38	11.75	10.82	12.25	13	13	12.75	13.13	12.55	10.505	11.125	10.62
Mean (mm)	10.298	10.112	9.339	10.959	11.230	10.499	11.445	11.508	10.807	9.717	10.203	9.673
Standard Error	0.087	0.112	0.116	0.093	0.115	0.136	0.086	0.096	0.092	0.069	0.070	0.076
Standard Deviation	0.614	0.795	0.787	0.642	0.777	0.899	0.610	0.671	0.618	0.464	0.467	0.513
Sample Variance	0.376	0.632	0.620	0.412	0.604	0.808	0.372	0.450	0.381	0.215	0.218	0.263
Coefficient of V	5.958	7.859	8.428	5.857	6.918	8.563	5.331	5.831	5.714	4.772	4.575	5.303
Males Only												
N	35	33	36	33	35	34	36	36	36	32	35	35
Range (mm)	3.47	4.32	4.38	2.97	4.43	4.46	2.55	2.6	3.68	1.955	2.64	2.84
Min (mm)	8.41	8.31	7.75	9.28	8.7	8.42	10	10.15	9.45	8.61	8.8	8.6
Max (mm)	11.88	12.63	12.13	12.25	13.13	12.88	12.55	12.75	13.13	10.565	11.44	11.44
Mean (mm)	10.520	10.685	9.831	11.214	11.633	11.121	11.583	11.773	11.150	9.832	10.512	10.163
Standard Error	0.138	0.145	0.146	0.115	0.155	0.167	0.103	0.106	0.130	0.094	0.103	0.115
Standard Deviation	0.819	0.831	0.877	0.658	0.920	0.973	0.619	0.637	0.778	0.533	0.606	0.679
Sample Variance	0.671	0.691	0.769	0.433	0.846	0.947	0.383	0.406	0.605	0.284	0.368	0.460
Coefficient of V	7.788	7.779	8.920	5.868	7.907	8.753	5.340	5.413	6.978	5.424	5.769	6.677

[1] Molar traits are defined in Appendix 1A.

Table P. Scaled Molar Variation in *Pan troglodytes*, by trait[1]

	UM1md	*UM2md*	*UM3md*	*UM1bl*	*UM2bl*	*UM3bl*	*LM1md*	*LM2md*	*LM3md*	*LM1bl*	*LM2bl*	*LM3bl*
Pan troglodytes												
Pooled Sex												
N	85	83	82	81	81	78	86	85	81	77	80	80
Range	0.174	0.258	0.239	0.154	0.251	0.277	0.257	0.190	0.221	0.209	0.136	0.216
Min	0.887	0.803	0.778	0.962	0.926	0.869	0.984	1.014	0.940	0.806	0.906	0.834
Max	1.060	1.061	1.017	1.115	1.177	1.145	1.241	1.204	1.160	1.014	1.042	1.050
Mean	0.982	0.975	0.898	1.041	1.073	1.010	1.088	1.098	1.032	0.922	0.973	0.930
Standard Error	0.005	0.005	0.006	0.004	0.005	0.007	0.005	0.004	0.005	0.004	0.003	0.005
Standard Deviation	0.043	0.047	0.051	0.036	0.047	0.061	0.047	0.039	0.048	0.035	0.030	0.042
Sample Variance	0.002	0.002	0.003	0.001	0.002	0.004	0.002	0.002	0.002	0.001	0.001	0.002
Coefficient of V	4.383	4.831	5.728	3.427	4.405	6.013	4.355	3.558	4.660	3.809	3.098	4.547
Females Only												
N	50	50	46	48	46	44	50	49	45	45	45	45
Range	0.165	0.252	0.208	0.144	0.192	0.276	0.257	0.189	0.204	0.136	0.136	0.216
Min	0.895	0.803	0.778	0.962	0.958	0.869	0.984	1.014	0.940	0.878	0.906	0.834
Max	1.060	1.056	0.986	1.106	1.150	1.145	1.241	1.204	1.144	1.014	1.042	1.050
Mean	0.987	0.967	0.890	1.048	1.072	0.998	1.098	1.103	1.031	0.930	0.975	0.924
Standard Error	0.005	0.007	0.008	0.005	0.007	0.009	0.007	0.006	0.007	0.005	0.005	0.006
Standard Deviation	0.038	0.049	0.053	0.035	0.044	0.062	0.050	0.041	0.047	0.033	0.034	0.044
Sample Variance	0.001	0.002	0.003	0.001	0.002	0.004	0.003	0.002	0.002	0.001	0.001	0.002
Coefficient of V	3.859	5.068	5.918	3.353	4.129	6.229	4.582	3.715	4.555	3.496	3.439	4.713
Males Only												
N	35	33	36	33	35	34	36	36	36	32	35	35
Range	0.172	0.140	0.209	0.145	0.251	0.275	0.175	0.145	0.219	0.172	0.107	0.153
Min	0.887	0.921	0.808	0.970	0.926	0.869	0.994	1.014	0.941	0.806	0.931	0.866
Max	1.059	1.061	1.017	1.115	1.177	1.144	1.169	1.160	1.160	0.977	1.038	1.019
Mean	0.975	0.988	0.909	1.032	1.074	1.027	1.074	1.092	1.034	0.911	0.971	0.939
Standard Error	0.008	0.007	0.008	0.006	0.009	0.010	0.007	0.006	0.008	0.006	0.004	0.007
Standard Deviation	0.049	0.042	0.049	0.035	0.052	0.056	0.040	0.036	0.050	0.036	0.025	0.040
Sample Variance	0.002	0.002	0.002	0.001	0.003	0.003	0.002	0.001	0.003	0.001	0.001	0.002
Coefficient of V	5.018	4.233	5.351	3.378	4.802	5.406	3.703	3.300	4.849	3.969	2.616	4.232

[1] Scaled data has been adjusted to correct for body size, where adjusted data is "trait/geometric mean of individual=scaled trait".

Table Q. Unscaled Molar Variation in *Papio hamadryas*, by trait[1]

	UM1md	*UM2md*	*UM3md*	*UM1bl*	*UM2bl*	*UM3bl*	*LM1md*	*LM2md*	*LM3md*	*LM1bl*	*LM2bl*	*LM3bl*
Papio hamadryas												
Pooled Sex												
N	316	379	304	300	361	347	314	380	300	295	360	288
Range (mm)	5.97	7.83	8.31	6.02	7.65	9.99	5.085	6.785	6.33	4.55	5.695	6.195
Min (mm)	7.13	7.79	8.09	6.48	7.65	10.13	6.79	7.255	7.67	5.48	7	6.92
Max (mm)	13.1	15.62	16.4	12.5	15.3	20.12	11.875	14.04	14	10.03	12.695	13.115
Mean (mm)	10.456	12.540	12.828	10.114	12.233	15.590	9.462	11.148	11.157	8.104	9.877	10.245
Standard Error	0.066	0.074	0.096	0.067	0.072	0.095	0.047	0.053	0.067	0.045	0.050	0.065
Standard Deviation	1.168	1.438	1.672	1.165	1.372	1.766	0.830	1.036	1.154	0.765	0.950	1.100
Sample Variance	1.364	2.067	2.794	1.357	1.883	3.117	0.689	1.073	1.332	0.585	0.902	1.210
Coefficient of V	11.169	11.467	13.031	11.517	11.218	11.325	8.773	9.290	10.344	9.437	9.617	10.737
Females Only												
N	132	138	122	126	132	117	131	140	118	125	132	114
Range (mm)	5.57	7.61	7.81	5.52	7.65	7.87	3.98	5.365	4.955	4.095	4.72	4.785
Min (mm)	7.13	7.79	8.09	6.48	7.65	10.13	6.79	7.255	7.67	5.48	7	6.92
Max (mm)	12.7	15.4	15.9	12	15.3	18	10.77	12.62	12.625	9.575	11.72	11.705
Mean (mm)	9.959	11.964	11.993	9.537	11.603	14.712	8.998	10.500	10.412	7.702	9.284	9.584
Standard Error	0.102	0.129	0.140	0.103	0.123	0.167	0.069	0.086	0.094	0.065	0.080	0.098
Standard Deviation	1.172	1.510	1.545	1.157	1.411	1.802	0.792	1.019	1.026	0.730	0.916	1.043
Sample Variance	1.375	2.279	2.386	1.339	1.990	3.247	0.627	1.038	1.053	0.533	0.839	1.088
Coefficient of V	11.772	12.618	12.880	12.133	12.158	12.248	8.802	9.704	9.857	9.476	9.864	10.882
Males Only												
N	184	241	182	174	229	230	183	240	182	170	228	174
Range (mm)	4.9	6.37	6.8	4.75	6.12	9.37	4.225	5.34	5.78	3.53	5.145	5.165
Min (mm)	8.2	9.25	9.6	7.75	9.13	10.75	7.65	8.7	8.22	6.5	7.55	7.95
Max (mm)	13.1	15.62	16.4	12.5	15.25	20.12	11.875	14.04	14	10.03	12.695	13.115
Mean (mm)	10.812	12.869	13.388	10.532	12.596	16.037	9.794	11.527	11.640	8.399	10.220	10.679
Standard Error	0.076	0.083	0.112	0.074	0.080	0.104	0.051	0.054	0.071	0.050	0.052	0.069
Standard Deviation	1.029	1.287	1.516	0.980	1.212	1.572	0.687	0.841	0.960	0.648	0.787	0.905
Sample Variance	1.058	1.655	2.297	0.960	1.468	2.470	0.471	0.707	0.922	0.419	0.620	0.820
Coefficient of V	9.513	9.997	11.320	9.303	9.619	9.801	7.011	7.292	8.251	7.711	7.704	8.477

[1] Molar traits are defined in Appendix 1A.

Table R. Scaled Molar Variation in *Papio hamadryas*, by trait[1]

	UM1md	*UM2md*	*UM3md*	*UM1bl*	*UM2bl*	*UM3bl*	*LM1md*	*LM2md*	*LM3md*	*LM1bl*	*LM2bl*	*LM3bl*
Papio hamadryas												
Pooled Sex												
N	316	379	304	300	361	347	314	380	300	295	360	288
Range	0.317	0.399	0.308	0.390	0.374	0.501	0.226	0.252	0.245	0.181	0.296	0.203
Min	0.823	0.930	1.022	0.764	0.925	1.092	0.777	0.853	0.895	0.651	0.759	0.851
Max	1.140	1.329	1.330	1.155	1.299	1.592	1.002	1.105	1.140	0.832	1.055	1.054
Mean	0.953	1.124	1.163	0.922	1.097	1.393	0.864	1.001	1.014	0.740	0.887	0.932
Standard Error	0.003	0.004	0.004	0.003	0.004	0.005	0.002	0.002	0.003	0.002	0.002	0.002
Standard Deviation	0.050	0.072	0.063	0.049	0.069	0.088	0.034	0.043	0.045	0.032	0.045	0.036
Sample Variance	0.002	0.005	0.004	0.002	0.005	0.008	0.001	0.002	0.002	0.001	0.002	0.001
Coefficient of V	5.206	6.393	5.415	5.362	6.295	6.284	3.970	4.311	4.417	4.351	5.032	3.881
Females Only												
N	132	138	122	126	132	117	131	140	118	125	132	114
Range	0.308	0.325	0.284	0.263	0.352	0.401	0.208	0.204	0.195	0.181	0.195	0.173
Min	0.832	1.003	1.022	0.780	0.947	1.192	0.795	0.901	0.913	0.651	0.803	0.851
Max	1.140	1.329	1.306	1.043	1.299	1.592	1.002	1.105	1.107	0.832	0.998	1.024
Mean	0.963	1.149	1.156	0.923	1.117	1.417	0.872	1.010	1.007	0.747	0.895	0.929
Standard Error	0.005	0.006	0.006	0.005	0.006	0.007	0.003	0.003	0.004	0.003	0.003	0.003
Standard Deviation	0.056	0.069	0.063	0.057	0.063	0.081	0.036	0.039	0.041	0.031	0.040	0.035
Sample Variance	0.003	0.005	0.004	0.003	0.004	0.007	0.001	0.002	0.002	0.001	0.002	0.001
Coefficient of V	5.808	5.982	5.437	6.194	5.669	5.713	4.139	3.888	4.101	4.210	4.486	3.796
Males Only												
N	184	241	182	174	229	230	183	240	182	170	228	174
Range	0.302	0.346	0.303	0.390	0.350	0.471	0.165	0.251	0.245	0.166	0.296	0.189
Min	0.823	0.930	1.027	0.764	0.925	1.092	0.777	0.853	0.895	0.666	0.759	0.865
Max	1.125	1.276	1.330	1.155	1.275	1.563	0.942	1.104	1.140	0.832	1.055	1.054
Mean	0.946	1.109	1.168	0.921	1.086	1.381	0.859	0.995	1.018	0.735	0.882	0.933
Standard Error	0.003	0.004	0.005	0.003	0.005	0.006	0.002	0.003	0.003	0.002	0.003	0.003
Standard Deviation	0.043	0.070	0.063	0.043	0.070	0.088	0.032	0.044	0.046	0.032	0.046	0.037
Sample Variance	0.002	0.005	0.004	0.002	0.005	0.008	0.001	0.002	0.002	0.001	0.002	0.001
Coefficient of V	4.587	6.273	5.377	4.682	6.429	6.404	3.734	4.455	4.565	4.349	5.260	3.932

[1] Scaled data has been adjusted to correct for body size, where adjusted data is “trait/geometric mean of individual=scaled trait”.

Table S. Unscaled Molar Variation in *Theropithecus gelada*, by trait[1]

	UM1md	*UM2md*	*UM3md*	*UM1bl*	*UM2bl*	*UM3bl*	*LM1md*	*LM2md*	*LM3md*	*LM1bl*	*LM2bl*	*LM3bl*
Theropithecus gelada												
Pooled Sex												
N	51	53	45	50	57	52	50	53	46	50	54	49
Range (mm)	4.23	4.1	3.75	3.74	4.53	4.53	2.77	3.225	3.7	1.64	2.13	2.88
Min (mm)	8.27	10.6	11.25	7.76	10.1	14.1	7.86	9.275	9.18	6.735	8	8.37
Max (mm)	12.5	14.7	15	11.5	14.63	18.63	10.63	12.5	12.88	8.375	10.13	11.25
Mean (mm)	10.422	12.726	13.318	9.925	12.402	16.070	9.086	10.713	11.122	7.703	9.154	9.597
Standard Error	0.119	0.142	0.140	0.125	0.144	0.134	0.076	0.100	0.135	0.054	0.069	0.084
Standard Deviation	0.849	1.034	0.938	0.886	1.088	0.963	0.537	0.730	0.918	0.383	0.510	0.591
Sample Variance	0.721	1.068	0.879	0.785	1.184	0.928	0.288	0.533	0.842	0.147	0.260	0.349
Coefficient of V	8.150	8.121	7.040	8.925	8.773	5.995	5.906	6.815	8.250	4.970	5.570	6.159
Females Only												
N	14	17	12	14	18	16	13	17	12	14	17	12
Range (mm)	2.1	2.22	2.25	2.65	2.83	2.13	1.25	1.33	1.625	1.47	1.205	1.45
Min (mm)	8.27	10.6	11.25	7.76	10.1	14.1	7.86	9.54	9.495	6.735	8.3	8.37
Max (mm)	10.37	12.82	13.5	10.41	12.93	16.23	9.11	10.87	11.12	8.205	9.505	9.82
Mean (mm)	9.636	11.799	12.319	9.001	11.381	15.287	8.609	10.245	10.342	7.359	8.787	9.214
Standard Error	0.153	0.160	0.174	0.204	0.168	0.140	0.106	0.094	0.153	0.094	0.091	0.121
Standard Deviation	0.571	0.658	0.602	0.764	0.713	0.560	0.381	0.388	0.531	0.353	0.373	0.420
Sample Variance	0.326	0.433	0.362	0.583	0.509	0.314	0.145	0.151	0.282	0.125	0.139	0.177
Coefficient of V	5.929	5.580	4.883	8.486	6.267	3.665	4.429	3.791	5.136	4.798	4.248	4.562
Males Only												
N	37	36	33	36	39	36	37	36	34	36	37	37
Range (mm)	3.69	4.06	2.88	2.73	4.31	3.89	2.435	3.225	3.7	1.275	2.13	2.58
Min (mm)	8.81	10.64	12.12	8.77	10.32	14.74	8.195	9.275	9.18	7.1	8	8.67
Max (mm)	12.5	14.7	15	11.5	14.63	18.63	10.63	12.5	12.88	8.375	10.13	11.25
Mean (mm)	10.720	13.164	13.682	10.285	12.873	16.418	9.253	10.934	11.397	7.838	9.322	9.722
Standard Error	0.122	0.147	0.132	0.106	0.143	0.150	0.079	0.125	0.149	0.051	0.079	0.097
Standard Deviation	0.744	0.880	0.758	0.638	0.892	0.902	0.482	0.753	0.869	0.305	0.478	0.589
Sample Variance	0.553	0.774	0.574	0.407	0.796	0.813	0.233	0.566	0.755	0.093	0.228	0.347
Coefficient of V	6.938	6.682	5.537	6.201	6.930	5.493	5.211	6.883	7.622	3.888	5.123	6.058

[1] Molar traits are defined in Appendix 1A.

Table T. Scaled Molar Variation in *Theropithecus gelada*, by trait[1]

	UM1md	*UM2md*	*UM3md*	*UM1bl*	*UM2bl*	*UM3bl*	*LM1md*	*LM2md*	*LM3md*	*LM1bl*	*LM2bl*	*LM3bl*
Theropithecus gelada												
Pooled Sex												
N	51	53	45	50	57	52	50	53	46	50	54	49
Range	0.247	0.362	0.245	0.357	0.350	0.292	0.108	0.184	0.207	0.129	0.173	0.187
Min	0.850	0.981	1.098	0.763	0.950	1.327	0.786	0.880	0.904	0.671	0.761	0.799
Max	1.097	1.343	1.343	1.121	1.300	1.619	0.894	1.064	1.111	0.800	0.933	0.987
Mean	0.967	1.174	1.225	0.923	1.150	1.483	0.844	0.988	1.021	0.718	0.848	0.885
Standard Error	0.008	0.009	0.008	0.009	0.011	0.010	0.004	0.006	0.007	0.004	0.005	0.005
Standard Deviation	0.054	0.068	0.055	0.063	0.080	0.071	0.030	0.045	0.047	0.029	0.036	0.036
Sample Variance	0.003	0.005	0.003	0.004	0.006	0.005	0.001	0.002	0.002	0.001	0.001	0.001
Coefficient of V	5.599	5.821	4.526	6.831	6.997	4.787	3.519	4.576	4.593	4.061	4.285	4.027
Females Only												
N	14	17	12	14	18	16	13	17	12	14	17	12
Range	0.228	0.337	0.206	0.357	0.346	0.241	0.085	0.147	0.110	0.073	0.140	0.112
Min	0.869	0.981	1.098	0.763	0.950	1.327	0.805	0.910	0.951	0.698	0.777	0.848
Max	1.097	1.318	1.304	1.121	1.296	1.568	0.890	1.056	1.061	0.771	0.918	0.960
Mean	0.956	1.146	1.206	0.893	1.113	1.476	0.857	0.994	1.012	0.729	0.860	0.901
Standard Error	0.017	0.021	0.018	0.024	0.024	0.019	0.007	0.011	0.011	0.006	0.012	0.008
Standard Deviation	0.063	0.088	0.061	0.091	0.103	0.077	0.024	0.043	0.037	0.023	0.048	0.026
Sample Variance	0.004	0.008	0.004	0.008	0.011	0.006	0.001	0.002	0.001	0.001	0.002	0.001
Coefficient of V	6.541	7.703	5.068	10.172	9.212	5.224	2.753	4.364	3.658	3.139	5.526	2.919
Males Only												
N	37	36	33	36	39	36	37	36	34	36	37	37
Range	0.225	0.258	0.217	0.199	0.275	0.277	0.108	0.184	0.207	0.129	0.173	0.187
Min	0.850	1.085	1.126	0.846	1.025	1.342	0.786	0.880	0.904	0.671	0.761	0.799
Max	1.075	1.343	1.343	1.045	1.300	1.619	0.894	1.064	1.111	0.800	0.933	0.987
Mean	0.972	1.187	1.232	0.934	1.167	1.486	0.839	0.985	1.025	0.714	0.843	0.880
Standard Error	0.008	0.009	0.009	0.007	0.010	0.011	0.005	0.008	0.009	0.005	0.005	0.006
Standard Deviation	0.051	0.053	0.053	0.045	0.062	0.069	0.030	0.046	0.050	0.030	0.029	0.037
Sample Variance	0.003	0.003	0.003	0.002	0.004	0.005	0.001	0.002	0.002	0.001	0.001	0.001
Coefficient of V	5.239	4.472	4.261	4.808	5.350	4.644	3.634	4.708	4.880	4.265	3.445	4.205

[1] Scaled data has been adjusted to correct for body size, where adjusted data is "trait/geometric mean of individual=scaled trait".

Table U. Unscaled Molar Variation in *Macaca fascicularis*, by trait[1]

	UM1md	*UM2md*	*UM3md*	*UM1bl*	*UM2bl*	*UM3bl*	*LM1md*	*LM2md*	*LM3md*	*LM1bl*	*LM2bl*	*LM3bl*
Macaca fascicularis												
Pooled Sex												
N	61	61	60	60	61	60	61	61	59	59	60	60
Range (mm)	2.2	2.44	3.05	2.49	2.69	4.38	1.615	2.305	2.43	1.685	1.605	1.75
Min (mm)	5.3	5.86	5.32	5.13	5.81	6.12	5.005	5.445	5.07	4.165	4.895	4.56
Max (mm)	7.5	8.3	8.37	7.62	8.5	10.5	6.62	7.75	7.5	5.85	6.5	6.31
Mean (mm)	6.145	7.022	6.710	6.137	7.089	8.369	5.900	6.667	6.282	4.851	5.669	5.472
Standard Error	0.061	0.071	0.076	0.059	0.067	0.113	0.051	0.063	0.077	0.048	0.051	0.059
Standard Deviation	0.478	0.558	0.591	0.457	0.524	0.877	0.396	0.492	0.588	0.372	0.391	0.456
Sample Variance	0.228	0.311	0.349	0.209	0.275	0.769	0.157	0.242	0.346	0.138	0.153	0.208
Coefficient of V	7.773	7.945	8.807	7.453	7.397	10.477	6.709	7.382	9.367	7.664	6.904	8.338
Females Only												
N	29	29	28	28	29	28	29	29	27	27	28	28
Range (mm)	1.9	2.44	2.18	1.57	1.99	3.13	1.495	2.055	2.18	1.685	1.605	1.435
Min (mm)	5.3	5.86	5.32	5.13	5.81	6.12	5.005	5.445	5.07	4.165	4.895	4.56
Max (mm)	7.2	8.3	7.5	6.7	7.8	9.25	6.5	7.5	7.25	5.85	6.5	5.995
Mean (mm)	5.988	6.808	6.400	5.909	6.813	7.868	5.751	6.433	5.967	4.684	5.463	5.193
Standard Error	0.086	0.100	0.095	0.067	0.088	0.161	0.076	0.093	0.111	0.069	0.068	0.076
Standard Deviation	0.463	0.541	0.504	0.353	0.473	0.850	0.408	0.503	0.575	0.360	0.359	0.404
Sample Variance	0.214	0.293	0.254	0.125	0.223	0.722	0.167	0.253	0.330	0.130	0.129	0.164
Coefficient of V	7.729	7.946	7.868	5.980	6.938	10.799	7.098	7.826	9.634	7.686	6.576	7.787
Males Only												
N	32	32	32	32	32	32	32	32	32	32	32	32
Range (mm)	2.11	1.9	2.22	2.47	1.87	2.73	1.335	1.765	1.96	1.465	1.255	1.42
Min (mm)	5.39	6.35	6.15	5.15	6.63	7.77	5.285	5.985	5.54	4.22	5.115	4.89
Max (mm)	7.5	8.25	8.37	7.62	8.5	10.5	6.62	7.75	7.5	5.685	6.37	6.31
Mean (mm)	6.288	7.216	6.982	6.337	7.339	8.807	6.035	6.880	6.547	4.993	5.849	5.716
Standard Error	0.080	0.090	0.094	0.079	0.078	0.113	0.059	0.067	0.081	0.057	0.058	0.062
Standard Deviation	0.452	0.507	0.530	0.449	0.441	0.640	0.336	0.377	0.460	0.324	0.327	0.349
Sample Variance	0.204	0.257	0.281	0.201	0.194	0.409	0.113	0.142	0.212	0.105	0.107	0.122
Coefficient of V	7.186	7.019	7.588	7.082	6.007	7.263	5.572	5.482	7.029	6.490	5.592	6.113

[1] Molar traits are defined in Appendix 1A.

Table V. Scaled Molar Variation in *Macaca fascicularis*, by trait[1]

	UM1md	*UM2md*	*UM3md*	*UM1bl*	*UM2bl*	*UM3bl*	*LM1md*	*LM2md*	*LM3md*	*LM1bl*	*LM2bl*	*LM3bl*
Macaca fascicularis												
Pooled Sex												
N	61	61	60	60	61	60	61	61	59	59	60	60
Range	0.162	0.170	0.290	0.157	0.195	0.474	0.158	0.162	0.240	0.140	0.109	0.181
Min	0.893	1.021	0.929	0.887	1.013	1.076	0.855	0.954	0.846	0.699	0.837	0.785
Max	1.055	1.191	1.220	1.044	1.208	1.551	1.013	1.116	1.086	0.840	0.946	0.967
Mean	0.975	1.114	1.066	0.973	1.125	1.329	0.937	1.058	0.996	0.769	0.899	0.870
Standard Error	0.005	0.005	0.006	0.005	0.005	0.011	0.004	0.004	0.006	0.003	0.004	0.005
Standard Deviation	0.035	0.039	0.049	0.035	0.038	0.083	0.032	0.032	0.044	0.026	0.029	0.037
Sample Variance	0.001	0.002	0.002	0.001	0.001	0.007	0.001	0.001	0.002	0.001	0.001	0.001
Coefficient of V	3.630	3.526	4.621	3.583	3.378	6.246	3.390	3.011	4.410	3.329	3.247	4.272
Females Only												
N	29	29	28	28	29	28	29	29	27	27	28	28
Range	0.139	0.124	0.229	0.137	0.195	0.353	0.113	0.162	0.235	0.096	0.106	0.181
Min	0.916	1.067	0.929	0.907	1.013	1.076	0.899	0.954	0.846	0.744	0.837	0.785
Max	1.055	1.191	1.158	1.044	1.208	1.429	1.013	1.116	1.081	0.840	0.943	0.967
Mean	0.987	1.122	1.061	0.974	1.124	1.302	0.948	1.061	0.986	0.771	0.900	0.861
Standard Error	0.006	0.006	0.009	0.007	0.008	0.018	0.005	0.007	0.009	0.004	0.005	0.008
Standard Deviation	0.033	0.031	0.049	0.038	0.044	0.093	0.030	0.038	0.049	0.023	0.027	0.040
Sample Variance	0.001	0.001	0.002	0.001	0.002	0.009	0.001	0.001	0.002	0.001	0.001	0.002
Coefficient of V	3.390	2.754	4.644	3.864	3.901	7.165	3.121	3.540	4.919	2.931	3.005	4.662
Males Only												
N	32	32	32	32	32	32	32	32	32	32	32	32
Range	0.132	0.166	0.262	0.136	0.133	0.315	0.133	0.102	0.160	0.119	0.101	0.125
Min	0.893	1.021	0.957	0.887	1.056	1.236	0.855	0.999	0.926	0.699	0.845	0.811
Max	1.025	1.187	1.220	1.023	1.189	1.551	0.987	1.101	1.086	0.818	0.946	0.936
Mean	0.965	1.108	1.071	0.972	1.127	1.352	0.927	1.056	1.005	0.766	0.898	0.878
Standard Error	0.006	0.008	0.009	0.006	0.006	0.012	0.005	0.005	0.007	0.005	0.006	0.006
Standard Deviation	0.034	0.045	0.050	0.033	0.033	0.066	0.031	0.026	0.038	0.028	0.031	0.033
Sample Variance	0.001	0.002	0.002	0.001	0.001	0.004	0.001	0.001	0.001	0.001	0.001	0.001
Coefficient of V	3.545	4.060	4.623	3.378	2.885	4.866	3.297	2.474	3.824	3.657	3.492	3.758

[1] Scaled data has been adjusted to correct for body size, where adjusted data is "trait/geometric mean of individual=scaled trait".

Table W. Unscaled Molar Variation in *Macaca nemestrina*, by trait[1]

	UM1md	*UM2md*	*UM3md*	*UM1bl*	*UM2bl*	*UM3bl*	*LM1md*	*LM2md*	*LM3md*	*LM1bl*	*LM2bl*	*LM3bl*
Macaca nemestrina												
Pooled Sex												
N	49	49	49	49	49	49	49	49	49	49	49	49
Range (mm)	2.07	2.07	3.59	1.75	1.97	4.62	2.19	2.985	3.515	1.8	1.725	2.545
Min (mm)	6.43	7.55	6.91	6.87	7.65	8.5	6.06	6.635	5.985	5.26	6.145	5.825
Max (mm)	8.5	9.62	10.5	8.62	9.62	13.12	8.25	9.62	9.5	7.06	7.87	8.37
Mean (mm)	7.580	8.723	8.824	7.563	8.606	11.038	7.341	8.474	8.457	6.031	7.162	7.381
Standard Error	0.066	0.065	0.107	0.060	0.066	0.141	0.066	0.078	0.103	0.059	0.061	0.089
Standard Deviation	0.461	0.458	0.752	0.419	0.463	0.985	0.463	0.545	0.721	0.411	0.429	0.621
Sample Variance	0.212	0.210	0.565	0.176	0.214	0.971	0.214	0.297	0.520	0.169	0.184	0.386
Coefficient of V	6.082	5.255	8.519	5.544	5.376	8.928	6.302	6.430	8.527	6.812	5.992	8.418
Females Only												
N	23	23	23	23	23	23	23	23	23	23	23	23
Range (mm)	1.82	1.95	3.21	0.87	1.47	4.62	2.19	2.485	3.515	1.675	1.475	2.425
Min (mm)	6.43	7.55	6.91	7	7.65	8.5	6.06	6.635	5.985	5.26	6.145	5.825
Max (mm)	8.25	9.5	10.12	7.87	9.12	13.12	8.25	9.12	9.5	6.935	7.62	8.25
Mean (mm)	7.413	8.539	8.465	7.400	8.385	10.530	7.217	8.295	8.180	5.887	6.954	7.123
Standard Error	0.094	0.100	0.144	0.063	0.091	0.196	0.114	0.128	0.173	0.083	0.095	0.131
Standard Deviation	0.449	0.480	0.690	0.300	0.434	0.938	0.545	0.614	0.830	0.396	0.457	0.629
Sample Variance	0.201	0.231	0.476	0.090	0.188	0.881	0.298	0.378	0.688	0.157	0.209	0.396
Coefficient of V	6.051	5.624	8.154	4.053	5.177	8.912	7.558	7.408	10.144	6.725	6.571	8.831
Males Only												
N	26	26	26	26	26	26	26	26	26	26	26	26
Range (mm)	1.63	1.25	2.75	1.75	1.37	3.37	1.27	1.87	1.88	1.565	1.06	2.06
Min (mm)	6.87	8.37	7.75	6.87	8.25	9.75	6.85	7.75	7.62	5.495	6.81	6.31
Max (mm)	8.5	9.62	10.5	8.62	9.62	13.12	8.12	9.62	9.5	7.06	7.87	8.37
Mean (mm)	7.727	8.886	9.142	7.707	8.802	11.488	7.451	8.633	8.703	6.157	7.345	7.608
Standard Error	0.084	0.074	0.130	0.090	0.079	0.157	0.069	0.084	0.100	0.076	0.061	0.103
Standard Deviation	0.428	0.377	0.665	0.461	0.401	0.801	0.350	0.427	0.509	0.388	0.309	0.527
Sample Variance	0.183	0.142	0.442	0.212	0.160	0.642	0.122	0.182	0.259	0.150	0.095	0.278
Coefficient of V	5.533	4.238	7.274	5.981	4.551	6.973	4.697	4.941	5.847	6.300	4.203	6.932

[1] Molar traits are defined in Appendix 1A.

Table X. Scaled Molar Variation in *Macaca nemestrina*, by trait[1]

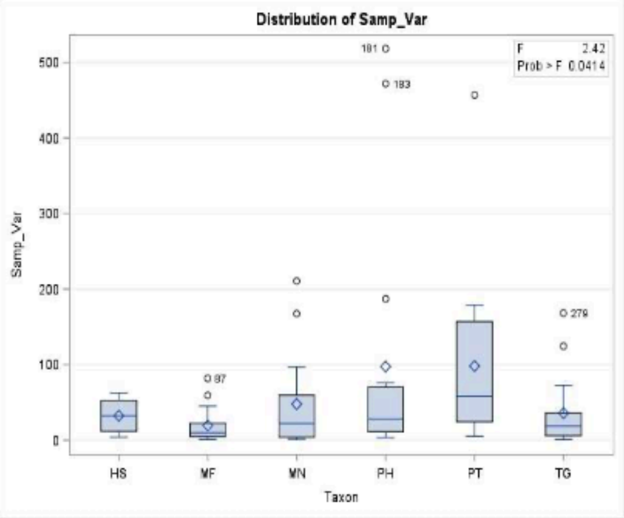
	UM1md	*UM2md*	*UM3md*	*UM1bl*	*UM2bl*	*UM3bl*	*LM1md*	*LM2md*	*LM3md*	*LM1bl*	*LM2bl*	*LM3bl*
Macaca nemestrina												
Pooled Sex												
N	49	49	49	49	49	49	49	49	49	49	49	49
Range	0.134	0.144	0.265	0.180	0.170	0.393	0.138	0.209	0.273	0.164	0.126	0.149
Min	0.869	1.029	1.015	0.872	1.003	1.123	0.835	0.969	0.875	0.678	0.821	0.846
Max	1.003	1.173	1.280	1.052	1.173	1.516	0.974	1.179	1.148	0.842	0.947	0.995
Mean	0.947	1.090	1.101	0.945	1.075	1.377	0.917	1.058	1.055	0.753	0.894	0.921
Standard Error	0.004	0.005	0.007	0.005	0.005	0.010	0.005	0.006	0.007	0.005	0.004	0.005
Standard Deviation	0.029	0.032	0.046	0.035	0.035	0.072	0.035	0.041	0.048	0.032	0.026	0.038
Sample Variance	0.001	0.001	0.002	0.001	0.001	0.005	0.001	0.002	0.002	0.001	0.001	0.001
Coefficient of V	3.029	2.960	4.186	3.661	3.247	5.210	3.763	3.867	4.507	4.312	2.945	4.104
Females Only												
N	23	23	23	23	23	23	23	23	23	23	23	23
Range	0.068	0.126	0.145	0.177	0.170	0.382	0.108	0.148	0.255	0.164	0.122	0.141
Min	0.917	1.047	1.015	0.875	1.003	1.123	0.865	0.975	0.875	0.678	0.821	0.854
Max	0.984	1.173	1.161	1.052	1.173	1.505	0.974	1.123	1.130	0.842	0.943	0.995
Mean	0.952	1.098	1.086	0.952	1.078	1.352	0.927	1.065	1.049	0.757	0.894	0.914
Standard Error	0.004	0.007	0.007	0.008	0.008	0.017	0.007	0.008	0.012	0.008	0.006	0.008
Standard Deviation	0.020	0.032	0.035	0.039	0.037	0.081	0.033	0.037	0.057	0.039	0.028	0.039
Sample Variance	0.000	0.001	0.001	0.002	0.001	0.007	0.001	0.001	0.003	0.001	0.001	0.002
Coefficient of V	2.069	2.884	3.188	4.145	3.427	5.978	3.543	3.496	5.457	5.112	3.089	4.291
Males Only												
N	26	26	26	26	26	26	26	26	26	26	26	26
Range	0.134	0.126	0.241	0.113	0.131	0.239	0.137	0.209	0.162	0.102	0.095	0.148
Min	0.869	1.029	1.039	0.872	1.011	1.277	0.835	0.969	0.986	0.706	0.852	0.846
Max	1.003	1.156	1.280	0.986	1.142	1.516	0.972	1.179	1.148	0.808	0.947	0.994
Mean	0.941	1.083	1.113	0.939	1.073	1.399	0.908	1.052	1.060	0.750	0.895	0.926
Standard Error	0.007	0.006	0.010	0.006	0.007	0.011	0.007	0.009	0.007	0.005	0.005	0.007
Standard Deviation	0.034	0.032	0.052	0.029	0.034	0.056	0.034	0.044	0.037	0.026	0.026	0.036
Sample Variance	0.001	0.001	0.003	0.001	0.001	0.003	0.001	0.002	0.001	0.001	0.001	0.001
Coefficient of V	3.645	2.938	4.643	3.078	3.125	3.972	3.768	4.160	3.518	3.485	2.870	3.912

[1] Scaled data has been adjusted to correct for body size, where adjusted data is “trait/geometric mean of individual=scaled trait”.

APPENDIX C

CRANIODENTAL ANALYSES OF VARIANCE

Cranial: Sample Variance, Unadjusted data, Pooled Sex

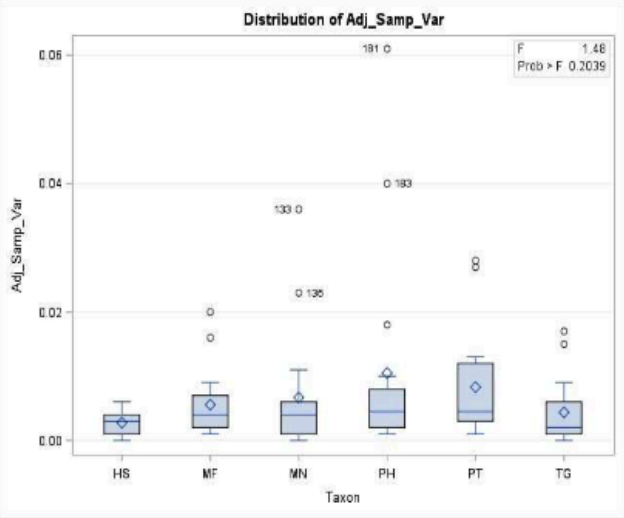


Generalized Linear Model (*a* = 0.05); *left*

Bonferroni Correction, *below*
(*a* = 0.05; Critical Value of t = 3.01557)

SVPC	**Minimum Significant Difference**	**93.684**	
Bon Grouping	**Mean**	**N**	**Taxon**
A	98.09	16	PT
A	97.52	16	PH
A	47.89	16	MN
A	35.91	16	TG
A	32.41	16	HS
A	19.54	16	MF

Cranial: Sample Variance, Adjusted data, Pooled sex

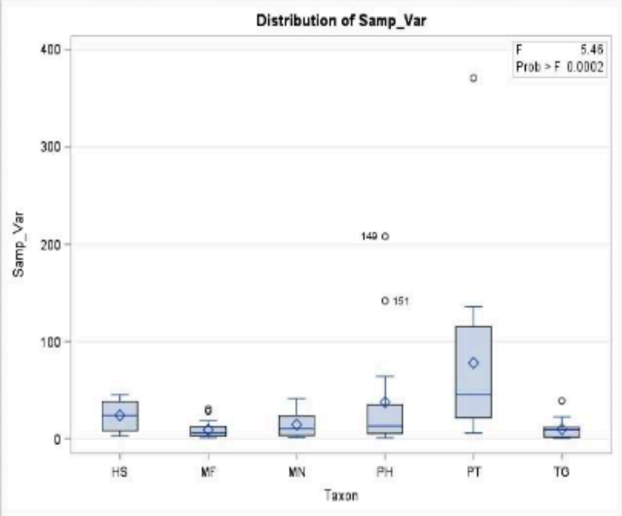


Generalized Linear Model (*a* = 0.05); *left*

Bonferroni Correction, *below*
(*a* = 0.05; Critical Value of t = 3.01557)

SVAPC	**Minimum Significant Difference**	***0.0097***	
Bon Grouping	**Mean**	**N**	**Taxon**
A	0.0105	16	PH
A	0.008313	16	PT
A	0.006688	16	MN
A	0.005563	16	MF
A	0.004375	16	TG
A	0.00275	16	HS

Cranial: Sample Variance, Unadjusted data, Females only

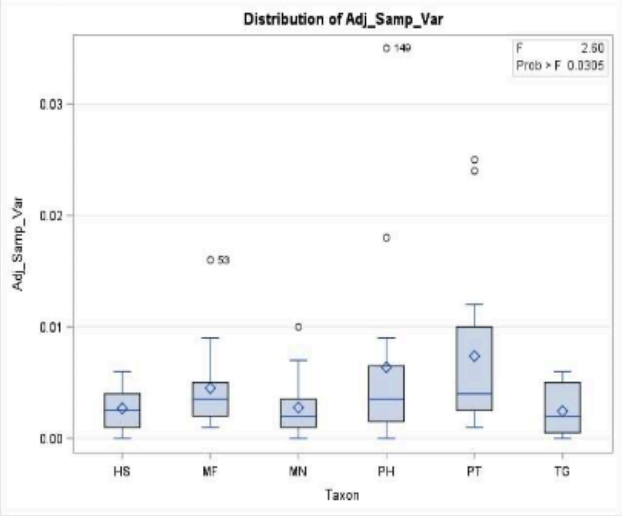


Generalized Linear Model (*a* = 0.05); *left*

Bonferroni Correction, *below*
(*a* = 0.05; Critical Value of t = 3.01557)

SVFC	**Minimum Significant Difference**	***47.998***		
Bon Grouping		**Mean**	**N**	**Taxon**
	A	78.07	16	PT
B	A	37.85	16	PH
B		24.2	16	HS
B		14.78	16	MN
B		9.95	16	TG
B		9.47	16	MF

Cranial: Sample Variance, Adjusted data, Females only

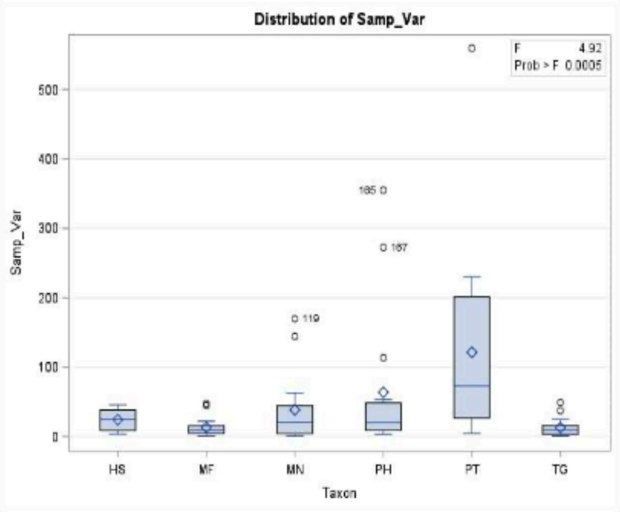


Generalized Linear Model (*a* = 0.05); *left*

Bonferroni Correction, *below*
(*a* = 0.05; Critical Value of t = 3.01557)

SVAFC	**Minimum Significant Difference**	***0.0056***	
Bon Grouping	**Mean**	**N**	**Taxon**
A	0.007375	16	PT
A	0.006375	16	PH
A	0.0045	16	MF
A	0.00275	16	MN
A	0.002688	16	HS
A	0.002438	16	TG

Cranial: Sample Variance, Unadjusted data, Males only

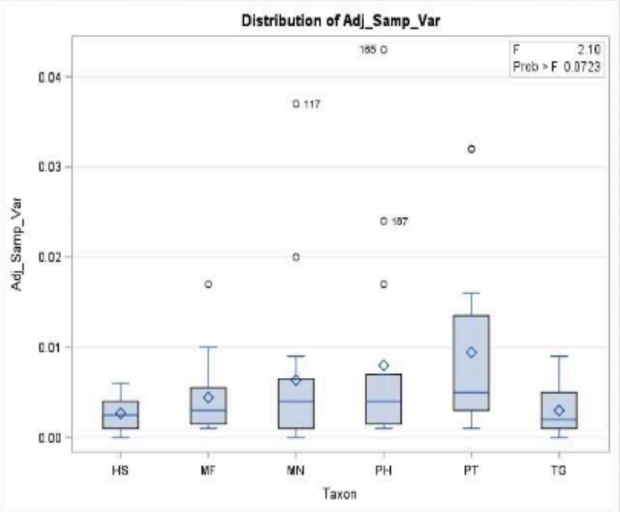


Generalized Linear Model (*a* = 0.05); *left*

Bonferroni Correction, *below*
(*a* = 0.05; Critical Value of t = 3.01557)

SVMC	**Minimum Significant Difference**	***80.109***		
Bon Grouping		**Mean**	**N**	**Taxon**
	A	121.32	16	PT
B	A	63.66	16	PH
B		38.43	16	MN
B		24.2	16	HS
B		13.15	16	MF
B		12.93	16	TG

Cranial: Sample Variance, Adjusted data, Males only

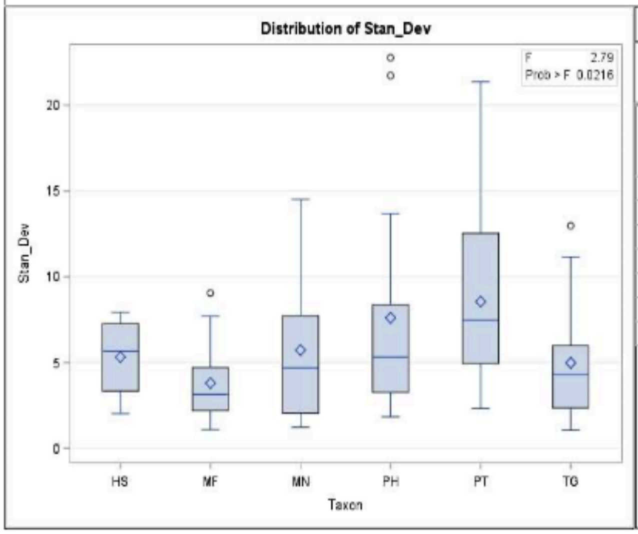


Generalized Linear Model (*a* = 0.05); *left*

Bonferroni Correction, *below*
(*a* = 0.05; Critical Value of t = 3.01557)

SVAMC	**Minimum Significant Difference**	**0.0081**	
Bon Grouping	**Mean**	**N**	**Taxon**
A	0.009438	16	PT
A	0.008	16	PH
A	0.006375	16	MN
A	0.004438	16	MF
A	0.003	16	TG
A	0.002688	16	HS

Cranial: Standard Deviation, Unadjusted data, Pooled sex

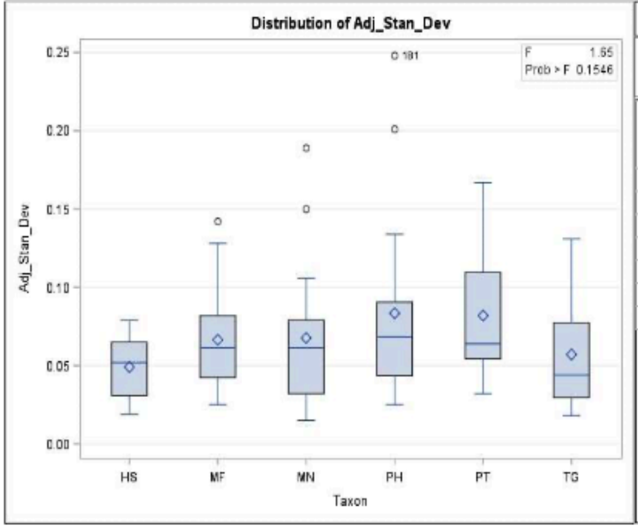


Generalized Linear Model (*a* = 0.05); *left*

Bonferroni Correction, *below*
(*a* = 0.05; Critical Value of t = 3.01557)

SDPC	**Minimum Significant Difference**	***4.4975***		
Bon Grouping		**Mean**	**N**	**Taxon**
	A	8.553	16	PT
B	A	7.607	16	PH
B	A	5.725	16	MN
B	A	5.315	16	HS
B	A	4.979	16	TG
B		3.798	16	MF

Cranial: Standard Deviation, Adjusted data, Pooled sex

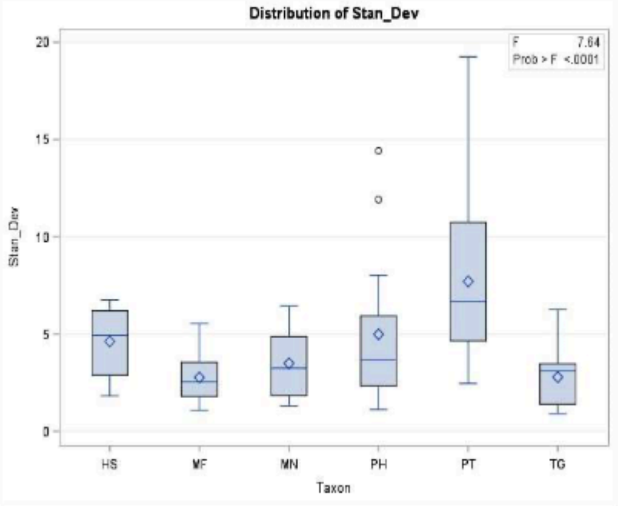


Generalized Linear Model (*a* = 0.05); *left*

Bonferroni Correction, *below*
(*a* = 0.05; Critical Value of t = 3.01557)

SDAPC	**Minimum Significant Difference**	***0.0448***	
Bon Grouping	**Mean**	**N**	**Taxon**
A	0.08344	16	PH
A	0.082	16	PT
A	0.06769	16	MN
A	0.0665	16	MF
A	0.05713	16	TG
A	0.04913	16	HS

Cranial: Standard Deviation, Unadjusted data, Females only

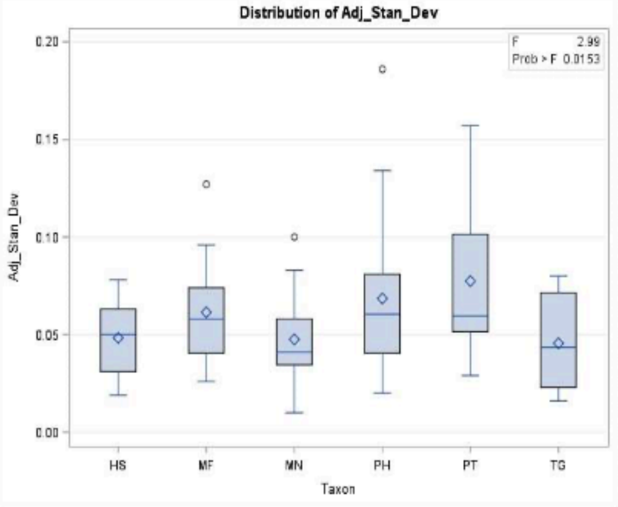


Generalized Linear Model ($a = 0.05$); *left*

Bonferroni Correction, *below*
($a = 0.05$; Critical Value of t = 3.01557)

SDFC		**Minimum Significant Difference**	***2.8829***	
Bon Grouping		**Mean**	**N**	**Taxon**
	A	7.7066	16	PT
B	A	4.9895	16	PH
B		4.6196	16	HS
B		3.4893	16	MN
B		2.7839	16	TG
B		2.7636	16	MF

Cranial: Standard Deviation, Adjusted data, Females only

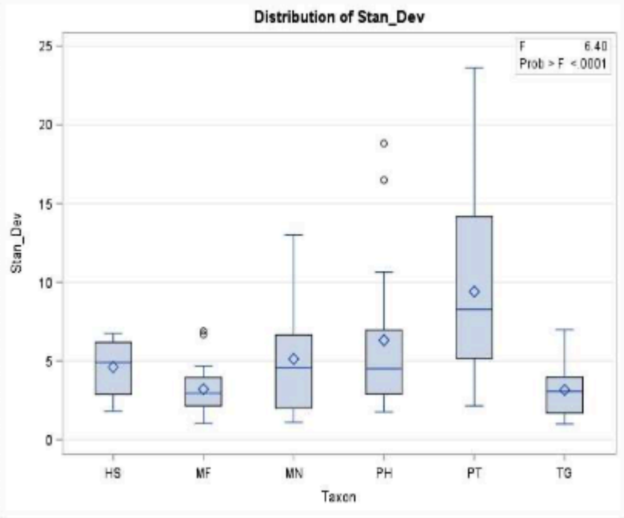


Generalized Linear Model ($a = 0.05$); *left*

Bonferroni Correction, *below*
($a = 0.05$; Critical Value of t = 3.01557)

SDAFC	**Minimum Significant Difference**	***0.0323***	
Bon Grouping	**Mean**	**N**	**Taxon**
A	0.07744	16	PT
A	0.0685	16	PH
A	0.06144	16	MF
A	0.04831	16	HS
A	0.04756	16	MN
A	0.04556	16	TG

Cranial: Standard Deviation, Unadjusted data, Males only

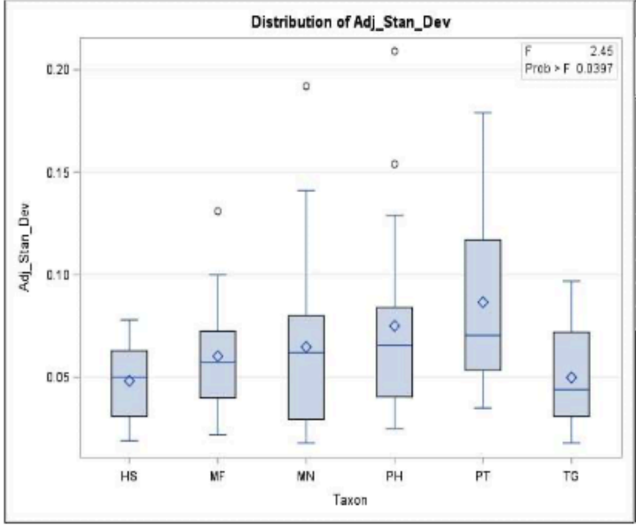


Generalized Linear Model (*a* = 0.05); *left*

Bonferroni Correction, *below*
(*a* = 0.05; Critical Value of t = 3.01557)

SDMC	**Minimum Significant Difference**	***3.9461***		
Bon Grouping		**Mean**	**N**	**Taxon**
	A	9.415	16	PT
B	A	6.326	16	PH
B		5.133	16	MN
B		4.62	16	HS
B		3.21	16	MF
B		3.163	16	TG

Cranial: Standard Deviation, Adjusted data, Males only

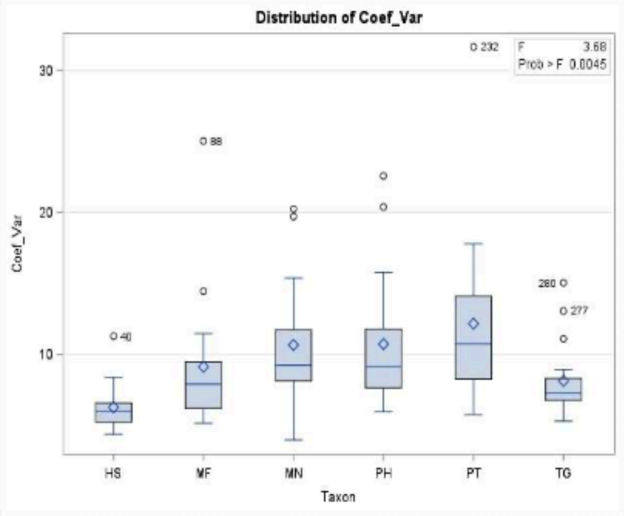


Generalized Linear Model (*a* = 0.05); *left*

Bonferroni Correction, *below*
(*a* = 0.05; Critical Value of t = 3.01557)

SDAMC	**Minimum Significant Difference**	***0.0403***	
Bon Grouping	**Mean**	**N**	**Taxon**
A	0.08663	16	PT
A	0.07506	16	PH
A	0.06481	16	MN
A	0.06031	16	MF
A	0.04988	16	TG
A	0.04831	16	HS

Cranial: Coefficient of Variance, Unadjusted data, Pooled sex

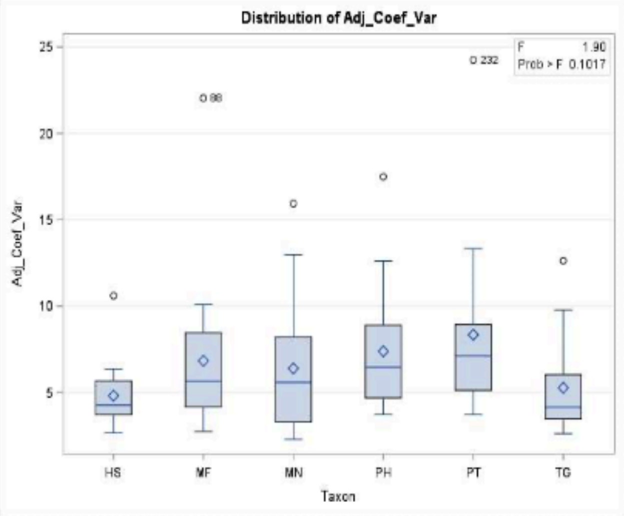


Generalized Linear Model (*a* = 0.05); *left*

Bonferroni Correction, *below*
(*a* = 0.05; Critical Value of t = 3.01557)

CVPC	**Minimum Significant Difference**	***4.7057***		
Bon Grouping		**Mean**	**N**	**Taxon**
	A	12.159	16	PT
B	A	10.723	16	PH
B	A	10.657	16	MN
B	A	9.122	16	MF
B	A	8.125	16	TG
B		6.267	16	HS

Cranial: Coefficient of Variance, Adjusted data, Pooled sex

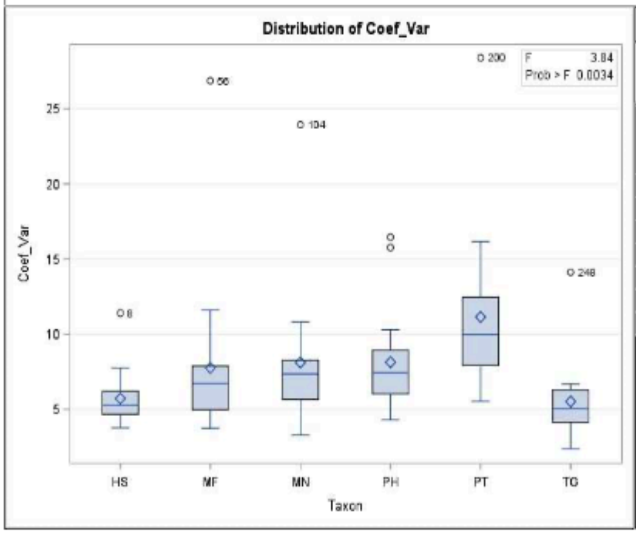


Generalized Linear Model (*a* = 0.05); *left*

Bonferroni Correction, *below*
(*a* = 0.05; Critical Value of t = 3.01557)

CVAPC	**Minimum Significant Difference**	***4.0683***	
Bon Grouping	**Mean**	**N**	**Taxon**
A	8.34	16	PT
A	7.384	16	PH
A	6.832	16	MF
A	6.391	16	MN
A	5.273	16	TG
A	4.809	16	HS

Cranial: Coefficient of Variance, Unadjusted data, Females only

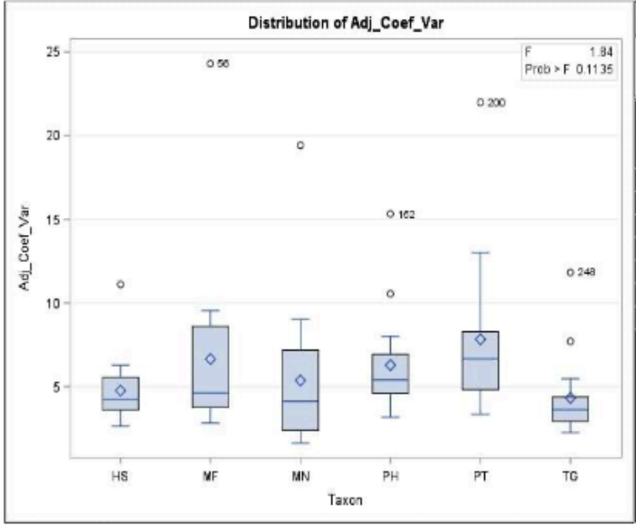


Generalized Linear Model (*a* = 0.05); *left*

Bonferroni Correction, *below*
(*a* = 0.05; Critical Value of t = 3.01557)

CVFC	**Minimum Significant Difference**	***4.4511***		
Bon Grouping		**Mean**	**N**	**Taxon**
	A	11.143	16	PT
B	A	8.135	16	PH
B	A	8.108	16	MN
B	A	7.76	16	MF
B		5.716	16	HS
B		5.518	16	TG

Cranial: Coefficient of Variance, Adjusted data, Females only

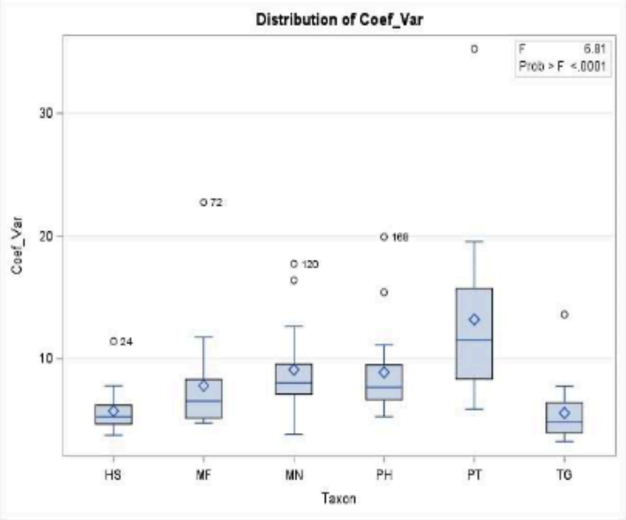


Generalized Linear Model (*a* = 0.05); *left*

Bonferroni Correction, *below*
(*a* = 0.05; Critical Value of t = 3.01557)

CVAFC	**Minimum Significant Difference**	***4.0957***	
Bon Grouping	**Mean**	**N**	**Taxon**
A	7.827	16	PT
A	6.645	16	MF
A	6.292	16	PH
A	5.37	16	MN
A	4.761	16	HS
A	4.325	16	TG

Cranial: Coefficient of Variance, Unadjusted data, Males only

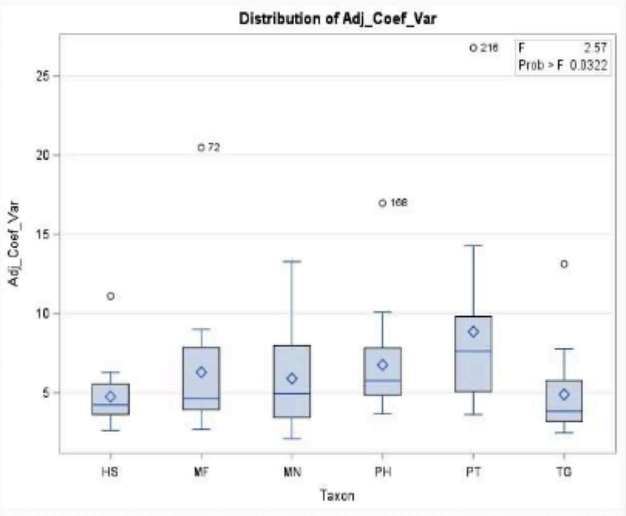


Generalized Linear Model (*a* = 0.05); *left*

Bonferroni Correction, *below*
(*a* = 0.05; Critical Value of t = 3.01557)

CVMC	**Minimum Significant Difference**	***4.5788***		
Bon Grouping		**Mean**	**N**	**Taxon**
	A	13.181	16	PT
B	A	9.094	16	MN
B	A	8.876	16	PH
B		7.788	16	MF
B		5.716	16	HS
B		5.553	16	TG

Cranial: Coefficient of Variance, Adjusted data, Males only



Generalized Linear Model (*a* = 0.05); *left*

Bonferroni Correction, *below*
(*a* = 0.05; Critical Value of t = 3.01557)

CVAMC	**Minimum Significant Difference**	***3.9899***		
Bon Grouping		**Mean**	**N**	**Taxon**
	A	8.855	16	PT
B	A	6.763	16	PH
B	A	6.295	16	MF
B	A	5.897	16	MN
B	A	4.893	16	TG
B		4.761	16	HS

APPENDIX D

POSTCRANIAL SKELETAL MEASUREMENT PROTOCOL

The focus of this protocol is on homologous anatomical landmarks between adult catarrhine taxa, and on equivalent measures throughout the epiphyseal fusion of the sample. Equivalent measures are provided, especially where data was collected from other sources; complete references for equivalent measurements are located at end of measurement list and numbered in brackets throughout. All measures were collected using sliding calipers or osteometric boards; all measures taken on the left if possible.

Humerus

1. **hLEN1.** *Humeral Length 1*. Linear distance from greater tuberosity to capitulum, in anterior view. This measure is typically the longest humeral measure in old world monkeys; in hominoids it is usually **hLEN2** (42). Measured using external jaws of sliding calipers; may require osteometric board if sufficiently large. Equivalent to the variables HLGTCP (PRIMO [1]) and HLGT (Frost [2]).
2. **hLEN2.** *Humeral Length 2*. Linear distance from humeral head to capitulum, in anterior view. This measure tends to be the longest humeral length in hominoids, but in old world monkeys it is usually **hLEN1** (41). Measured using external jaws of sliding calipers; may require osteometric board if sufficiently large. Equivalent to the variables HLHDCP [1] and HLHD [2].

3. **hLEN3**. *Humeral Length 3*. Maximum linear distance, proximal limit of humerus to distal limit, in anterior view. This measure gives the longest possible proximodistal measure of the humerus. Measured using external jaws of sliding calipers; may require osteometric board if sufficiently large. Equivalent to the variable HumMaxLng (Terry [3]).

4. **hPML.** *Humeral Proximal End Mediolateral Breadth*. Mediolateral linear distance of the proximal end in superior view, including the tuberosities, with the deltoid insertion as the lateralmost landmark. Measured using external jaws of sliding calipers. Equivalent to the variables HHDWTR [1], HHWTR [2], and HumProxEpiBr [3].

5. **hPAP**. *Humeral Proximal End Anteroposterior Breadth*. Anteroposterior linear distance of the proximal end, including tuberosities, with the bicipital groove as the anteriormost landmark, in superior view. Measured using external jaws of sliding calipers. Equivalent to the variables HHDWAP [1], HHWAP [2], and HPAP (Guthrie [4]).

6. **hHEAP**. *Humeral Head Anteroposterior Breadth*. Anteroposterior linear distance of the articular surface of the head, in medial view. Measured using external jaws of sliding calipers. Equivalent to the variables HHDWAP (head only ap) [1] and HHWAP (head only) [2].

7. **hHEML**. *Humeral Head Mediolateral Breadth*. Mediolateral linear distance of the articular surface of the head, in medial view. Measured using external jaws of sliding calipers. Equivalent to the variables HHDWTR (head only tr) [1], HHWTR (head only) [2], and HumMxVertHeadDia [3].

8. **hLEN4.** *Humeral Length 4*. Length from proximal limit of the brachioradialis flange to capitulum, in anterior view. Measured using external jaws of sliding calipers. Equivalent to the variables HBRFLC [1] and HBRCP [2].
9. **hDML.** *Humeral Distal End Mediolateral Breadth*. Mediolateral linear distance from medial epicondyle to lateral epicondyle, in anterior view. Measured using external jaws of sliding calipers. Equivalent to the variables HDTRWX [1], HDWTR [2], HumDistEpiBr [3], and HDML [4].
10. **hDASML.** *Humeral Distal Articular Surface Breadth*. Linear distance from medial limit of trochlea to lateral limit of capitulum, in anterior view. Measured using external jaws of sliding calipers. Equivalent to the variables HDTRWA [1], HDWA [2], and HDTA [4].
11. **hDHA**. *Humeral Harrison's Breadth*. Lateral epicondyle to medial limit of trochlea, in anterior view. Measured using external jaws of sliding calipers. Equivalent to the variables HDTRWH [1] and HDWH [2].
12. **hTRPD**. *Humeral Trochlear Flange Length*. Proximodistal length of the trochlear flange, anterior view. Measured using external jaws of sliding calipers. Equivalent to the variables HDLENT [1] and HDTL [2].
13. **hTRML**. *Humeral Trochlear Mediolateral Breadth*. Mediolateral linear distance of trochlea, in posterior view; from the medial aspect of the articular surface of the trochlea, measure transversely to the point where the three lines of the trochlea, capitulum, and humeral shaft meet on the lateral aspect of the trochlea. Measured using internal jaws of sliding calipers. Equivalent to the variables HDTRWT [1] and HDTTR [2].

14. **hDAP**. *Humeral Distal End Anteroposterior Breadth*. Anteroposterior linear distance of the distal end, in inferior view. Measured using external jaws of sliding calipers. Equivalent to the variables HDAPWX [1] and HDAP [2].

Radius

15. **rLEN1.** *Radial Length 1*. Length from proximal articular surface of head to distal articular surface, in anterior view. External caliper jaw across head, aiming the point of the other jaw to the middle of the distal articular surface, with the bone flat on a tabletop and parallel to the caliper beam. Or, this measure can be taken with an osteometric board with the styloid oriented off the edge of the measuring plane. Equivalent to the variable LENFUN [1].
16. **rLEN2**. *Radial Length 2*. Maximum linear distance of the total radius; proximal articular surface of head to styloid, in anterior view. External caliper jaw across head, aiming the point of the other jaw to the tip of the styloid process, with the bone flat on a tabletop and parallel to the caliper beam. Or, this measure can be taken with an osteometric board. Equivalent to the variables LENSTYL [1], LENGTH [2], and RadMxLng [3].
17. **rPAP.** *Radial Head Anteroposterior Breadth*. Maximum anteroposterior diameter, in superior view. Measured using external jaws of sliding calipers. Equivalent to the variables HDIAM [1], MAXDIAM [2], RadMxHeadDia [3], and RHAP [4].
18. **rPML.** *Radial Head Mediolateral Breadth*. Maximum mediolateral diameter, in superior view. Measured using external jaws of sliding calipers. Equivalent to the variables HPERP [1], PERP [2], and RHML [4].

19. **rNE1.** *Radial Neck Length 1*. The proximodistal linear distance of the radial neck in medial view; from the distal limit of head to the proximal limit of tuberosity. Measured using internal jaws of sliding calipers. Equivalent to the variable NECK [1].

20. **rNE2**. *Radial Neck Length 2*. The distal limit of the head to the mid-radial tuberosity in medial view. Measured using internal jaws of sliding calipers

21. **rNE3**. *Radial Neck Length 3*. Distance from mid-radial tuberosity to proximal limit of the head, in medial view. Measured using external jaws of sliding calipers. Equivalent to the variables NECKLEV [1] and TUBER [2].

22. **rTUB**. *Radial Tuberosity Length*. This measure is proximodistal linear distance of radial tuberosity, in medial view; gives a functional assessment of the biceps brachii insertion point. Measured using internal jaws of sliding calipers.

23. **rDML**. *Radial Distal End Mediolateral Breadth*. Mediolateral linear distance of the distal end, in inferior view; from the flat radial notch to other side. Measured using external jaws of sliding calipers. Equivalent to the variables DTR [1], DISTML [2], and RDML [3].

24. **rDAP**. *Radial Distal End Anteroposterior Breadth*. This measure is the anteroposterior linear distance of the distal end, in inferior view. Measured using external jaws of sliding calipers. Equivalent to the variables DAP [1], DISTAP [2], and RDAP [3].

Femur

25. **fLEN1**. *Femur Length 1*. Linear distance from distal end across condyles to greater trochanter, in anterior view. Measured using external jaws of calipers, or with osteometric board flat across distal end. Equivalent to the variables LENGTR [1] and FemTrocLng [3].

26. **fLEN2**. *Femur Length 2*. Linear distance from distal end across condyles to the femoral head, in anterior view. Measured using external jaws of calipers, or with osteometric board flat across distal end. Equivalent to the variables LENHD [1] and FemMxLng [3].

27. **fPML.** *Femoral Proximal End Mediolateral Breadth*. Mediolateral linear distance of the proximal end, in anterior view. Measured using external jaws. Equivalent to the variable MAXML [1].

28. **fMLLESS.** *Lesser Trochanter Mediolateral Breadth*. Mediolateral breadth at lesser trochanter, in anterior view. This is more precisely measuring mediolateral midshaft breadth at the lesser trochanter, not necessarily the depth the lesser trochanter imparts to the diaphysis; the latter varies by taxon and individual enthesial robusticity. Among cercopithecines, the lesser trochanter tends to extend laterally; in hominoids, it tends to extend posteriorly. Measure can include lesser trochanter, but the external jaws of sliding calipers should be flat across the medial and lateral portions of the diaphysis as possible.

29. **fGT.** *Proximal Projection of Greater Trochanter*. Projection of greater trochanter above the femoral neck, in anterior view. This measure varies substantially by taxa and is reflective of rotational ability around the hip. Best measured using the sliding caliper’s depth measuring rod. Equivalent to the variable GTRPROJ [1].

30. **fAPLESS.** *Lesser Trochanter Anteroposterior Breadth*. Anteroposterior linear distance of the lesser trochanter, in medial view. This is more precisely measuring mid-shaft at lesser trochanter, not the depth the lesser trochanter imparts to the diaphysis; the latter varies by taxon and individual enthesial robusticity. Among cercopithecines, the lesser trochanter tends to extend laterally; in hominoids, it tends to extend posteriorly. Measured including lesser trochanter, but with external jaws of sliding calipers still flat across the anterior portion of the diaphysis.

31. **fHEPD**. *Femoral Head Proximodistal Length*. Proximodistal linear distance of femoral head articular surface, in medial view. Measured using external jaws of sliding calipers. Equivalent to the variables HEADPD [1], HPD [2], and FemHeadSIDia [3].

32. **fHEML**. *Femoral Head Mediolateral Breadth*. Mediolateral linear distance from fovea capitis to lateral limit of femoral head articular surface, in anterior view. Measured using internal jaws of sliding calipers, avoiding the greater trochanter while measuring the medial limit of the femoral head. Equivalent to the variables HEADML [1] and HML [2].

33. **fHEAP**. *Femoral Head Anteroposterior Breadth*. Anteroposterior linear distance of femoral head articular surface, in medial view. Measured using external jaws of sliding calipers. Equivalent to the variables HEADAP [1], HAP [2], and FemHeadHzDia [3].

34. **fPSPD**. *Patellar Surface Proximodistal Length*. Distal limit of patellar sulcus to proximal limit of articular surface, in anterior view. Measured using external jaws of sliding calipers. Equivalent to the variable GRVAP [1].

35. **fPSML**. *Patellar Surface Mediolateral Breadth*. Distal linear distance from medial patellar ridge to lateral ridge, in anterior view; caliper points are positioned in the midline of the proximodistal distance of the patellar ridge. Measured using external jaws of sliding calipers.

36. **fDML**. *Femoral Bi-Epicondylar Mediolateral Breadth*. Linear distance from medial limit of medial epicondyle to lateral limit of lateral epicondyle, in anterior view. Measured using external jaws of sliding calipers. Equivalent to the variables BICML [1], DML [2], and FemEpicBr [3].

37. **fDAP**. *Femoral Distal End Anteroposterior Breadth*. Anteroposterior linear distance of the distal end, in inferior view. Measured using external jaws of sliding calipers. Equivalent to the variables DISTAP [1], DAP [2], and FemAPLatCond [3].

38. **fCPD**. *Femoral Condylar Proximodistal Length*. Proximodistal linear distance of condyles, in posterior view. Measured using external jaws of sliding calipers. Equivalent to the variable CONDPD [1].

39. **fCML**. *Femoral Condylar Mediolateral Breadth*. Mediolateral linear distance of condyles at mid-point, in posterior view. Measured using external jaws of sliding calipers. Equivalent to the variable FemBiConBr [3].

40. **fICGPD**. *Femoral Intercondylar Groove Proximodistal Length*. Proximodistal linear distance of the intercondylar groove, in posterior view. Measured using internal jaws of sliding calipers.

41. **fICGML**. *Femoral Intercondylar Groove Mediolateral Breadth*. Mediolateral linear distance of the intercondylar groove, in posterior view. Measured using internal jaws of sliding calipers.

Tibia

42. **tLEN1**. *Tibia Length 1*. Linear distance from intercondylar tubercles to distal limit of medial malleolus, in anterior view. Measured using external jaws of sliding calipers. Equivalent to the variables LENMAL [2] and TibCondMalLng [3].

43. **tLEN2**. *Tibia Length 2*. Linear distance from the intercondylar tubercles to the distal articular surface, in anterior view. Measured using external jaws of sliding calipers. Equivalent to the variables LENFAC [1] and LENFUN [2].

44. **tPML**. *Tibial Proximal End Mediolateral Breadth*. Mediolateral linear distance of the proximal end, in superior view. Measured using external jaws of sliding calipers; tibial plateau should be parallel to the caliper beam. Equivalent to the variables BICONML [1], PRML [2], TibMaxBrProxEpi [3], TPML [4], and to the linear distances between 3D landmarks 7,13 (Turley [5]).

45. **tPAP.** *Tibial Proximal End Anteroposterior Breadth*. Anteroposterior linear distance of the proximal end, in superior view. Measured using external jaws of sliding calipers. Anterior lip of tibial plateau is guiding ridge for measurement,

and external jaw is placed there. The bone is then at an oblique angle relative to the caliper beam, is the plateau is tilted posteriorly. Equivalent to the variables PROXAP [1], PRAP [2], and TPAP [4].

46. **tLFAP**. *Tibial Lateral Condyle Anteroposterior Breadth*. Anteroposterior linear distance of the lateral condyle, in superior view. Measured using external jaws of sliding calipers. Equivalent to the variables LFACAP [1], LFAC [2], TLCL [4], and the linear distance between the 3D landmarks 11,15 [5].

47. **tMFAP**. *Tibial Medial Condyle Anteroposterior Breadth*. Anteroposterior linear distance of the medial condyle, in superior view. Measured using external jaws of sliding calipers. Equivalent to the variables MFACAP [1], MFAC [2], TMCL [4], and the linear distance between the 3D landmarks 1,5 [5].

48. **tLFML**. *Tibial Lateral Condyle Mediolateral Breadth*. Mediolateral linear distance of the lateral condyle, in superior view. Measured using external jaws of sliding calipers. Equivalent to the variable TLCW [4].

49. **tMFML**. *Tibial Medial Condyle Mediolateral Breadth*. Mediolateral linear distance of the medial condyle, in superior view. Measured using external jaws of sliding calipers. Equivalent to the variable TMCW [4].

50. **tDAP**. *Tibial Distal End Anteroposterior Breadth*. Anteroposterior linear distance of the distal end, in inferior view. Measured using external jaws of sliding calipers. Equivalent to the variables DISTAP [1], DAP [2], and the linear distance between the 3D landmarks 23,27 [5].

51. **tDML**. *Tibial Distal End Mediolateral Breadth.* Mediolateral linear distance of the distal end, in inferior view. Measured using external jaws of sliding calipers.

Equivalent to the variables DISTML [1], DML [2], TibMaxBrDistEpi [3], and TDML [4].

52. **tMMPD**. *Tibial Medial Malleolus Proximodistal Length*. Proximodistal linear distance of medial malleolus, in anterior view. Measured using depth rod of sliding calipers. Equivalent to the variable TMMW [4].

53. **tDASML**. *Tibial Distal Articular Surface Mediolateral Breadth*. Linear distance from lateral limit of medial malleolus to lateral limit of distal articular surface, in anterior view. Measured using internal jaws of sliding calipers. Equivalent to the variable TASW [4].

References and Acknowledgements

[1] PRIMO (Primate Morphometrics Online), the NYCEP Primate Morphometric database, is a resource for researchers who use metrical (including 3D) data to study aspects of primate morphology and evolution. Some data for this project were downloaded from PRIMO, the NYCEP Primate Morphology Online database (http://primo.nycep.org). I thank Dr. Eric Delson and colleagues for access to these data.

[2] Frost, S.R. Personal communication and sharing of his postcranial caliper data from various primate taxa. Data has appeared in publication, such as: Frost, S.R., 2014. Fossil Cercopithecidae of the Konso Formation. *Konso-Gardula Research Project*, 5, p.41. I thank Dr. Kieran McNulty and colleagues for access to these data.

[3] The Robert J. Terry Anatomical Skeletal Collection, housed at the National Museum of Natural History, offers public access to an osteometric database of the collection available here: https://anthropology.si.edu/cm/terry.htm. This database includes a protocol with additional citations listed below. I thank Collections Manager of the Terry Collection Dr. David Hunt, and colleagues, for continued public access to this data.

[4] Guthrie, E.H. Personal communication and sharing of her postcranial caliper data from various primate taxa. Data has appeared in publication, such as: Guthrie, E.H., 2011. Functional morphology of the postcranium of *Theropithecus brumpti* (Primates: Cercopithecidae) (Doctoral dissertation, University of Oregon). I thank Dr. Emily Guthrie for access to these data.

[5] Turley, K., Guthrie, E.H. and Frost, S.R., 2011. Geometric morphometric analysis of tibial shape and presentation among catarrhine taxa. *The Anatomical Record: Advances in Integrative Anatomy and Evolutionary Biology*, *294*(2), pp.217-230.

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APPENDIX E

POSTCRANIAL MEASURES OF VARIANCE

Measures of variance are reported per individual linear bony measure, by bony element and subsample. Subsamples are grouped by species and sex. All samples are reported on unadjusted data, and data which has been adjusted by the geometric mean to control for differences due to absolute body size. Each subsection is ordered by taxon pairs: *H. sapiens*, *P. troglodytes*, *P. hamadryas*, *T. gelada*, *M. fascicularis*, and *M. nemestrina*. Where split sex measures of variance are reported, females are always listed first.

Humeral Measures of Variance, Pooled Sexes

***Homo sapiens*, pooled sexes, humerus**

	hLEN1	*hLEN2*	*hLEN3*	*hPML*	*hPAP*	*hHEAP*	*hHEML*	*hLEN4*	*hDML*	*hDASML*	*hDHA*	*hTRPD*	*hTRML*	*hDAP*
Count	18	18	18	18	18	18	18	18	18	18	18	18	18	18
Range	67.00	67.50	69.00	12.26	12.21	14.09	22.92	65.93	23.04	20.05	21.19	9.58	10.86	8.93
Minimum	268.00	273.50	276.50	43.13	40.40	36.28	29.15	83.29	48.47	33.96	37.32	19.11	20.91	22.25
Maximum	335.00	341.00	345.50	55.39	52.61	50.37	52.07	149.22	71.51	54.01	58.51	28.69	31.77	31.18
Mean	302.67	309.61	313.94	48.39	45.98	42.72	40.18	114.92	58.70	39.58	43.22	22.93	25.51	26.00
Standard Error	4.63	4.85	4.92	0.88	0.89	0.99	1.30	4.50	1.62	1.15	1.38	0.60	0.73	0.61
Standard Deviation	19.63	20.59	20.87	3.74	3.77	4.20	5.51	19.09	6.85	4.89	5.84	2.54	3.09	2.57
Sample Variance	385.53	423.81	435.73	14.00	14.20	17.67	30.31	364.34	46.96	23.88	34.07	6.46	9.55	6.63
CV	6.49	6.65	6.65	7.73	8.20	9.84	13.70	16.61	11.68	12.35	13.51	11.08	12.11	9.90

***Pan troglodytes*, pooled sexes, humerus**

	hLEN1	*hLEN2*	*hLEN3*	*hPML*	*hPAP*	*hHEAP*	*hHEML*	*hLEN4*	*hDML*	*hDASML*	*hDHA*	*hTRPD*	*hTRML*	*hDAP*
Count	14	14	14	15	15	15	15	15	15	15	15	15	15	15
Range	69.5	73.5	77	11.96	10.19	10.31	12.74	30.31	17.99	10.2	12.42	11.77	7.21	6.95
Minimum	250	251	252	37.92	37.9	34.68	31.78	87.76	50.95	38.87	43.14	18.13	20.97	23.52
Maximum	319.5	324.5	329	49.88	48.09	44.99	44.52	118.07	68.94	49.07	55.56	29.9	28.18	30.47
Mean	294.00	296.64	299.64	43.73	42.82	39.53	37.65	102.68	60.65	43.69	48.64	22.64	23.71	27.50
Standard Error	5.1	5.29	5.39	0.82	0.88	0.81	0.81	2.31	1.34	0.75	0.84	0.88	0.53	0.48
Standard Deviation	19.10	19.81	20.18	3.19	3.40	3.14	3.13	8.96	5.18	2.92	3.24	3.42	2.06	1.86
Sample Variance	365.00	392.32	407.09	10.18	11.53	9.83	9.82	80.23	26.80	8.55	10.47	11.68	4.23	3.45
CV	6.50	6.68	6.73	7.30	7.93	7.93	8.32	8.72	8.53	6.69	6.65	15.10	8.67	6.76

Humeral Measures of Variance, Pooled Sexes

***Papio hamadryas*, pooled sexes, humerus**

	hLEN1	*hLEN2*	*hLEN3*	*hPML*	*hPAP*	*hHEAP*	*hHEML*	*hLEN4*	*hDML*	*hDASML*	*hDHA*	*hTRPD*	*hTRML*	*hDAP*
Count	21	21	7	22	22	21	21	22	23	23	19	23	23	23
Range	72.72	71.64	39.33	12.42	11.51	9.99	11.16	43.09	16.1	11.22	16.19	9.39	8.99	9.34
Minimum	184.78	182	202.71	24.75	24.67	21.55	17.36	50.62	31.12	21.7	25.26	14.94	12.04	20.66
Maximum	257.5	253.64	242.04	37.17	36.18	31.54	28.52	93.71	47.22	32.92	41.45	24.33	21.03	30
Mean	220.02	217.95	225.86	31.19	31.34	26.43	24.38	68.23	38.91	28.26	34.23	20.08	15.98	25.35
Standard Error	4.48	4.53	4.59	0.79	0.76	0.74	0.67	2.03	0.98	0.74	0.94	0.61	0.55	0.63
Standard Deviation	20.55	20.76	12.14	3.71	3.54	3.40	3.07	9.53	4.70	3.57	4.08	2.92	2.64	3.04
Sample Variance	422.17	431.02	147.45	13.74	12.56	11.57	9.45	90.87	22.06	12.71	16.64	8.51	6.98	9.26
CV	9.34	9.53	5.38	11.89	11.31	12.87	12.61	13.97	12.07	12.62	11.92	14.53	16.53	12.00

***Theropithecus gelada*, pooled sexes, humerus**

	hLEN1	*hLEN2*	*hLEN3*	*hPML*	*hPAP*	*hHEAP*	*hHEML*	*hLEN4*	*hDML*	*hDASML*	*hDHA*	*hTRPD*	*hTRML*	*hDAP*
Count	13	13	4	12	13	9	9	13	13	13	10	13	13	13
Range	43.73	43.09	32.29	5.85	8.63	6.4	4.73	14.94	8.69	6.23	5.67	5.07	7	4.78
Minimum	161.38	161.31	169.5	22.57	23.87	21.49	18.13	47.56	27.23	19.17	24.85	14.72	10.52	18.7
Maximum	205.11	204.4	201.79	28.42	32.5	27.89	22.86	62.5	35.92	25.4	30.52	19.79	17.52	23.48
Mean	187.45	186.07	185.44	25.79	28.35	23.88	20.33	56.28	32.39	22.72	27.70	17.04	13.25	21.60
Standard Error	4.44	4.31	7.94	0.68	0.90	0.78	0.62	1.27	0.78	0.52	0.69	0.41	0.57	0.49
Standard Deviation	16.00	15.54	15.87	2.37	3.23	2.34	1.85	4.57	2.82	1.87	2.19	1.46	2.04	1.77
Sample Variance	256.01	241.37	251.95	5.62	10.42	5.49	3.42	20.87	7.94	3.50	4.79	2.14	4.18	3.15
CV	8.54	8.35	8.56	9.19	11.38	9.81	9.09	8.12	8.70	8.23	7.90	8.58	15.43	8.21

Humeral Measures of Variance, Pooled Sexes

***Macaca fascicularis*, pooled sexes, humerus**

	hLEN1	*hLEN2*	*hLEN3*	*hPML*	*hPAP*	*hHEAP*	*hHEML*	*hLEN4*	*hDML*	*hDASML*	*hDHA*	*hTRPD*	*hTRML*	*hDAP*
Count	9	9	5	9	9	9	9	11	11	11	11	11	11	11
Range	45.79	44.26	44.98	6.36	6.5	6.34	6.56	18.14	10.9	7.89	13.9	5.06	5.5	5.96
Minimum	103.91	105.39	106.69	12.95	13.21	10.68	10.43	26.87	15.55	11.34	13.3	8.11	7.07	9.81
Maximum	149.7	149.65	151.67	19.31	19.71	17.02	16.99	45.01	26.45	19.23	27.2	13.17	12.57	15.77
Mean	120.10	120.31	125.17	15.80	16.10	13.67	13.18	38.06	20.52	14.76	17.87	9.77	8.64	12.21
Standard Error	4.39	4.28	7.59	0.78	0.78	0.68	0.79	1.69	1.04	0.69	1.19	0.51	0.52	0.63
Standard Deviation	13.16	12.84	16.96	2.33	2.33	2.05	2.37	5.61	3.45	2.29	3.93	1.68	1.72	2.09
Sample Variance	173.23	164.98	287.74	5.41	5.41	4.21	5.61	31.48	11.87	5.22	15.46	2.83	2.95	4.38
CV	10.96	10.68	13.55	14.73	14.45	15.01	17.96	14.74	16.79	15.48	22.01	17.23	19.89	17.14

***Macaca nemestrina*, pooled sexes, humerus**

	hLEN1	*hLEN2*	*hLEN3*	*hPML*	*hPAP*	*hHEAP*	*hHEML*	*hLEN4*	*hDML*	*hDASML*	*hDHA*	*hTRPD*	*hTRML*	*hDAP*
Count	3	3	2	3	3	3	3	3	3	3	3	3	3	3
Range	34	32.92	18.18	6.44	4.56	5.31	5.5	8.54	4.54	3.54	4.27	3.56	2.49	2.91
Minimum	155.5	155.58	155.6	20.24	20.61	17.45	17.98	46.9	27.04	20.03	23.66	12.75	10.87	17.02
Maximum	189.5	188.5	173.78	26.68	25.17	22.76	23.48	55.44	31.58	23.57	27.93	16.31	13.36	19.93
Mean	172.54	171.22	164.69	23.73	23.00	20.21	20.04	50.92	29.97	21.67	25.26	14.90	12.32	18.79
Standard Error	9.82	9.54	9.09	1.88	1.32	1.54	1.73	2.48	1.47	1.03	1.35	1.09	0.75	0.90
Standard Deviation	17.00	16.52	12.86	3.25	2.29	2.66	3.00	4.29	2.54	1.78	2.33	1.89	1.29	1.56
Sample Variance	289.00	272.95	165.26	10.59	5.23	7.08	9.00	18.42	6.47	3.18	5.43	3.59	1.68	2.42
CV	9.85	9.65	7.81	13.71	9.95	13.17	14.98	8.43	8.49	8.23	9.22	12.71	10.51	8.28

Humeral Measures of Variance, Split Sexes

***Homo sapiens*, female only, humerus**

	hLEN1	*hLEN2*	*hLEN3*	*hPML*	*hPAP*	*hHEAP*	*hHEML*	*hLEN4*	*hDML*	*hDASML*	*hDHA*	*hTRPD*	*hTRML*	*hDAP*
Count	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Range	40.00	42.00	43.50	5.74	5.01	7.15	12.82	47.50	14.03	5.84	6.25	3.95	6.46	3.82
Minimum	268.00	273.50	276.50	43.13	40.40	36.56	29.15	83.29	48.47	33.96	37.32	19.11	20.91	22.25
Maximum	308.00	315.50	320.00	48.87	45.41	43.71	41.97	130.79	62.50	39.80	43.57	23.06	27.37	26.07
Mean	290.56	297.00	300.78	45.55	42.90	40.38	36.89	108.04	54.35	36.80	39.16	21.54	23.94	24.03
Standard Error	4.37	4.57	4.68	0.66	0.54	0.80	1.31	4.67	1.49	0.65	0.71	0.44	0.72	0.38
Standard Deviation	13.12	13.71	14.04	1.98	1.61	2.40	3.94	14.00	4.48	1.96	2.13	1.32	2.16	1.15
Sample Variance	172.03	187.88	197.26	3.92	2.60	5.78	15.52	196.13	20.07	3.84	4.52	1.75	4.66	1.33
CV	4.51	4.62	4.67	4.34	3.76	5.95	10.68	12.96	8.24	5.32	5.43	6.15	9.02	4.79

***Homo sapiens*, male only, humerus**

	hLEN1	*hLEN2*	*hLEN3*	*hPML*	*hPAP*	*hHEAP*	*hHEML*	*hLEN4*	*hDML*	*hDASML*	*hDHA*	*hTRPD*	*hTRML*	*hDAP*
Count	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Range	55.5	56	52.5	7.88	7.03	14.09	16.91	61.33	15.7	17.24	18.16	9.17	9.11	6.67
Minimum	279.5	285	293	47.51	45.58	36.28	35.16	87.89	55.81	36.77	40.35	19.52	22.66	24.51
Maximum	335	341	345.5	55.39	52.61	50.37	52.07	149.22	71.51	54.01	58.51	28.69	31.77	31.18
Mean	314.78	322.22	327.11	51.23	49.06	45.07	43.46	121.80	63.04	42.36	47.27	24.31	27.08	27.97
Standard Error	5.94	6.28	6.13	0.92	0.83	1.47	1.65	7.24	2.03	1.81	1.85	0.92	1.06	0.67
Standard Deviation	17.81	18.84	18.40	2.77	2.49	4.40	4.96	21.72	6.10	5.44	5.55	2.77	3.17	2.01
Sample Variance	317.19	354.88	338.61	7.68	6.19	19.37	24.59	471.66	37.25	29.55	30.82	7.67	10.06	4.04
CV	5.66	5.85	5.63	5.41	5.07	9.77	11.41	17.83	9.68	12.83	11.74	11.39	11.71	7.19

Humeral Measures of Variance, Split Sexes

***Pan troglodytes*, female only, humerus**

	hLEN1	*hLEN2*	*hLEN3*	*hPML*	*hPAP*	*hHEAP*	*hHEML*	*hLEN4*	*hDML*	*hDASML*	*hDHA*	*hTRPD*	*hTRML*	*hDAP*
Count	8	8	8	9	9	9	9	9	9	9	9	9	9	9
Range	68.5	73.5	77	9.09	10.19	8.83	8.46	28.65	13.98	7.92	8.26	8.21	7.21	5.77
Minimum	250	251	252	37.92	37.9	34.68	31.78	89.42	50.95	38.87	43.14	18.13	20.97	23.52
Maximum	318.5	324.5	329	47.01	48.09	43.51	40.24	118.07	64.93	46.79	51.4	26.34	28.18	29.29
Mean	286.31	289.00	292.56	42.55	41.50	38.36	36.48	103.92	58.30	42.49	47.51	21.43	23.45	26.82
Standard Error	6.69	7.14	7.43	0.85	1.06	0.90	0.82	3.49	1.48	0.83	0.97	0.97	0.80	0.59
Standard Deviation	18.93	20.19	21.01	2.55	3.17	2.70	2.45	10.47	4.43	2.48	2.90	2.90	2.41	1.77
Sample Variance	358.21	407.50	441.60	6.49	10.03	7.27	5.98	109.58	19.62	6.16	8.40	8.43	5.80	3.13
CV	6.61	6.98	7.18	5.99	7.63	7.03	6.70	10.07	7.60	5.84	6.10	13.55	10.27	6.60

***Pan troglodytes*, male only, humerus**

	hLEN1	*hLEN2*	*hLEN3*	*hPML*	*hPAP*	*hHEAP*	*hHEML*	*hLEN4*	*hDML*	*hDASML*	*hDHA*	*hTRPD*	*hTRML*	*hDAP*
Count	6	6	6	6	6	6	6	6	6	6	6	6	6	6
Range	32	31.5	36	8.43	7.55	7.39	9.39	16.64	12.39	6.44	9.2	9.36	3.64	4.14
Minimum	287.5	290.5	290	41.45	39.99	37.6	35.13	87.76	56.55	42.63	46.36	20.54	22.39	26.33
Maximum	319.5	322	326	49.88	47.54	44.99	44.52	104.4	68.94	49.07	55.56	29.9	26.03	30.47
Mean	304.25	306.83	309.08	45.50	44.81	41.28	39.40	100.82	64.19	45.50	50.33	24.45	24.11	28.51
Standard Error	6.15	6.21	6.49	1.41	1.18	1.27	1.40	2.66	1.76	1.12	1.30	1.45	0.61	0.66
Standard Deviation	15.06	15.21	15.91	3.45	2.89	3.12	3.43	6.51	4.32	2.75	3.18	3.56	1.50	1.61
Sample Variance	226.88	231.47	253.04	11.88	8.35	9.75	11.79	42.41	18.66	7.58	10.12	12.66	2.24	2.61
CV	4.95	4.96	5.15	7.58	6.45	7.57	8.71	6.46	6.73	6.05	6.32	14.55	6.21	5.66

Humeral Measures of Variance, Split Sexes

***Papio hamadryas*, female only, humerus**

	hLEN1	*hLEN2*	*hLEN3*	*hPML*	*hPAP*	*hHEAP*	*hHEML*	*hLEN4*	*hDML*	*hDASML*	*hDHA*	*hTRPD*	*hTRML*	*hDAP*
Count	7	7	2	8	8	8	8	8	8	8	7	8	8	8
Range	35.61	36.14	18.53	5.7	5.56	3.92	6.25	15.85	6.97	6.25	16.19	4.53	7.53	4.41
Minimum	184.78	182	202.71	24.75	24.67	21.55	17.36	50.62	31.12	21.7	25.26	14.94	12.04	20.66
Maximum	220.39	218.14	221.24	30.45	30.23	25.47	23.61	66.47	38.09	27.95	41.45	19.47	19.57	25.07
Mean	200.57	198.25	211.98	27.53	27.53	23.53	21.26	60.12	34.49	24.76	31.78	17.12	14.68	22.22
Standard Error	5.12	5.29	9.27	0.62	0.66	0.54	0.74	1.86	0.80	0.78	1.87	0.47	1.05	0.53
Standard Deviation	13.56	14.01	13.10	1.75	1.87	1.52	2.10	5.27	2.27	2.20	4.94	1.33	2.98	1.50
Sample Variance	183.83	196.22	171.68	3.07	3.50	2.30	4.42	27.81	5.13	4.84	24.42	1.76	8.88	2.26
CV	6.76	7.07	6.18	6.36	6.80	6.44	9.90	8.77	6.57	8.89	15.55	7.76	20.31	6.77

***Papio hamadryas*, male only, humerus**

	hLEN1	*hLEN2*	*hLEN3*	*hPML*	*hPAP*	*hHEAP*	*hHEML*	*hLEN4*	*hDML*	*hDASML*	*hDHA*	*hTRPD*	*hTRML*	*hDAP*
Count	14	14	5	14	14	13	13	14	15	15	12	15	15	15
Range	53.8	50.47	16.54	10.07	7.37	8.76	6.52	32.16	14.92	9.52	8.79	8.73	7.93	6.94
Minimum	203.7	203.17	225.5	27.1	28.81	22.78	22	61.55	32.3	23.4	31.3	15.6	13.1	23.06
Maximum	257.5	253.64	242.04	37.17	36.18	31.54	28.52	93.71	47.22	32.92	40.09	24.33	21.03	30
Mean	229.74	227.81	231.41	33.29	33.52	28.21	26.31	72.86	41.27	30.13	35.66	21.65	16.68	27.02
Standard Error	4.30	4.30	2.95	0.73	0.56	0.83	0.45	2.21	1.00	0.67	0.81	0.57	0.58	0.57
Standard Deviation	16.10	16.09	6.59	2.75	2.08	2.99	1.63	8.26	3.87	2.61	2.80	2.20	2.24	2.20
Sample Variance	259.05	258.89	43.39	7.56	4.33	8.93	2.66	68.21	14.98	6.79	7.86	4.83	5.03	4.84
CV	7.01	7.06	2.85	8.26	6.21	10.59	6.20	11.34	9.38	8.65	7.86	10.15	13.44	8.14

Humeral Measures of Variance, Split Sexes

***Theropithecus gelada*, female only, humerus**

	hLEN1	*hLEN2*	*hLEN3*	*hPML*	*hPAP*	*hHEAP*	*hHEML*	*hLEN4*	*hDML*	*hDASML*	*hDHA*	*hTRPD*	*hTRML*	*hDAP*
Count	5	5	2	5	5	4	4	5	5	5	4	5	5	5
Range	12.44	11.01	4.9	1.58	2.13	0.93	0.99	7.71	3.77	3.32	1.29	1.58	5.91	1.81
Minimum	161.38	161.31	169.5	22.57	23.87	21.49	18.13	47.56	27.23	19.17	24.85	14.72	10.52	18.7
Maximum	173.82	172.32	174.4	24.15	26	22.42	19.12	55.27	31	22.49	26.14	16.3	16.43	20.51
Mean	169.25	168.50	171.95	23.33	24.91	21.84	18.50	52.36	29.34	20.85	25.42	15.55	12.82	19.54
Standard Error	2.33	2.18	2.45	0.31	0.38	0.21	0.22	1.36	0.77	0.58	0.31	0.28	1.10	0.30
Standard Deviation	5.20	4.89	3.46	0.69	0.85	0.42	0.44	3.04	1.73	1.29	0.63	0.62	2.46	0.67
Sample Variance	27.03	23.87	12.01	0.48	0.72	0.17	0.19	9.22	2.99	1.65	0.39	0.38	6.04	0.45
CV	3.07	2.90	2.02	2.96	3.40	1.91	2.36	5.80	5.90	6.17	2.46	3.96	19.17	3.44

***Theropithecus gelada*, male only, humerus**

	hLEN1	*hLEN2*	*hLEN3*	*hPML*	*hPAP*	*hHEAP*	*hHEML*	*hLEN4*	*hDML*	*hDASML*	*hDHA*	*hTRPD*	*hTRML*	*hDAP*
Count	8	8	2	7	8	5	5	8	8	8	6	8	8	8
Range	17.54	18.14	5.74	3.28	4.77	4.54	2	11.78	3.1	2.95	3.48	3.19	5.82	1.02
Minimum	187.57	186.26	196.05	25.14	27.73	23.35	20.86	50.72	32.82	22.45	27.04	16.6	11.7	22.46
Maximum	205.11	204.4	201.79	28.42	32.5	27.89	22.86	62.5	35.92	25.4	30.52	19.79	17.52	23.48
Mean	198.83	197.06	198.92	27.54	30.51	25.51	21.81	58.73	34.30	23.89	29.22	17.98	13.52	22.90
Standard Error	2.20	2.28	2.87	0.44	0.68	0.82	0.35	1.26	0.37	0.35	0.49	0.33	0.66	0.15
Standard Deviation	6.21	6.45	4.06	1.17	1.91	1.83	0.78	3.56	1.04	0.99	1.21	0.93	1.87	0.43
Sample Variance	38.62	41.58	16.47	1.37	3.65	3.36	0.61	12.66	1.08	0.99	1.47	0.86	3.50	0.19
CV	3.13	3.27	2.04	4.25	6.27	7.18	3.57	6.06	3.04	4.16	4.14	5.16	13.83	1.90

Humeral Measures of Variance, Split Sexes

***Macaca fascicularis*, female only, humerus**

	hLEN 1	*hLEN 2*	*hLEN 3*	*hPML*	*hPAP*	*hHEAP*	*hHEML*	*hLEN 4*	*hDML*	*hDASML*	*hDHA*	*hTRPD*	*hTRML*	*hDAP*
Count	5	5	2	5	5	5	5	6	6	6	6	6	6	6
Range	15.59	14.01	13.91	2.74	1.82	2.84	2.72	12.16	4.07	3.46	3.61	1.6	1.1	2.13
Minimum	103.91	105.39	106.69	12.95	13.21	10.68	10.43	26.87	15.55	11.34	13.3	8.11	7.07	9.81
Maximum	119.5	119.4	120.6	15.69	15.03	13.52	13.15	39.03	19.62	14.8	16.91	9.71	8.17	11.94
Mean	112.61	113.08	113.65	14.13	14.32	12.25	11.55	34.91	17.97	13.15	15.29	8.66	7.54	10.70
Standard Error	2.70	2.47	6.96	0.46	0.31	0.58	0.44	2.13	0.61	0.51	0.62	0.24	0.18	0.34
Standard Deviation	6.03	5.53	9.84	1.03	0.70	1.29	0.99	5.21	1.50	1.25	1.51	0.58	0.45	0.84
Sample Variance	36.35	30.60	96.74	1.07	0.48	1.67	0.98	27.19	2.25	1.56	2.28	0.34	0.20	0.70
CV	5.35	4.89	8.65	7.32	4.86	10.56	8.57	14.94	8.34	9.50	9.88	6.73	5.92	7.84

***Macaca fascicularis*, male only, humerus**

	hLEN 1	*hLEN 2*	*hLEN 3*	*hPML*	*hPAP*	*hHEAP*	*hHEML*	*hLEN 4*	*hDML*	*hDASML*	*hDHA*	*hTRPD*	*hTRML*	*hDAP*
Count	4	4	3	4	4	4	4	5	5	5	5	5	5	5
Range	32.36	31.94	34.56	3.26	2.71	2.58	3.71	8.07	5.1	4.18	8.9	3.88	4.41	2.95
Minimum	117.34	117.71	117.11	16.05	17	14.44	13.28	36.94	21.35	15.05	18.3	9.29	8.16	12.82
Maximum	149.7	149.65	151.67	19.31	19.71	17.02	16.99	45.01	26.45	19.23	27.2	13.17	12.57	15.77
Mean	129.45	129.34	132.86	17.89	18.32	15.46	15.23	41.84	23.58	16.70	20.96	11.10	9.95	14.03
Standard Error	7.13	7.13	10.09	0.80	0.70	0.59	0.95	1.54	1.04	0.71	1.66	0.72	0.80	0.71
Standard Deviation	14.26	14.26	17.48	1.60	1.40	1.18	1.91	3.45	2.32	1.58	3.72	1.61	1.78	1.58
Sample Variance	203.39	203.31	305.65	2.55	1.97	1.40	3.63	11.93	5.39	2.50	13.84	2.61	3.16	2.49
CV	11.02	11.02	13.16	8.93	7.66	7.65	12.51	8.25	9.84	9.47	17.74	14.55	17.87	11.24

Humeral Measures of Variance, Split Sexes

***Macaca nemestrina*, female only, humerus**

	hLEN1	*hLEN2*	*hLEN3*	*hPML*	*hPAP*	*hHEAP*	*hHEML*	*hLEN4*	*hDML*	*hDASML*	*hDHA*	*hTRPD*	*hTRML*	*hDAP*
Count	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Range	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Minimum	155.5	155.58	155.6	20.24	20.61	17.45	17.98	46.9	27.04	20.03	23.66	12.75	10.87	17.02
Maximum	155.5	155.58	155.6	20.24	20.61	17.45	17.98	46.9	27.04	20.03	23.66	12.75	10.87	17.02
Mean	155.5	155.58	155.6	20.24	20.61	17.45	17.98	46.9	27.04	20.03	23.66	12.75	10.87	17.02
Standard Error	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Standard Deviation	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Sample Variance	.	.	.	.	.	.	.	.	.	.	.	.	.	.
CV	.	.	.	.	.	.	.	.	.	.	.	.	.	.

***Macaca nemestrina*, male only, humerus**

	hLEN1	*hLEN2*	*hLEN3*	*hPML*	*hPAP*	*hHEAP*	*hHEML*	*hLEN4*	*hDML*	*hDASML*	*hDHA*	*hTRPD*	*hTRML*	*hDAP*
Count	2	2	1	2	2	2	2	2	2	2	2	2	2	2
Range	16.88	18.92	0	2.4	1.96	2.34	4.83	5.02	0.28	2.16	3.75	0.66	0.63	0.5
Minimum	172.62	169.58	173.78	24.28	23.21	20.42	18.65	50.42	31.3	21.41	24.18	15.65	12.73	19.43
Maximum	189.5	188.5	173.78	26.68	25.17	22.76	23.48	55.44	31.58	23.57	27.93	16.31	13.36	19.93
Mean	181.06	179.04	173.78	25.48	24.19	21.59	21.065	52.93	31.44	22.49	26.055	15.98	13.045	19.68
Standard Error	8.44	9.46	.	1.2	0.98	1.17	2.415	2.51	0.14	1.08	1.875	0.33	0.315	0.25
Standard Deviation	11.94	13.38	.	1.70	1.39	1.65	3.42	3.55	0.20	1.53	2.65	0.47	0.45	0.35
Sample Variance	142.47	178.98	.	2.88	1.92	2.74	11.66	12.60	0.04	2.33	7.03	0.22	0.20	0.13
CV	6.59	7.47	.	6.66	5.73	7.66	16.21	6.71	0.63	6.79	10.18	2.92	3.41	1.80

Radial Measures of Variance, Pooled Sexes

***Homo sapiens*, pooled sexes, radius**

	rLEN1	*rLEN2*	*rPAP*	*rPML*	*rNE1*	*rNE2*	*rNE3*	*rTUB*	*rDML*	*rDAP*
Count	18	18	18	18	18	18	18	18	18	18
Range	67.5	65	7.01	5.99	8.46	9.57	9.44	7.93	15.42	16.19
Minimum	196.5	206	19.91	19.15	7.7	17.88	27.51	19.18	23.23	18.87
Maximum	264	271	26.92	25.14	16.16	27.45	36.95	27.11	38.65	35.06
Mean	231.72	237.97	22.09	21.11	13.45	22.90	32.42	22.61	31.47	22.54
Standard Error	4.40	4.30	0.40	0.34	0.49	0.53	0.56	0.55	0.93	0.86
Standard Deviation	18.66	18.26	1.69	1.45	2.08	2.24	2.37	2.32	3.95	3.66
Sample Variance	348.30	333.51	2.85	2.09	4.32	5.03	5.63	5.40	15.61	13.40
CV	8.05	7.67	7.64	6.85	15.45	9.80	7.32	10.28	12.56	16.24

***Pan troglodytes*, pooled sexes, radius**

	rLEN1	*rLEN2*	*rPAP*	*rPML*	*rNE1*	*rNE2*	*rNE3*	*rTUB*	*rDML*	*rDAP*
Count	15	15	15	15	15	15	15	15	15	15
Range	69.5	70	7.27	7.68	9.01	7.27	11.24	18.04	8.89	7.26
Minimum	231	234.5	20.07	19.72	17.19	29.23	35.52	16.25	27.52	20.05
Maximum	300.5	304.5	27.34	27.4	26.2	36.5	46.76	34.29	36.41	27.31
Mean	271.60	274.33	24.45	23.90	21.81	32.30	40.83	24.06	32.53	22.85
Standard Error	5.58	5.50	0.55	0.49	0.68	0.58	0.83	1.28	0.69	0.55
Standard Deviation	21.62	21.31	2.13	1.90	2.62	2.23	3.22	4.95	2.67	2.12
Sample Variance	467.22	453.92	4.53	3.62	6.89	4.98	10.39	24.48	7.13	4.50
CV	7.96	7.77	8.70	7.96	12.03	6.91	7.90	20.57	8.21	9.28

Radial Measures of Variance, Pooled Sexes

***Papio hamadryas*, pooled sexes, radius**										
	rLEN1	*rLEN2*	*rPAP*	*rPML*	*rNE1*	*rNE2*	*rNE3*	*rTUB*	*rDML*	*rDAP*
Count	7	18	33	33	18	7	18	7	23	23
Range	35.94	76	8.62	8.32	8.3	6.48	15.71	11.13	9.80	8.35
Minimum	208.44	194	13.72	13.19	5.19	15.88	17.56	22.2	18.7	14.64
Maximum	244.38	270	22.34	21.51	13.49	22.36	33.27	33.33	28.5	22.99
Mean	231.47	231.13	18.68	17.69	9.59	18.87	24.82	25.27	23.59	18.67
Standard Error	4.37	4.76	0.41	0.40	0.51	0.83	1.05	1.49	0.61	0.49
Standard Deviation	11.57	20.18	2.37	2.29	2.18	2.20	4.46	3.94	2.92	2.34
Sample Variance	133.94	407.06	5.63	5.23	4.77	4.84	19.88	15.49	8.51	5.49
CV	5.00	8.73	12.70	12.94	22.76	11.66	17.96	15.57	12.37	12.55

***Theropithecus gelada*, pooled sexes, radius**										
	rLEN1	*rLEN2*	*rPAP*	*rPML*	*rNE1*	*rNE2*	*rNE3*	*rTUB*	*rDML*	*rDAP*
Count	4	11	12	12	11	4	11	4	10	10
Range	26.59	36.14	3.39	4.92	3.89	3.07	6.44	5.79	7.65	3.06
Minimum	182.84	180.88	13.18	12.21	4.9	11.02	14.32	21.19	13.99	13.76
Maximum	209.43	217.02	16.57	17.13	8.79	14.09	20.76	26.98	21.64	16.82
Mean	191.98	197.50	15.03	14.88	6.58	12.70	17.54	24.45	17.98	15.37
Standard Error	6.13	4.16	0.37	0.46	0.43	0.73	0.61	1.26	0.70	0.35
Standard Deviation	12.26	13.81	1.28	1.58	1.41	1.46	2.01	2.53	2.22	1.12
Sample Variance	150.31	190.78	1.63	2.51	1.99	2.12	4.06	6.39	4.94	1.25
CV	6.39	6.99	8.48	10.64	21.45	11.47	11.48	10.34	12.36	7.28

Radial Measures of Variance, Pooled Sexes

***Macaca fascicularis*, pooled sexes, radius**

	rLEN1	*rLEN2*	*rPAP*	*rPML*	*rNE1*	*rNE2*	*rNE3*	*rTUB*	*rDML*	*rDAP*
Count	5	5	12	12	5	5	5	5	12	12
Range	46.1	47.48	4.46	3.97	6.85	9.68	11.12	6.62	6.37	4.12
Minimum	96.21	98.89	7.34	7.27	4.2	8.36	11.29	8.83	9.62	7.49
Maximum	142.31	146.37	11.8	11.24	11.05	18.04	22.41	15.45	15.99	11.61
Mean	116.01	119.44	9.76	9.07	6.92	12.05	14.98	12.14	12.16	9.44
Standard Error	7.57	7.92	0.41	0.35	1.27	1.71	2.03	1.18	0.53	0.43
Standard Deviation	16.94	17.70	1.42	1.21	2.83	3.82	4.54	2.65	1.85	1.50
Sample Variance	286.80	313.30	2.03	1.45	8.02	14.61	20.66	7.00	3.41	2.25
CV	14.60	14.82	14.60	13.30	40.93	31.71	30.34	21.80	15.18	15.91

***Macaca nemestrina*, pooled sexes, radius**

	rLEN1	*rLEN2*	*rPAP*	*rPML*	*rNE1*	*rNE2*	*rNE3*	*rTUB*	*rDML*	*rDAP*
Count	3	3	10	10	4	3	4	3	10	10
Range	38.13	38.23	6.57	6.42	5.56	3.83	4.84	3.92	8.86	6.25
Minimum	133.85	138.27	9.90	9.70	4.38	10.33	14.86	12.25	13.09	10.07
Maximum	171.98	176.50	16.47	16.12	9.94	14.16	19.70	16.17	21.95	16.32
Mean	152.71	157.41	13.21	12.77	8.00	12.65	18.09	14.29	17.65	13.25
Standard Error	11.01	11.04	0.81	0.71	1.23	1.18	1.14	1.13	0.97	0.78
Standard Deviation	19.07	19.12	2.55	2.25	2.47	2.04	2.28	1.96	3.07	2.47
Sample Variance	363.60	365.39	6.52	5.08	6.09	4.16	5.21	3.86	9.44	6.09
CV	12.49	12.14	19.32	17.64	30.86	16.12	12.62	13.75	17.41	18.62

Radial Measures of Variance, Split Sexes

***Homo sapiens*, female only, radius**										
	rLEN1	*rLEN2*	*rPAP*	*rPML*	*rNE1*	*rNE2*	*rNE3*	*rTUB*	*rDML*	*rDAP*
Count	9	9	9	9	9	9	9	9	9	9
Range	48	42	2.8	2.47	4.42	4.47	5.98	6.64	5.2	2.65
Minimum	196.5	206	19.91	19.15	10.81	19.27	27.51	19.79	27.5	18.87
Maximum	244.5	248	22.71	21.62	15.23	23.74	33.49	26.43	32.7	21.52
Mean	221.00	226.89	21.30	20.32	13.25	22.25	31.00	22.03	29.44	20.30
Standard Error	5.09	4.78	0.28	0.29	0.56	0.49	0.70	0.62	0.56	0.34
Standard Deviation	15.27	14.33	0.83	0.86	1.67	1.48	2.09	1.87	1.69	1.02
Sample Variance	233.13	205.49	0.68	0.74	2.80	2.20	4.35	3.50	2.85	1.03
CV	6.91	6.32	3.88	4.22	12.63	6.67	6.73	8.50	5.74	5.01

***Homo sapiens*, male only, radius**										
	rLEN1	*rLEN2*	*rPAP*	*rPML*	*rNE1*	*rNE2*	*rNE3*	*rTUB*	*rDML*	*rDAP*
Count	9	9	9	9	9	9	9	9	9	9
Range	52.5	51	6.59	5.04	8.46	9.57	5.34	7.93	15.42	12.98
Minimum	211.5	220	20.33	20.1	7.7	17.88	31.61	19.18	23.23	22.08
Maximum	264	271	26.92	25.14	16.16	27.45	36.95	27.11	38.65	35.06
Mean	242.44	249.06	22.87	21.90	13.66	23.55	33.83	23.20	33.50	24.79
Standard Error	5.25	5.02	0.67	0.51	0.84	0.91	0.59	0.90	1.53	1.34
Standard Deviation	15.76	15.06	2.00	1.52	2.51	2.74	1.77	2.69	4.59	4.01
Sample Variance	248.34	226.84	3.99	2.30	6.29	7.53	3.14	7.22	21.06	16.10
CV	6.50	6.05	8.74	6.92	18.37	11.65	5.24	11.58	13.70	16.19

Radial Measures of Variance, Split Sexes

***Pan troglodytes*, female only, radius**

	rLEN1	*rLEN2*	*rPAP*	*rPML*	*rNE1*	*rNE2*	*rNE3*	*rTUB*	*rDML*	*rDAP*
Count	9	9	9	9	9	9	9	9	9	9
Range	67.5	66.5	5.77	4.95	8.4	5.29	8.58	18.04	8.45	4.3
Minimum	231	234.5	20.07	19.72	17.19	29.23	35.52	16.25	27.52	20.05
Maximum	298.5	301	25.84	24.67	25.59	34.52	44.1	34.29	35.97	24.35
Mean	265.00	267.61	23.58	22.98	21.25	31.62	39.80	23.19	31.81	22.24
Standard Error	7.74	7.66	0.66	0.51	0.78	0.63	0.87	1.91	0.91	0.63
Standard Deviation	23.21	22.99	1.97	1.53	2.35	1.90	2.61	5.74	2.73	1.88
Sample Variance	538.81	528.42	3.90	2.34	5.50	3.61	6.80	32.92	7.45	3.53
CV	8.76	8.59	8.37	6.66	11.04	6.01	6.55	24.74	8.58	8.44

***Pan troglodytes*, male only, radius**

	rLEN1	*rLEN2*	*rPAP*	*rPML*	*rNE1*	*rNE2*	*rNE3*	*rTUB*	*rDML*	*rDAP*
Count	6	6	6	6	6	6	6	6	6	6
Range	40	40.5	4.63	4.37	8.11	6.19	9.19	10.08	5.15	6.78
Minimum	260.5	264	22.71	23.03	18.09	30.31	37.57	19.47	31.26	20.53
Maximum	300.5	304.5	27.34	27.4	26.2	36.5	46.76	29.55	36.41	27.31
Mean	281.50	284.42	25.74	25.28	22.65	33.34	42.38	25.36	33.60	23.76
Standard Error	6.46	6.08	0.72	0.65	1.23	1.00	1.50	1.44	0.98	0.94
Standard Deviation	15.81	14.90	1.75	1.60	3.01	2.46	3.67	3.54	2.39	2.30
Sample Variance	250.10	222.14	3.08	2.57	9.07	6.04	13.44	12.50	5.73	5.30
CV	5.62	5.24	6.81	6.34	13.30	7.37	8.65	13.95	7.13	9.69

Radial Measures of Variance, Split Sexes

***Papio hamadryas*, female only, radius**

	rLEN1	*rLEN2*	*rPAP*	*rPML*	*rNE1*	*rNE2*	*rNE3*	*rTUB*	*rDML*	*rDAP*
Count	2	5	10	10	5	2	5	2	8	8
Range	25.56	46.39	4.26	4.32	4.45	1.08	4.83	1.39	3.51	3.08
Minimum	208.44	194	13.72	13.19	5.19	15.88	17.56	22.98	18.7	14.64
Maximum	234	240.39	17.98	17.51	9.64	16.96	22.39	24.37	22.21	17.72
Mean	221.22	213.98	15.77	15.05	7.91	16.42	20.09	23.68	20.53	15.95
Standard Error	12.78	7.85	0.42	0.43	0.74	0.54	0.95	0.70	0.48	0.34
Standard Deviation	18.07	17.56	1.33	1.35	1.64	0.76	2.11	0.98	1.36	0.96
Sample Variance	326.66	308.43	1.76	1.82	2.70	0.58	4.47	0.97	1.85	0.93
CV	8.17	8.21	8.42	8.96	20.80	4.65	10.53	4.15	6.63	6.03

***Papio hamadryas*, male only, radius**

	rLEN1	*rLEN2*	*rPAP*	*rPML*	*rNE1*	*rNE2*	*rNE3*	*rTUB*	*rDML*	*rDAP*
Count	5	13	23	23	13	5	13	5	15	15
Range	16.38	61	4.92	5.78	6.19	4.13	12.43	11.13	7.88	4.93
Minimum	228	209	17.42	15.73	7.3	18.23	20.84	22.2	20.62	18.06
Maximum	244.38	270	22.34	21.51	13.49	22.36	33.27	33.33	28.5	22.99
Mean	235.58	237.73	19.94	18.83	10.24	19.85	26.64	25.91	25.22	20.12
Standard Error	3.02	4.84	0.29	0.32	0.57	0.76	1.03	2.06	0.53	0.33
Standard Deviation	6.76	17.44	1.40	1.53	2.05	1.71	3.70	4.61	2.07	1.30
Sample Variance	45.64	304.13	1.95	2.34	4.21	2.91	13.72	21.21	4.27	1.68
CV	2.87	7.34	7.01	8.13	20.04	8.60	13.90	17.78	8.19	6.45

Radial Measures of Variance, Split Sexes

***Theropithecus gelada*, female only, radius**										
	rLEN1	*rLEN2*	*rPAP*	*rPML*	*rNE1*	*rNE2*	*rNE3*	*rTUB*	*rDML*	*rDAP*
Count	2	5	5	5	5	2	5	2	4	4
Range	1.22	7.26	1.4	2.67	3.08	1.77	3.21	2.66	3.25	0.93
Minimum	182.84	180.88	13.18	12.21	4.9	11.96	14.32	21.19	13.99	13.76
Maximum	184.06	188.14	14.58	14.88	7.98	13.73	17.53	23.85	17.24	14.69
Mean	183.45	184.39	13.76	13.52	6.12	12.85	15.83	22.52	15.81	14.18
Standard Error	0.61	1.38	0.24	0.50	0.70	0.89	0.62	1.33	0.70	0.22
Standard Deviation	0.86	3.08	0.55	1.11	1.56	1.25	1.39	1.88	1.41	0.44
Sample Variance	0.74	9.51	0.30	1.23	2.43	1.57	1.94	3.54	1.99	0.19
CV	0.47	1.67	3.96	8.21	25.44	9.74	8.79	8.35	8.92	3.08

***Theropithecus gelada*, male only, radius**										
	rLEN1	*rLEN2*	*rPAP*	*rPML*	*rNE1*	*rNE2*	*rNE3*	*rTUB*	*rDML*	*rDAP*
Count	2	6	7	7	6	2	6	2	6	6
Range	17.84	21.96	1.93	2.65	3.22	3.07	2.92	1.2	3.50	1.17
Minimum	191.59	195.06	14.64	14.48	5.57	11.02	17.84	25.78	18.14	15.65
Maximum	209.43	217.02	16.57	17.13	8.79	14.09	20.76	26.98	21.64	16.82
Mean	200.51	208.42	15.94	15.86	6.96	12.56	18.97	26.38	19.42	16.16
Standard Error	8.92	3.13	0.26	0.40	0.53	1.54	0.44	0.60	0.48	0.20
Standard Deviation	12.61	7.67	0.68	1.05	1.29	2.17	1.09	0.85	1.19	0.49
Sample Variance	159.13	58.87	0.47	1.11	1.66	4.71	1.19	0.72	1.41	0.24
CV	6.29	3.68	4.29	6.65	18.52	17.29	5.74	3.22	6.11	3.06

Radial Measures of Variance, Split Sexes

***Macaca fascicularis*, female only, radius**

	rLEN1	*rLEN2*	*rPAP*	*rPML*	*rNE1*	*rNE2*	*rNE3*	*rTUB*	*rDML*	*rDAP*
Count	2	2	6	6	2	2	2	2	6	6
Range	12.44	11.84	2.71	1.76	0.89	1.31	0.03	2.49	3.2	2.62
Minimum	96.21	98.89	7.34	7.27	4.2	8.36	11.29	8.83	9.62	7.49
Maximum	108.65	110.73	10.05	9.03	5.09	9.67	11.32	11.32	12.82	10.11
Mean	102.43	104.81	8.69	8.17	4.65	9.02	11.31	10.08	11.02	8.43
Standard Error	6.22	5.92	0.43	0.30	0.45	0.66	0.02	1.25	0.52	0.49
Standard Deviation	8.80	8.37	1.06	0.74	0.63	0.93	0.02	1.76	1.28	1.19
Sample Variance	77.38	70.09	1.13	0.55	0.40	0.86	0.00	3.10	1.64	1.42
CV	8.59	7.99	12.22	9.11	13.55	10.28	0.19	17.48	11.62	14.14

***Macaca fascicularis*, male only, radius**

	rLEN1	*rLEN2*	*rPAP*	*rPML*	*rNE1*	*rNE2*	*rNE3*	*rTUB*	*rDML*	*rDAP*
Count	3	3	6	6	3	3	3	3	6	6
Range	27.97	29.46	2.22	2.59	5.37	7.22	7.92	4.5	4.24	2.52
Minimum	114.34	116.91	9.58	8.65	5.68	10.82	14.49	10.95	11.75	9.09
Maximum	142.31	146.37	11.8	11.24	11.05	18.04	22.41	15.45	15.99	11.61
Mean	125.07	129.19	10.83	9.96	8.43	14.08	17.43	13.51	13.30	10.45
Standard Error	8.71	8.85	0.31	0.34	1.55	2.11	2.50	1.34	0.67	0.42
Standard Deviation	15.08	15.33	0.77	0.84	2.69	3.66	4.34	2.31	1.65	1.04
Sample Variance	227.37	235.03	0.59	0.71	7.22	13.40	18.80	5.36	2.72	1.08
CV	12.06	11.87	7.10	8.44	31.87	26.00	24.88	17.13	12.40	9.94

Radial Measures of Variance, Split Sexes

***Macaca nemestrina*, female only, radius**

	rLEN1	*rLEN2*	*rPAP*	*rPML*	*rNE1*	*rNE2*	*rNE3*	*rTUB*	*rDML*	*rDAP*
Count	2	2	4	4	2	2	2	2	4	4
Range	18.44	19.2	3.1	2.33	4.38	3.83	3.22	3.92	2.89	2.61
Minimum	133.85	138.27	9.9	9.7	4.38	10.33	14.86	12.25	13.09	10.07
Maximum	152.29	157.47	13	12.03	8.76	14.16	18.08	16.17	15.98	12.68
Mean	143.07	147.87	11.17	11.11	6.57	12.245	16.47	14.21	15.03	11.3375
Standard Error	9.22	9.60	0.66	0.51	2.19	1.92	1.61	1.96	0.66	0.53
Standard Deviation	13.04	13.58	1.32	1.02	3.10	2.71	2.28	2.77	1.31	1.07
Sample Variance	170.02	184.32	1.74	1.03	9.59	7.33	5.18	7.68	1.72	1.14
CV	9.11	9.18	11.80	9.14	47.14	22.12	13.82	19.51	8.72	9.41

***Macaca nemestrina*, male only, radius**

	rLEN1	*rLEN2*	*rPAP*	*rPML*	*rNE1*	*rNE2*	*rNE3*	*rTUB*	*rDML*	*rDAP*
Count	1	1	6	6	2	1	2	1	6	6
Range	0.00	0.00	6.36	6.30	1.03	0.00	0.00	0.00	7.15	6.05
Minimum	171.98	176.50	10.11	9.82	8.91	13.46	19.70	14.45	14.80	10.27
Maximum	171.98	176.50	16.47	16.12	9.94	13.46	19.70	14.45	21.95	16.32
Mean	171.98	176.50	14.57	13.88	9.43	13.46	19.70	14.45	19.39	14.53
Standard Error	.	.	0.92	0.90	0.52	.	.	.	1.07	0.95
Standard Deviation	.	.	2.27	2.20	0.73	.	.	.	2.61	2.32
Sample Variance	.	.	5.13	4.84	0.53	.	.	.	6.83	5.38
CV	.	.	15.54	15.85	7.73	.	.	.	13.47	15.97

Femoral Measures of Variance, Pooled Sexes

***Homo sapiens*, pooled sexes, femur**

	fLEN1	*fLEN2*	*fPML*	*fMLLESS*	*fGT*	*fAPLESS*	*fHEPD*	*fHEML*	*fHEAP*	*fPSPD*	*fPSML*	*fDML*	*fDAP*	*fCPD*	*fCML*	*fICGPD*	*fICGML*
Count	18	18	18	18	18	18	18	18	18	18	18	18	18	18	18	18	18
Range	87	96.5	24.38	17.3	10.3	12.42	13.06	14.42	12.62	7.36	16.12	22.04	12.04	11.74	20.36	9.06	11.36
Minimum	367	386	76.26	26.94	4.14	26.04	37.37	32.42	37.52	30.19	36.93	67.6	56.75	33.05	61.24	21.65	14.04
Maximum	454	482.5	100.64	44.24	14.44	38.46	50.43	46.84	50.14	37.55	53.05	89.64	68.79	44.79	81.6	30.71	25.4
Mean	415.28	436.19	87.61	35.36	8.67	30.47	43.99	37.98	43.72	33.17	41.99	76.36	61.09	38.61	70.62	26.50	20.25
Standard Error	6.25	6.25	1.78	0.94	0.76	0.73	0.84	0.91	0.88	0.51	1.07	1.39	0.89	0.86	1.45	0.66	0.65
Standard Deviation	26.53	26.52	7.57	3.98	3.21	3.09	3.54	3.88	3.74	2.18	4.53	5.90	3.78	3.65	6.14	2.79	2.75
Sample Variance	703.68	703.47	57.35	15.84	10.32	9.55	12.56	15.03	14.00	4.76	20.56	34.78	14.31	13.29	37.74	7.77	7.56
CV	6.39	6.08	8.64	11.26	37.08	10.14	8.06	10.21	8.56	6.58	10.80	7.72	6.19	9.44	8.70	10.52	13.57

***Pan troglodytes*, pooled sexes, femur**

	fLEN1	*fLEN2*	*fPML*	*fMLLESS*	*fGT*	*fAPLESS*	*fHEPD*	*fHEML*	*fHEAP*	*fPSPD*	*fPSML*	*fDML*	*fDAP*	*fCPD*	*fCML*	*fICGPD*	*fICGML*
Count	13	13	15	15	15	15	15	15	15	14	14	14	14	14	14	14	14
Range	64	61.5	19.11	14.65	8.36	15.7	8.87	14.13	8.85	10.58	9.01	13.54	27.25	7.21	32.82	9.43	7.29
Minimum	251.5	253	53.05	24.27	9.26	22.24	28.26	21.48	28.32	22.21	26.83	53.87	33.88	25.41	28.55	13.39	13.77
Maximum	315.5	314.5	72.16	38.92	17.62	37.94	37.13	35.61	37.17	32.79	35.84	67.41	61.13	32.62	61.37	22.82	21.06
Mean	285.58	289.04	63.77	32.90	13.58	29.19	32.57	29.02	32.70	27.28	32.09	59.70	41.01	29.45	53.47	18.39	17.17
Standard Error	4.76	4.71	1.54	1.18	0.64	0.96	0.67	0.98	0.63	0.75	0.65	1.12	1.80	0.56	2.14	0.69	0.52
Standard Deviation	17.17	17.00	5.95	4.55	2.48	3.73	2.58	3.78	2.46	2.81	2.42	4.19	6.73	2.11	8.01	2.59	1.95
Sample Variance	294.70	288.98	35.45	20.73	6.14	13.92	6.68	14.26	6.04	7.91	5.85	17.57	45.23	4.44	64.13	6.70	3.81
CV	6.01	5.88	9.34	13.84	18.24	12.78	7.94	13.01	7.52	10.31	7.54	7.02	16.40	7.16	14.98	14.08	11.36

Femoral Measures of Variance, Pooled Sexes

***Papio hamadryas*, pooled sexes, femur**

	fLEN1	*fLEN2*	*fPML*	*fMLLESS*	*fGT*	*fAPLESS*	*fHEPD*	*fHEML*	*fHEAP*	*fPSPD*	*fPSML*	*fDML*	*fDAP*	*fCPD*	*fCML*	*fICGPD*	*fICGML*
Count	19	19	19	7	17	7	19	19	19	19	7	19	19	19	7	7	7
Range	85.95	83.08	16.51	5.59	8.2	3.37	6.48	7.21	6.18	9.14	4.95	14.21	10.36	7.76	7.55	5.06	1.86
Minimum	215.29	208.06	41.09	20.88	11.6	18.86	19.72	18.37	19.76	15.94	19.95	32.01	26.52	17.46	33.03	11.39	10.67
Maximum	301.24	291.14	57.6	26.47	19.8	22.23	26.2	25.58	25.94	25.08	24.9	46.22	36.88	25.22	40.58	16.45	12.53
Mean	254.89	246.76	49.30	23.24	15.26	20.33	23.36	21.45	23.71	20.28	22.87	39.28	32.39	22.08	38.06	14.11	11.58
Standard Error	5.82	5.49	1.21	0.82	0.63	0.43	0.48	0.55	0.47	0.68	0.73	1.01	0.83	0.57	1.07	0.62	0.27
Standard Deviation	25.37	23.93	5.26	2.18	2.60	1.14	2.10	2.39	2.07	2.99	1.94	4.39	3.60	2.47	2.82	1.63	0.71
Sample Variance	643.74	572.70	27.70	4.74	6.78	1.29	4.43	5.73	4.28	8.91	3.77	19.28	12.96	6.12	7.95	2.66	0.50
CV	9.95	9.70	10.68	9.37	17.05	5.59	9.01	11.16	8.72	14.72	8.49	11.18	11.11	11.21	7.41	11.57	6.10

***Theropithecus gelada*, pooled sexes, femur**

	fLEN1	*fLEN2*	*fPML*	*fMLLESS*	*fGT*	*fAPLESS*	*fHEPD*	*fHEML*	*fHEAP*	*fPSPD*	*fPSML*	*fDML*	*fDAP*	*fCPD*	*fCML*	*fICGPD*	*fICGML*
Count	10	10	10	4	9	4	10	10	10	9	4	9	9	9	4	4	4
Range	40.05	39.41	7.24	4.01	5.52	5.86	4.8	5.75	4.01	6.27	6.11	6.46	6.22	4.51	6.53	2.88	2.13
Minimum	179.28	173.79	35.56	15.18	9.23	18.19	17.12	14.98	17.78	15.02	18.03	30.62	24.02	15.78	29.22	10.88	10.03
Maximum	219.33	213.2	42.8	19.19	14.75	24.05	21.92	20.73	21.79	21.29	24.14	37.08	30.24	20.29	35.75	13.76	12.16
Mean	197.40	191.61	39.21	16.62	12.04	20.58	19.49	17.76	19.69	17.23	20.45	33.97	27.08	18.07	32.15	12.02	10.97
Standard Error	5.09	4.49	0.86	0.89	0.68	1.37	0.50	0.61	0.46	0.72	1.33	0.90	0.90	0.52	1.63	0.65	0.44
Standard Deviation	16.09	14.18	2.72	1.78	2.05	2.75	1.58	1.93	1.45	2.16	2.66	2.69	2.71	1.56	3.26	1.29	0.88
Sample Variance	258.83	201.21	7.41	3.18	4.19	7.54	2.51	3.71	2.12	4.68	7.05	7.24	7.36	2.42	10.62	1.68	0.78
CV	8.15	7.40	6.94	10.73	17.00	13.34	8.12	10.84	7.39	12.55	12.99	7.92	10.01	8.61	10.13	10.77	8.05

Femoral Measures of Variance, Pooled Sexes

***Macaca fascicularis*, pooled sexes, femur**

	fLEN1	*fLEN2*	*fPML*	*fMLLESS*	*fGT*	*fAPLESS*	*fHEPD*	*fHEML*	*fHEAP*	*fPSPD*	*fPSML*	*fDML*	*fDAP*	*fCPD*	*fCML*	*fICGPD*	*fICGML*
Count	10	10	11	5	11	5	11	11	11	10	5	10	10	10	5	5	5
Range	55.79	50.48	10.91	9.98	3.36	3.94	4.15	4.97	4	7.12	5.1	7.41	8.47	3.41	7.86	2.35	2.14
Minimum	113.27	112.97	19.77	7.98	5.11	8.75	9.85	8.5	10.28	8.83	7.85	16.79	13.24	9.95	16.03	6.05	4.9
Maximum	169.06	163.45	30.68	17.96	8.47	12.69	14	13.47	14.28	15.95	12.95	24.2	21.71	13.36	23.89	8.4	7.04
Mean	133.66	130.99	23.92	13.52	6.49	10.57	11.64	11.46	11.95	11.17	9.90	19.72	16.05	11.31	19.87	7.30	5.94
Standard Error	4.96	4.55	1.04	1.68	0.31	0.75	0.38	0.52	0.42	0.81	0.88	0.78	0.86	0.40	1.67	0.41	0.39
Standard Deviation	15.69	14.38	3.44	3.75	1.04	1.68	1.27	1.72	1.40	2.56	1.96	2.47	2.71	1.26	3.74	0.93	0.88
Sample Variance	246.30	206.66	11.82	14.07	1.07	2.83	1.60	2.95	1.97	6.55	3.85	6.08	7.37	1.60	14.01	0.86	0.77
CV	11.74	10.98	14.37	27.74	15.97	15.92	10.87	14.98	11.73	22.91	19.81	12.50	16.92	11.17	18.83	12.67	14.73

***Macaca nemestrina*, pooled sexes, femur**

	fLEN1	*fLEN2*	*fPML*	*fMLLESS*	*fGT*	*fAPLESS*	*fHEPD*	*fHEML*	*fHEAP*	*fPSPD*	*fPSML*	*fDML*	*fDAP*	*fCPD*	*fCML*	*fICGPD*	*fICGML*
Count	4	4	4	3	4	3	4	4	4	4	3	4	4	4	3	3	3
Range	64.44	60.34	10.33	8.39	4.61	5.72	4.82	4.83	5.68	5.63	8.25	7.62	6.89	3.8	9.14	5.8	2.34
Minimum	158.56	158.66	25.96	14.03	5.97	10.35	13.17	11.52	12.68	13.04	11.79	22.44	18.9	12.93	21.27	7.79	7.38
Maximum	223	219	36.29	22.42	10.58	16.07	17.99	16.35	18.36	18.67	20.04	30.06	25.79	16.73	30.41	13.59	9.72
Mean	187.24	185.13	32.16	18.34	7.89	13.68	15.99	13.76	16.21	15.55	14.71	27.09	22.76	15.06	25.49	10.24	8.51
Standard Error	14.31	13.41	2.31	2.42	1.14	1.72	1.03	1.00	1.26	1.42	2.67	1.81	1.65	0.79	2.66	1.73	0.68
Standard Deviation	28.62	26.83	4.63	4.20	2.29	2.97	2.05	2.00	2.51	2.84	4.62	3.61	3.31	1.58	4.61	3.00	1.17
Sample Variance	818.92	719.85	21.43	17.64	5.24	8.84	4.20	4.00	6.32	8.06	21.37	13.05	10.94	2.48	21.25	9.01	1.37
CV	15.28	14.49	14.39	22.90	29.00	21.74	12.82	14.53	15.51	18.26	31.43	13.34	14.53	10.46	18.09	29.30	13.76

Femoral Measures of Variance, Split Sexes

***Homo sapiens*, female only, femur**																	
	fLEN1	*fLEN2*	*fPML*	*fMLLESS*	*fGT*	*fAPLESS*	*fHEPD*	*fHEML*	*fHEAP*	*fPSPD*	*fPSML*	*fDML*	*fDAP*	*fCPD*	*fCML*	*fICGPD*	*fICGML*
Count	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Range	71	64	19.27	13.93	9.06	6.88	9.19	6.56	8.6	5.33	6.26	11.19	4.68	11.11	9.02	6.69	8.11
Minimum	367	386	76.26	26.94	5.18	26.04	37.37	32.42	37.52	30.19	36.93	67.6	56.75	33.68	61.24	21.86	14.04
Maximum	438	450	95.53	40.87	14.24	32.92	46.56	38.98	46.12	35.52	43.19	78.79	61.43	44.79	70.26	28.55	22.15
Mean	400.28	421.50	83.81	33.70	10.02	28.53	41.56	35.67	41.19	32.55	39.50	72.50	58.97	38.55	66.22	25.23	19.48
Standard Error	6.60	6.69	2.04	1.31	0.91	0.72	0.90	0.81	0.85	0.68	0.60	1.31	0.57	1.19	1.13	0.80	0.98
Standard Deviation	19.79	20.07	6.11	3.94	2.72	2.15	2.70	2.43	2.55	2.03	1.81	3.93	1.70	3.57	3.39	2.39	2.94
Sample Variance	391.63	402.69	37.30	15.52	7.40	4.64	7.31	5.91	6.51	4.13	3.27	15.41	2.88	12.72	11.53	5.72	8.63
CV	4.94	4.76	7.29	11.69	27.15	7.55	6.50	6.82	6.19	6.25	4.58	5.41	2.88	9.25	5.13	9.48	15.08

***Homo sapiens*, male only, femur**																	
	fLEN1	*fLEN2*	*fPML*	*fMLLESS*	*fGT*	*fAPLESS*	*fHEPD*	*fHEML*	*fHEAP*	*fPSPD*	*fPSML*	*fDML*	*fDAP*	*fCPD*	*fCML*	*fICGPD*	*fICGML*
Count	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Range	74	75.5	19.96	10.95	10.3	10.2	7.34	11.78	7.84	7.06	15.76	14.31	11.35	11.66	13.91	9.06	8.57
Minimum	380	407	80.68	33.29	4.14	28.26	43.09	35.06	42.3	30.49	37.29	75.33	57.44	33.05	67.69	21.65	16.83
Maximum	454	482.5	100.64	44.24	14.44	38.46	50.43	46.84	50.14	37.55	53.05	89.64	68.79	44.71	81.6	30.71	25.4
Mean	430.28	450.89	91.41	37.01	7.31	32.41	46.42	40.30	46.24	33.80	44.47	80.21	63.21	38.67	75.02	27.77	21.03
Standard Error	8.15	8.21	2.40	1.15	1.08	0.89	0.82	1.25	1.00	0.75	1.72	1.67	1.39	1.31	1.67	0.89	0.82
Standard Deviation	24.44	24.62	7.21	3.46	3.23	2.68	2.47	3.74	2.99	2.26	5.15	5.01	4.17	3.94	5.01	2.68	2.47
Sample Variance	597.44	606.36	52.05	11.97	10.41	7.18	6.10	13.97	8.91	5.10	26.57	25.07	17.42	15.51	25.06	7.16	6.09
CV	5.68	5.46	7.89	9.35	44.14	8.27	5.32	9.27	6.46	6.68	11.59	6.24	6.60	10.18	6.67	9.64	11.74

Femoral Measures of Variance, Split Sexes

***Pan troglodytes*, female only, femur**

	fLEN1	*fLEN2*	*fPML*	*fMLLESS*	*fGT*	*fAPLESS*	*fHEPD*	*fHEML*	*fHEAP*	*fPSPD*	*fPSML*	*fDML*	*fDAP*	*fCPD*	*fCML*	*fICGPD*	*fICGML*
Count	8	8	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Range	51	57	16.68	12.9	7.25	15.7	6.78	11.16	6.68	6.46	8.31	8.74	27.25	6.2	32.82	7.14	5.19
Minimum	251.5	253	53.05	24.27	9.26	22.24	28.26	21.48	28.32	22.21	26.83	53.87	33.88	25.41	28.55	15.68	13.79
Maximum	302.5	310	69.73	37.17	16.51	37.94	35.04	32.64	35	28.67	35.14	62.61	61.13	31.61	61.37	22.82	18.98
Mean	278.19	282.50	60.82	30.77	12.87	28.66	31.30	27.86	31.56	26.09	31.59	58.37	40.11	28.55	51.58	18.61	16.80
Standard Error	5.58	6.09	1.77	1.37	0.80	1.56	0.69	1.09	0.68	0.82	0.81	1.09	2.77	0.61	3.08	0.86	0.51
Standard Deviation	15.78	17.23	5.32	4.12	2.41	4.67	2.06	3.27	2.04	2.47	2.43	3.28	8.32	1.84	9.25	2.57	1.54
Sample Variance	248.92	296.71	28.31	17.01	5.80	21.79	4.26	10.70	4.18	6.11	5.90	10.77	69.19	3.40	85.62	6.60	2.36
CV	5.67	6.10	8.75	13.40	18.70	16.28	6.60	11.74	6.48	9.47	7.69	5.62	20.74	6.46	17.94	13.80	9.15

***Pan troglodytes*, male only, femur**

	fLEN1	*fLEN2*	*fPML*	*fMLLESS*	*fGT*	*fAPLESS*	*fHEPD*	*fHEML*	*fHEAP*	*fPSPD*	*fPSML*	*fDML*	*fDAP*	*fCPD*	*fCML*	*fICGPD*	*fICGML*
Count	5	5	6	6	6	6	6	6	6	5	5	5	5	5	5	5	5
Range	28	24.5	9.29	8.86	6.68	4.63	5.13	11.99	5.32	5.99	6.12	10.77	5.04	4.12	9.27	7.56	7.29
Minimum	287.5	290	62.87	30.06	10.94	27.59	32	23.62	31.85	26.8	29.72	56.64	39.44	28.5	51.86	13.39	13.77
Maximum	315.5	314.5	72.16	38.92	17.62	32.22	37.13	35.61	37.17	32.79	35.84	67.41	44.48	32.62	61.13	20.95	21.06
Mean	297.40	299.50	68.20	36.10	14.65	29.97	34.48	30.77	34.41	29.40	32.99	62.09	42.62	31.07	56.88	17.98	17.83
Standard Error	5.74	5.01	1.57	1.32	0.97	0.69	0.88	1.67	0.86	0.97	1.06	2.21	0.85	0.71	1.71	1.29	1.17
Standard Deviation	12.83	11.20	3.84	3.23	2.38	1.70	2.15	4.09	2.10	2.17	2.37	4.94	1.89	1.59	3.82	2.87	2.61
Sample Variance	164.55	125.38	14.77	10.41	5.66	2.87	4.62	16.69	4.39	4.72	5.62	24.41	3.58	2.54	14.57	8.26	6.80
CV	4.31	3.74	5.64	8.94	16.24	5.66	6.24	13.27	6.09	7.39	7.19	7.96	4.44	5.13	6.71	15.98	14.62

Femoral Measures of Variance, Split Sexes

***Papio hamadryas*, female only, femur**

	fLEN1	*fLEN2*	*fPML*	*fMLLESS*	*fGT*	*fAPLESS*	*fHEPD*	*fHEML*	*fHEAP*	*fPSPD*	*fPSML*	*fDML*	*fDAP*	*fCPD*	*fCML*	*fICGPD*	*fICGML*
Count	6	6	6	2	4	2	6	6	6	6	2	6	6	6	2	2	2
Range	38.09	38.02	6.52	0.33	1.77	0.9	3.37	2.4	3.35	4.85	0.49	4.75	3.32	2.73	2.14	3.1	0.82
Minimum	215.29	208.06	41.09	20.88	11.6	18.86	19.72	18.37	19.76	16.11	19.95	32.01	26.52	17.46	33.03	11.39	10.67
Maximum	253.38	246.08	47.61	21.21	13.37	19.76	23.09	20.77	23.11	20.96	20.44	36.76	29.84	20.19	35.17	14.49	11.49
Mean	227.41	221.26	43.30	21.05	12.09	19.31	20.98	19.43	21.24	17.93	20.20	34.25	28.13	18.98	34.10	12.94	11.08
Standard Error	5.83	5.59	1.04	0.17	0.43	0.45	0.55	0.32	0.49	0.94	0.25	0.66	0.57	0.38	1.07	1.55	0.41
Standard Deviation	14.29	13.70	2.54	0.23	0.85	0.64	1.34	0.78	1.21	2.30	0.35	1.61	1.39	0.94	1.51	2.19	0.58
Sample Variance	204.10	187.75	6.44	0.05	0.73	0.41	1.79	0.61	1.47	5.28	0.12	2.60	1.93	0.88	2.29	4.80	0.34
CV	6.28	6.19	5.86	1.11	7.05	3.30	6.37	4.01	5.71	12.81	1.72	4.71	4.93	4.94	4.44	16.94	5.23

***Papio hamadryas*, male only, femur**

	fLEN1	*fLEN2*	*fPML*	*fMLLESS*	*fGT*	*fAPLESS*	*fHEPD*	*fHEML*	*fHEAP*	*fPSPD*	*fPSML*	*fDML*	*fDAP*	*fCPD*	*fCML*	*fICGPD*	*fICGML*
Count	13	13	13	5	13	5	13	13	13	13	5	13	13	13	5	5	5
Range	63.05	58.49	12.51	5	6.5	2.35	4.32	6.16	4.04	9.14	1.89	12.68	8.55	4.23	1.47	3.78	1.82
Minimum	238.19	232.65	45.09	21.47	13.3	19.88	21.88	19.42	21.9	15.94	23.01	33.54	28.33	20.99	39.11	12.67	10.71
Maximum	301.24	291.14	57.6	26.47	19.8	22.23	26.2	25.58	25.94	25.08	24.9	46.22	36.88	25.22	40.58	16.45	12.53
Mean	267.58	258.52	52.07	24.12	16.24	20.74	24.46	22.39	24.84	21.37	23.94	41.61	34.36	23.51	39.65	14.57	11.78
Standard Error	5.03	4.85	0.98	0.86	0.59	0.47	0.37	0.64	0.32	0.74	0.35	0.85	0.64	0.37	0.27	0.61	0.31
Standard Deviation	18.13	17.49	3.54	1.93	2.11	1.05	1.33	2.32	1.17	2.67	0.78	3.05	2.31	1.33	0.61	1.36	0.70
Sample Variance	328.67	305.83	12.55	3.72	4.47	1.11	1.77	5.36	1.37	7.13	0.61	9.31	5.35	1.77	0.37	1.84	0.49
CV	6.78	6.76	6.80	8.00	13.02	5.09	5.44	10.34	4.71	12.50	3.25	7.33	6.73	5.66	1.53	9.31	5.93

Femoral Measures of Variance, Split Sexes

***Theropithecus gelada*, female only, femur**

	fLEN1	*fLEN2*	*fPML*	*fMLLESS*	*fGT*	*fAPLESS*	*fHEPD*	*fHEML*	*fHEAP*	*fPSPD*	*fPSML*	*fDML*	*fDAP*	*fCPD*	*fCML*	*fICGPD*	*fICGML*
Count	5	5	5	2	4	2	5	5	5	4	2	4	4	4	2	2	2
Range	8.56	10.91	3.89	0.54	1.67	3.32	1.95	3.35	1.8	2.22	1.12	0.98	0.57	2.18	0.35	0.33	0.84
Minimum	179.28	173.79	35.56	15.18	9.23	18.19	17.12	14.98	17.78	15.02	18.03	30.62	24.02	15.78	29.22	10.88	10.03
Maximum	187.84	184.7	39.45	15.72	10.9	21.51	19.07	18.33	19.58	17.24	19.15	31.6	24.59	17.96	29.57	11.21	10.87
Mean	182.80	179.05	36.98	15.45	10.08	19.85	18.19	16.55	18.53	15.66	18.59	31.18	24.29	16.85	29.40	11.05	10.45
Standard Error	1.89	2.10	0.75	0.27	0.36	1.66	0.38	0.64	0.37	0.53	0.56	0.21	0.14	0.50	0.18	0.17	0.42
Standard Deviation	4.23	4.69	1.68	0.38	0.71	2.35	0.84	1.43	0.83	1.06	0.79	0.41	0.28	1.00	0.25	0.23	0.59
Sample Variance	17.85	22.00	2.83	0.15	0.51	5.51	0.71	2.04	0.68	1.13	0.63	0.17	0.08	0.99	0.06	0.05	0.35
CV	2.31	2.62	4.55	2.47	7.05	11.83	4.64	8.63	4.45	6.78	4.26	1.33	1.15	5.91	0.84	2.11	5.68

***Theropithecus gelada*, male only, femur**

	fLEN1	*fLEN2*	*fPML*	*fMLLESS*	*fGT*	*fAPLESS*	*fHEPD*	*fHEML*	*fHEAP*	*fPSPD*	*fPSML*	*fDML*	*fDAP*	*fCPD*	*fCML*	*fICGPD*	*fICGML*
Count	5	5	5	2	5	2	5	5	5	5	2	5	5	5	2	2	2
Range	14.37	15.02	2.64	2.81	2.47	5.47	2.19	3.66	1.82	4.93	3.67	1.34	1.92	3.11	1.69	1.53	1.36
Minimum	204.96	198.18	40.16	16.38	12.28	18.58	19.73	17.07	19.97	16.36	20.47	35.74	28.32	17.18	34.06	12.23	10.8
Maximum	219.33	213.2	42.8	19.19	14.75	24.05	21.92	20.73	21.79	21.29	24.14	37.08	30.24	20.29	35.75	13.76	12.16
Mean	211.99	204.17	41.45	17.79	13.61	21.32	20.80	18.97	20.85	18.48	22.31	36.20	29.32	19.04	34.91	13.00	11.48
Standard Error	2.53	2.69	0.52	1.41	0.46	2.74	0.37	0.73	0.38	0.90	1.84	0.27	0.35	0.54	0.84	0.77	0.68
Standard Deviation	5.65	6.01	1.16	1.99	1.04	3.87	0.82	1.62	0.84	2.02	2.60	0.60	0.79	1.20	1.20	1.08	0.96
Sample Variance	31.90	36.15	1.34	3.95	1.08	14.96	0.68	2.64	0.71	4.09	6.73	0.35	0.62	1.43	1.43	1.17	0.92
CV	2.66	2.94	2.79	11.17	7.63	18.15	3.96	8.56	4.04	10.95	11.63	1.65	2.69	6.28	3.42	8.33	8.38

Femoral Measures of Variance, Split Sexes

***Macaca fascicularis*, female only, femur**

	fLEN1	*fLEN2*	*fPML*	*fMLLESS*	*fGT*	*fAPLESS*	*fHEPD*	*fHEML*	*fHEAP*	*fPSPD*	*fPSML*	*fDML*	*fDAP*	*fCPD*	*fCML*	*fICGPD*	*fICGML*
Count	6	6	6	2	6	2	6	6	6	6	2	6	6	6	2	2	2
Range	16.58	14.56	4.05	4.16	1.29	0.2	1.79	4.36	1.44	1.87	1.17	2.56	2.73	2.06	0.87	1.17	1.08
Minimum	113.27	112.97	19.77	7.98	5.11	8.75	9.85	8.5	10.28	8.83	7.85	16.79	13.24	9.95	16.03	6.05	4.9
Maximum	129.85	127.53	23.82	12.14	6.4	8.95	11.64	12.86	11.72	10.7	9.02	19.35	15.97	12.01	16.9	7.22	5.98
Mean	124.76	122.82	21.42	10.06	5.77	8.85	10.75	10.85	10.88	9.78	8.44	18.21	14.43	10.63	16.47	6.64	5.44
Standard Error	2.77	2.41	0.60	2.08	0.24	0.10	0.28	0.76	0.24	0.30	0.59	0.38	0.38	0.30	0.43	0.59	0.54
Standard Deviation	6.78	5.91	1.46	2.94	0.60	0.14	0.69	1.86	0.58	0.74	0.83	0.93	0.94	0.74	0.62	0.83	0.76
Sample Variance	45.92	34.92	2.14	8.65	0.36	0.02	0.48	3.47	0.34	0.55	0.68	0.86	0.88	0.55	0.38	0.68	0.58
CV	5.43	4.81	6.83	29.24	10.34	1.60	6.45	17.17	5.32	7.59	9.81	5.10	6.49	6.97	3.74	12.47	14.04

***Macaca fascicularis*, male only, femur**

	fLEN1	*fLEN2*	*fPML*	*fMLLESS*	*fGT*	*fAPLESS*	*fHEPD*	*fHEML*	*fHEAP*	*fPSPD*	*fPSML*	*fDML*	*fDAP*	*fCPD*	*fCML*	*fICGPD*	*fICGML*
Count	4	4	5	3	5	3	5	5	5	4	3	4	4	4	3	3	3
Range	38.71	35.79	5.91	3.85	1.77	1.52	2.17	3.21	1.83	6.24	3.85	4.2	6.41	2.52	5.1	1.53	1.76
Minimum	130.35	127.66	24.77	14.11	6.7	11.17	11.83	10.26	12.45	9.71	9.1	20	15.3	10.84	18.79	6.87	5.28
Maximum	169.06	163.45	30.68	17.96	8.47	12.69	14	13.47	14.28	15.95	12.95	24.2	21.71	13.36	23.89	8.4	7.04
Mean	147.01	143.24	26.92	15.83	7.36	11.72	12.72	12.20	13.24	13.26	10.88	22.00	18.47	12.34	22.15	7.75	6.28
Standard Error	8.16	7.55	1.12	1.13	0.32	0.49	0.39	0.60	0.38	1.50	1.12	1.15	1.38	0.62	1.68	0.46	0.52
Standard Deviation	16.32	15.11	2.50	1.96	0.71	0.84	0.87	1.34	0.85	3.00	1.94	2.30	2.76	1.24	2.91	0.79	0.90
Sample Variance	266.28	228.17	6.27	3.83	0.51	0.71	0.75	1.78	0.72	9.03	3.77	5.28	7.63	1.53	8.45	0.62	0.82
CV	11.10	10.55	9.30	12.37	9.70	7.17	6.81	10.94	6.42	22.66	17.84	10.45	14.96	10.03	13.13	10.20	14.40

Femoral Measures of Variance, Split Sexes

***Macaca nemestrina*, female only, femur**

	fLEN1	*fLEN2*	*fPML*	*fMLLESS*	*fGT*	*fAPLESS*	*fHEPD*	*fHEML*	*fHEAP*	*fPSPD*	*fPSML*	*fDML*	*fDAP*	*fCPD*	*fCML*	*fICGPD*	*fICGML*
Count	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
Range	12.28	10.84	5.42	4.55	0.04	4.27	2.82	1.74	3.55	0.21	0.51	3.58	2.22	2.27	3.52	1.56	1.06
Minimum	158.56	158.66	25.96	14.03	5.97	10.35	13.17	11.52	12.68	13.04	11.79	22.44	18.9	12.93	21.27	7.79	7.38
Maximum	170.84	169.5	31.38	18.58	6.01	14.62	15.99	13.26	16.23	13.25	12.3	26.02	21.12	15.2	24.79	9.35	8.44
Mean	164.70	164.08	28.67	16.31	5.99	12.49	14.58	12.39	14.46	13.15	12.05	24.23	20.01	14.07	23.03	8.57	7.91
Standard Error	6.14	5.42	2.71	2.27	0.02	2.14	1.41	0.87	1.78	0.11	0.26	1.79	1.11	1.14	1.76	0.78	0.53
Standard Deviation	8.68	7.67	3.83	3.22	0.03	3.02	1.99	1.23	2.51	0.15	0.36	2.53	1.57	1.61	2.49	1.10	0.75
Sample Variance	75.40	58.75	14.69	10.35	0.00	9.12	3.98	1.51	6.30	0.02	0.13	6.41	2.46	2.58	6.20	1.22	0.56
CV	5.27	4.67	13.37	19.73	0.47	24.18	13.68	9.93	17.37	1.13	2.99	10.45	7.84	11.41	10.81	12.87	9.48

***Macaca nemestrina*, male only, femur**

	fLEN1	*fLEN2*	*fPML*	*fMLLESS*	*fGT*	*fAPLESS*	*fHEPD*	*fHEML*	*fHEAP*	*fPSPD*	*fPSML*	*fDML*	*fDAP*	*fCPD*	*fCML*	*fICGPD*	*fICGML*
Count	2	2	2	1	2	1	2	2	2	2	1	2	2	2	1	1	1
Range	26.46	25.66	1.27	0	1.57	0	1.19	2.44	0.78	1.43	0	0.22	0.57	1.35	0	0	0
Minimum	196.54	193.34	35.02	22.42	9.01	16.07	16.8	13.91	17.58	17.24	20.04	29.84	25.22	15.38	30.41	13.59	9.72
Maximum	223	219	36.29	22.42	10.58	16.07	17.99	16.35	18.36	18.67	20.04	30.06	25.79	16.73	30.41	13.59	9.72
Mean	209.77	206.17	35.66	22.42	9.80	16.07	17.40	15.13	17.97	17.96	20.04	29.95	25.51	16.06	30.41	13.59	9.72
Standard Error	13.23	12.83	0.63	.	0.79	.	0.59	1.22	0.39	0.72	.	0.11	0.29	0.68	.	.	.
Standard Deviation	18.71	18.14	0.90	.	1.11	.	0.84	1.73	0.55	1.01	.	0.16	0.40	0.95	.	.	.
Sample Variance	350.07	329.22	0.81	.	1.23	.	0.71	2.98	0.30	1.02	.	0.02	0.16	0.91	.	.	.
CV	8.92	8.80	2.52	.	11.33	.	4.84	11.40	3.07	5.63	.	0.52	1.58	5.95	.	.	.

Tibial Measures of Variance, Pooled Sexes

***Homo sapiens*, pooled sexes, tibia**

	tLEN1	*tLEN2*	*tPML*	*tPAP*	*tLFAP*	*tMFAP*	*tLFML*	*tMFML*	*tDAP*	*tDML*	*tMMPD*	*tDASML*
Count	17	17	17	17	17	17	17	17	17	17	17	17
Range	87	86.5	16.12	13.95	13.95	11.57	8.34	10.18	10.53	10.15	8.92	11.58
Minimum	314.5	307	64.02	43.33	30.06	38.35	23.79	23.47	31.86	38.64	8.73	22.82
Maximum	401.5	393.5	80.14	57.28	44.01	49.92	32.13	33.65	42.39	48.79	17.65	34.4
Mean	362.41	354.03	71.98	49.47	37.08	43.34	27.57	27.63	37.48	44.66	13.35	26.33
Standard Error	6.43	6.68	1.21	0.98	0.78	1.04	0.63	0.68	0.77	0.88	0.53	0.70
Standard Deviation	26.50	27.55	5.01	4.04	3.21	4.28	2.60	2.79	3.16	3.61	2.17	2.87
Sample Variance	702.44	758.80	25.07	16.32	10.33	18.30	6.79	7.80	10.01	13.02	4.71	8.25
CV	7.31	7.78	6.96	8.17	8.67	9.87	9.45	10.11	8.44	8.08	16.25	10.91

***Pan troglodytes*, pooled sexes, tibia**

	tLEN1	*tLEN2*	*tPML*	*tPAP*	*tLFAP*	*tMFAP*	*tLFML*	*tMFML*	*tDAP*	*tDML*	*tMMPD*	*tDASML*
Count	15	14	15	15	15	15	15	15	15	15	15	15
Range	62	61	13.1	10.31	9.38	12.66	5.42	6.63	8.45	13.15	5.89	12.12
Minimum	213	203.5	49.25	32.24	24.07	25.78	22.01	21.05	22.97	29.12	11.44	17.78
Maximum	275	264.5	62.35	42.55	33.45	38.44	27.43	27.68	31.42	42.27	17.33	29.9
Mean	245.90	237.00	56.82	37.28	29.59	32.04	24.06	24.11	25.94	35.37	13.58	24.15
Standard Error	4.61	4.53	0.99	0.70	0.74	0.99	0.43	0.50	0.56	0.88	0.43	0.91
Standard Deviation	17.86	16.95	3.84	2.70	2.86	3.82	1.65	1.94	2.18	3.42	1.66	3.53
Sample Variance	319.04	287.35	14.74	7.29	8.16	14.62	2.72	3.78	4.74	11.72	2.77	12.47
CV	7.26	7.15	6.76	7.24	9.65	11.94	6.85	8.06	8.39	9.68	12.26	14.63

Tibial Measures of Variance, Pooled Sexes

***Papio hamadryas*, pooled sexes, tibia**

	tLEN1	*tLEN2*	*tPML*	*tPAP*	*tLFAP*	*tMFAP*	*tLFML*	*tMFML*	*tDAP*	*tDML*	*tMMPD*	*tDASML*
Count	20	20	35	35	35	35	23	23	20	35	23	23
Range	80.39	77.87	15.08	14.9	10.68	12.89	7.45	6.76	6.61	11.36	6.7	6.82
Minimum	184.61	175.13	31.46	23.51	17.65	18.67	13.98	12.47	18.43	18.88	5.73	12.57
Maximum	265	253	46.54	38.41	28.33	31.56	21.43	19.23	25.04	30.24	12.43	19.39
Mean	221.90	212.68	39.80	30.30	23.06	25.34	17.51	16.48	21.38	25.22	8.52	16.07
Standard Error	4.91	4.91	0.72	0.63	0.48	0.53	0.40	0.38	0.48	0.50	0.38	0.39
Standard Deviation	21.96	21.97	4.26	3.75	2.83	3.13	1.94	1.80	2.14	2.93	1.84	1.86
Sample Variance	482.21	482.49	18.17	14.09	8.03	9.80	3.77	3.25	4.57	8.58	3.38	3.45
CV	9.90	10.33	10.71	12.39	12.29	12.35	11.08	10.94	9.99	11.62	21.59	11.55

***Theropithecus gelada*, pooled sexes, tibia**

	tLEN1	*tLEN2*	*tPML*	*tPAP*	*tLFAP*	*tMFAP*	*tLFML*	*tMFML*	*tDAP*	*tDML*	*tMMPD*	*tDASML*
Count	11	11	12	12	12	12	10	10	11	12	10	10
Range	41.67	43.89	7.16	7.48	4.24	8.29	4.65	2.88	3.43	5.5	4.69	4.55
Minimum	176.33	164.11	31.67	22.37	17.92	18.15	12.67	13.33	16.07	18.92	5.74	12.46
Maximum	218	208	38.83	29.85	22.16	26.44	17.32	16.21	19.5	24.42	10.43	17.01
Mean	195.48	185.76	35.32	26.22	19.54	21.45	14.57	14.41	17.73	22.13	7.60	14.75
Standard Error	4.75	4.62	0.82	0.73	0.39	0.66	0.58	0.30	0.36	0.54	0.54	0.52
Standard Deviation	15.74	15.32	2.86	2.54	1.34	2.29	1.84	0.96	1.18	1.85	1.70	1.66
Sample Variance	247.88	234.78	8.16	6.44	1.79	5.26	3.38	0.92	1.40	3.44	2.88	2.75
CV	8.05	8.25	8.09	9.68	6.84	10.69	12.61	6.64	6.67	8.38	22.31	11.24

Tibial Measures of Variance, Pooled Sexes

***Macaca fascicularis*, pooled sexes, tibia**

	tLEN1	*tLEN2*	*tPML*	*tPAP*	*tLFAP*	*tMFAP*	*tLFML*	*tMFML*	*tDAP*	*tDML*	*tMMPD*	*tDASML*
Count	5	5	12	12	12	12	12	12	5	12	12	12
Range	52.04	50.6	8.53	6.68	5.9	6.68	5.33	4.9	4.94	5.45	2.96	4.7
Minimum	109.21	105.1	16.83	12.02	10.82	9.77	6.17	6.6	8.56	10.57	3.36	6.28
Maximum	161.25	155.7	25.36	18.7	16.72	16.45	11.5	11.5	13.5	16.02	6.32	10.98
Mean	129.17	124.60	20.95	15.44	13.05	13.21	9.48	8.74	10.81	13.30	4.48	8.93
Standard Error	9.25	9.00	0.85	0.64	0.53	0.62	0.46	0.48	0.96	0.56	0.28	0.39
Standard Deviation	20.68	20.12	2.94	2.23	1.85	2.16	1.61	1.66	2.14	1.94	0.98	1.35
Sample Variance	427.80	404.71	8.67	4.96	3.43	4.65	2.58	2.75	4.57	3.76	0.96	1.83
CV	16.01	16.15	14.05	14.43	14.19	16.33	16.95	18.97	19.77	14.59	21.91	15.14

***Macaca nemestrina*, pooled sexes, tibia**

	tLEN1	*tLEN2*	*tPML*	*tPAP*	*tLFAP*	*tMFAP*	*tLFML*	*tMFML*	*tDAP*	*tDML*	*tMMPD*	*tDASML*
Count	4	4	9	9	9	9	8	8	4	9	8	8
Range	49.73	47.15	14.61	12.38	6.66	7.44	10.19	6.34	5.4	7.81	3.43	5.69
Minimum	146.77	140.85	21.77	15.3	12.72	13.24	7.64	8.53	11.27	13.85	4.35	7.6
Maximum	196.5	188	36.38	27.68	19.38	20.68	17.83	14.87	16.67	21.66	7.78	13.29
Mean	169.98	162.48	28.20	20.26	16.07	16.66	12.34	11.43	14.43	17.26	5.71	10.67
Standard Error	10.81	10.14	1.80	1.50	0.96	0.90	1.12	0.79	1.17	0.89	0.45	0.67
Standard Deviation	21.63	20.27	5.41	4.51	2.87	2.70	3.15	2.23	2.35	2.68	1.27	1.90
Sample Variance	467.80	411.04	29.24	20.38	8.24	7.27	9.95	4.96	5.51	7.17	1.60	3.60
CV	12.72	12.48	19.18	22.28	17.86	16.18	25.56	19.47	16.26	15.51	22.17	17.77

Tibial Measures of Variance, Split Sexes

***Homo sapiens*, female only, tibia**

	tLEN1	*tLEN2*	*tPML*	*tPAP*	*tLFAP*	*tMFAP*	*tLFML*	*tMFML*	*tDAP*	*tDML*	*tMMPD*	*tDASML*
Count	9	9	9	9	9	9	9	9	9	9	9	9
Range	69.5	67.5	8.4	7.6	8.34	8.62	6.31	4.46	6.83	8.81	7.86	4.94
Minimum	314.5	307	64.02	43.33	30.06	38.35	23.79	23.47	31.86	38.64	8.73	22.82
Maximum	384	374.5	72.42	50.93	38.4	46.97	30.1	27.93	38.69	47.45	16.59	27.76
Mean	347.83	340.28	68.37	46.82	35.37	40.56	26.39	26.05	35.42	42.15	12.61	25.00
Standard Error	7.41	7.19	1.13	0.93	0.84	0.92	0.80	0.62	0.72	1.05	0.80	0.48
Standard Deviation	22.24	21.56	3.40	2.78	2.52	2.76	2.39	1.87	2.15	3.14	2.39	1.45
Sample Variance	494.50	464.88	11.57	7.71	6.34	7.61	5.73	3.49	4.61	9.85	5.73	2.10
CV	6.39	6.34	4.98	5.93	7.12	6.80	9.07	7.17	6.06	7.45	18.98	5.80

***Homo sapiens*, male only, tibia**

	tLEN1	*tLEN2*	*tPML*	*tPAP*	*tLFAP*	*tMFAP*	*tLFML*	*tMFML*	*tDAP*	*tDML*	*tMMPD*	*tDASML*
Count	9	9	9	9	9	9	9	9	9	9	9	9
Range	67.5	83	9.85	9.04	8.27	8.68	6.01	8.79	7.83	3.52	4.99	9.69
Minimum	334	310.5	70.29	48.24	35.74	41.24	26.12	24.86	34.56	45.27	12.66	24.71
Maximum	401.5	393.5	80.14	57.28	44.01	49.92	32.13	33.65	42.39	48.79	17.65	34.4
Mean	377.50	368.00	75.54	52.56	38.91	46.10	28.80	28.90	39.65	47.25	14.30	27.63
Standard Error	6.81	8.31	1.04	0.95	0.91	1.14	0.72	0.97	0.78	0.42	0.53	1.08
Standard Deviation	20.44	24.92	3.11	2.86	2.72	3.42	2.15	2.90	2.34	1.25	1.59	3.24
Sample Variance	417.81	620.88	9.69	8.16	7.40	11.72	4.60	8.43	5.46	1.57	2.52	10.50
CV	5.41	6.77	4.12	5.43	6.99	7.43	7.45	10.05	5.89	2.65	11.10	11.73

Tibial Measures of Variance, Split Sexes

***Pan troglodytes*, female only, tibia**

	tLEN1	*tLEN2*	*tPML*	*tPAP*	*tLFAP*	*tMFAP*	*tLFML*	*tMFML*	*tDAP*	*tDML*	*tMMPD*	*tDASML*
Count	9	8	9	9	9	9	9	9	9	9	9	9
Range	54	52.5	12.76	7.28	9.38	11.65	5.42	5.06	8.45	7.34	5.49	11.01
Minimum	213	203.5	49.25	32.24	24.07	26.79	22.01	21.05	22.97	29.12	11.84	17.78
Maximum	267	256	62.01	39.52	33.45	38.44	27.43	26.11	31.42	36.46	17.33	28.79
Mean	241.06	230.31	55.59	36.32	29.21	31.22	23.91	23.30	25.65	33.92	13.31	22.88
Standard Error	5.45	5.85	1.24	0.81	0.98	1.25	0.53	0.48	0.89	0.80	0.56	1.07
Standard Deviation	16.36	16.55	3.72	2.42	2.94	3.74	1.59	1.43	2.66	2.40	1.69	3.21
Sample Variance	267.72	273.85	13.87	5.88	8.67	13.97	2.54	2.04	7.08	5.76	2.85	10.32
CV	6.79	7.19	6.70	6.67	10.08	11.97	6.66	6.13	10.37	7.07	12.68	14.04

***Pan troglodytes*, male only, tibia**

	tLEN1	*tLEN2*	*tPML*	*tPAP*	*tLFAP*	*tMFAP*	*tLFML*	*tMFML*	*tDAP*	*tDML*	*tMMPD*	*tDASML*
Count	6	6	6	6	6	6	6	6	6	6	6	6
Range	49.5	37	8.94	6.92	6.92	10.61	4.66	5.98	3.41	8.92	4.22	8.64
Minimum	225.5	227.5	53.41	35.63	26.35	25.78	22.01	21.7	24.31	33.35	11.44	21.26
Maximum	275	264.5	62.35	42.55	33.27	36.39	26.67	27.68	27.72	42.27	15.66	29.9
Mean	253.17	245.92	58.66	38.73	30.15	33.26	24.30	25.31	26.38	37.54	13.98	26.05
Standard Error	7.74	5.73	1.43	1.07	1.18	1.61	0.76	0.86	0.51	1.54	0.69	1.36
Standard Deviation	18.96	14.03	3.51	2.62	2.89	3.95	1.85	2.10	1.25	3.76	1.70	3.34
Sample Variance	359.37	196.74	12.31	6.85	8.34	15.63	3.44	4.41	1.56	14.16	2.88	11.16
CV	7.49	5.70	5.98	6.76	9.58	11.89	7.63	8.29	4.74	10.02	12.13	12.83

Tibial Measures of Variance, Split Sexes

***Papio hamadryas*, female only, tibia**

	tLEN1	*tLEN2*	*tPML*	*tPAP*	*tLFAP*	*tMFAP*	*tLFML*	*tMFML*	*tDAP*	*tDML*	*tMMPD*	*tDASML*
Count	6	6	11	11	11	11	8	8	6	11	8	8
Range	39.61	40.31	6.33	4.88	5.42	5.31	2.32	3.03	2.27	5.31	4.64	2.52
Minimum	184.61	175.13	31.46	23.51	17.65	18.67	13.98	12.47	18.43	18.88	5.73	12.57
Maximum	224.22	215.44	37.79	28.39	23.07	23.98	16.3	15.5	20.7	24.19	10.37	15.09
Mean	202.32	192.72	34.44	26.32	20.01	21.98	15.24	14.39	19.00	22.03	7.39	14.07
Standard Error	7.07	7.10	0.57	0.55	0.49	0.46	0.27	0.37	0.37	0.50	0.57	0.32
Standard Deviation	17.33	17.39	1.89	1.83	1.62	1.53	0.75	1.06	0.90	1.65	1.62	0.92
Sample Variance	300.29	302.34	3.59	3.34	2.63	2.35	0.57	1.12	0.80	2.73	2.61	0.84
CV	8.56	9.02	5.50	6.95	8.10	6.98	4.93	7.34	4.71	7.50	21.89	6.50

***Papio hamadryas*, male only, tibia**

	tLEN1	*tLEN2*	*tPML*	*tPAP*	*tLFAP*	*tMFAP*	*tLFML*	*tMFML*	*tDAP*	*tDML*	*tMMPD*	*tDASML*
Count	14	14	24	24	24	24	15	15	14	24	15	15
Range	64	61	11.13	12.06	7.37	9.66	4.72	2.85	6.32	8.79	5.29	4.34
Minimum	201	192	35.41	26.35	20.96	21.9	16.71	16.38	18.72	21.45	7.14	15.05
Maximum	265	253	46.54	38.41	28.33	31.56	21.43	19.23	25.04	30.24	12.43	19.39
Mean	230.30	221.24	42.26	32.12	24.46	26.88	18.72	17.60	22.41	26.67	9.12	17.14
Standard Error	4.90	4.83	0.47	0.59	0.42	0.48	0.28	0.22	0.43	0.43	0.44	0.31
Standard Deviation	18.34	18.06	2.30	2.89	2.06	2.36	1.07	0.85	1.62	2.11	1.70	1.22
Sample Variance	336.49	326.07	5.27	8.34	4.23	5.58	1.15	0.72	2.62	4.43	2.89	1.48
CV	7.97	8.16	5.43	8.99	8.41	8.79	5.73	4.83	7.22	7.89	18.62	7.11

Tibial Measures of Variance, Split Sexes

***Theropithecus gelada*, female only, tibia**

	tLEN1	*tLEN2*	*tPML*	*tPAP*	*tLFAP*	*tMFAP*	*tLFML*	*tMFML*	*tDAP*	*tDML*	*tMMPD*	*tDASML*
Count	5	5	5	5	5	5	4	4	5	5	4	4
Range	7.2	11.69	1.37	2.58	0.72	2.96	1.12	0.6	1.26	2.29	2.83	1.63
Minimum	176.33	164.11	31.67	22.37	17.92	18.15	12.77	13.33	16.07	18.92	5.74	12.46
Maximum	183.53	175.8	33.04	24.95	18.64	21.11	13.89	13.93	17.33	21.21	8.57	14.09
Mean	179.92	170.86	32.27	23.89	18.41	19.87	13.47	13.62	16.72	20.33	7.22	13.30
Standard Error	1.35	2.05	0.27	0.59	0.13	0.49	0.24	0.14	0.25	0.43	0.71	0.37
Standard Deviation	3.01	4.59	0.60	1.32	0.30	1.09	0.49	0.28	0.56	0.97	1.42	0.73
Sample Variance	9.05	21.08	0.36	1.74	0.09	1.18	0.24	0.08	0.31	0.94	2.01	0.54
CV	1.67	2.69	1.86	5.52	1.62	5.48	3.61	2.03	3.35	4.78	19.65	5.52

***Theropithecus gelada*, male only, tibia**

	tLEN1	*tLEN2*	*tPML*	*tPAP*	*tLFAP*	*tMFAP*	*tLFML*	*tMFML*	*tDAP*	*tDML*	*tMMPD*	*tDASML*
Count	6	6	7	7	7	7	6	6	6	7	6	6
Range	18.28	16.83	3.12	4.5	3.24	6.42	4.65	2.66	1.82	2.51	4.01	3.67
Minimum	199.72	191.17	35.71	25.35	18.92	20.02	12.67	13.55	17.68	21.91	6.42	13.34
Maximum	218	208	38.83	29.85	22.16	26.44	17.32	16.21	19.5	24.42	10.43	17.01
Mean	208.44	198.18	37.50	27.88	20.35	22.58	15.30	14.94	18.57	23.42	7.86	15.71
Standard Error	2.74	2.75	0.45	0.64	0.44	0.87	0.85	0.36	0.34	0.38	0.79	0.55
Standard Deviation	6.71	6.75	1.19	1.70	1.18	2.29	2.08	0.88	0.82	1.01	1.94	1.36
Sample Variance	45.08	45.53	1.42	2.89	1.38	5.26	4.34	0.77	0.68	1.02	3.77	1.84
CV	3.22	3.40	3.17	6.10	5.78	10.16	13.62	5.86	4.43	4.32	24.73	8.65

Tibial Measures of Variance, Split Sexes

***Macaca fascicularis*, female only, tibia**

	tLEN1	*tLEN2*	*tPML*	*tPAP*	*tLFAP*	*tMFAP*	*tLFML*	*tMFML*	*tDAP*	*tDML*	*tMMPD*	*tDASML*
Count	2	2	6	6	6	6	6	6	2	6	6	6
Range	0.180	0.218	0.117	0.128	0.096	0.220	0.158	0.039	0.002	0.114	0.115	0.189
Minimum	8.190	7.882	1.219	0.883	0.772	0.733	0.463	0.495	0.642	0.773	0.232	0.451
Maximum	8.370	8.099	1.336	1.011	0.867	0.953	0.620	0.534	0.644	0.887	0.347	0.640
Mean	8.280	7.990	1.290	0.950	0.816	0.813	0.572	0.509	0.643	0.821	0.274	0.553
Standard Error	0.090	0.109	0.018	0.022	0.015	0.036	0.024	0.006	0.001	0.020	0.018	0.025
Standard Deviation	0.127	0.154	0.045	0.055	0.038	0.087	0.059	0.015	0.002	0.048	0.043	0.061
Sample Variance	0.016	0.024	0.002	0.003	0.001	0.008	0.003	0.000	0.000	0.002	0.002	0.004
CV	1.537	1.927	3.514	5.761	4.630	10.700	10.248	2.933	0.252	5.883	15.844	10.986

***Macaca fascicularis*, male only, tibia**

	tLEN1	*tLEN2*	*tPML*	*tPAP*	*tLFAP*	*tMFAP*	*tLFML*	*tMFML*	*tDAP*	*tDML*	*tMMPD*	*tDASML*
Count	3	3	6	6	6	6	6	6	3	6	6	6
Range	0.645	0.611	0.118	0.093	0.102	0.136	0.069	0.081	0.010	0.128	0.129	0.076
Minimum	7.193	6.958	1.211	0.892	0.711	0.712	0.550	0.496	0.647	0.736	0.212	0.499
Maximum	7.839	7.569	1.329	0.985	0.813	0.848	0.619	0.577	0.656	0.863	0.341	0.575
Mean	7.478	7.210	1.264	0.932	0.776	0.795	0.580	0.549	0.651	0.800	0.272	0.536
Standard Error	0.190	0.184	0.019	0.016	0.018	0.021	0.010	0.013	0.003	0.021	0.022	0.011
Standard Deviation	0.329	0.319	0.046	0.039	0.043	0.052	0.025	0.031	0.005	0.051	0.053	0.028
Sample Variance	0.108	0.102	0.002	0.002	0.002	0.003	0.001	0.001	0.000	0.003	0.003	0.001
CV	4.401	4.427	3.610	4.190	5.561	6.489	4.237	5.719	0.753	6.406	19.484	5.188

Tibial Measures of Variance, Split Sexes

***Macaca nemestrina*, female only, tibia**

	tLEN1	*tLEN2*	*tPML*	*tPAP*	*tLFAP*	*tMFAP*	*tLFML*	*tMFML*	*tDAP*	*tDML*	*tMMPD*	*tDASML*
Count	2	2	4	4	4	4	4	4	2	4	4	4
Range	0.753	0.714	0.062	0.055	0.082	0.055	0.063	0.062	0.032	0.107	0.102	0.118
Minimum	7.522	7.227	1.255	0.863	0.674	0.747	0.551	0.524	0.635	0.761	0.232	0.475
Maximum	8.275	7.941	1.317	0.918	0.756	0.801	0.614	0.586	0.668	0.868	0.334	0.594
Mean	7.899	7.584	1.279	0.884	0.723	0.781	0.585	0.543	0.652	0.813	0.284	0.535
Standard Error	0.376	0.357	0.013	0.013	0.017	0.012	0.013	0.015	0.016	0.022	0.027	0.025
Standard Deviation	0.532	0.505	0.027	0.025	0.035	0.024	0.026	0.029	0.023	0.045	0.055	0.049
Sample Variance	0.283	0.255	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.002	0.003	0.002
CV	6.739	6.659	2.090	2.840	4.790	3.050	4.460	5.393	3.515	5.486	19.205	9.243

***Macaca nemestrina*, female only, tibia**

	tLEN1	*tLEN2*	*tPML*	*tPAP*	*tLFAP*	*tMFAP*	*tLFML*	*tMFML*	*tDAP*	*tDML*	*tMMPD*	*tDASML*
Count	2	2	5	5	5	5	4	4	2	5	4	4
Range	1.187	1.202	0.194	0.262	0.077	0.066	0.265	0.100	0.009	0.081	0.083	0.108
Minimum	7.123	6.748	1.222	0.895	0.731	0.740	0.429	0.479	0.661	0.762	0.230	0.427
Maximum	8.310	7.951	1.416	1.157	0.808	0.807	0.694	0.579	0.670	0.843	0.313	0.534
Mean	7.717	7.349	1.336	0.985	0.769	0.775	0.572	0.536	0.666	0.802	0.257	0.477
Standard Error	0.593	0.601	0.035	0.047	0.014	0.013	0.056	0.022	0.005	0.016	0.019	0.023
Standard Deviation	0.839	0.850	0.078	0.105	0.031	0.029	0.112	0.045	0.007	0.035	0.038	0.045
Sample Variance	0.704	0.723	0.006	0.011	0.001	0.001	0.013	0.002	0.000	0.001	0.001	0.002
CV	10.875	11.569	5.852	10.641	3.992	3.777	19.647	8.345	0.985	4.400	14.596	9.512

Humeral Measures of Variance, Pooled Sexes, GM adjusted

***Homo sapiens*, pooled sexes, humerus**

	hLEN1	*hLEN2*	*hLEN3*	*hPML*	*hPAP*	*hHEAP*	*hHEML*	*hLEN4*	*hDML*	*hDASML*	*hDHA*	*hTRPD*	*hTRML*	*hDAP*
Count	18	18	18	18	18	18	18	18	18	18	18	18	18	18
Range	0.809	0.740	0.724	0.144	0.116	0.192	0.174	0.737	0.192	0.146	0.141	0.069	0.103	0.059
Minimum	4.345	4.456	4.521	0.701	0.671	0.518	0.516	1.394	0.829	0.561	0.624	0.317	0.354	0.377
Maximum	5.154	5.195	5.246	0.845	0.787	0.710	0.690	2.131	1.021	0.707	0.766	0.387	0.458	0.436
Mean	4.744	4.852	4.920	0.758	0.720	0.669	0.627	1.792	0.916	0.618	0.674	0.358	0.399	0.406
Standard Error	0.050	0.049	0.049	0.008	0.007	0.010	0.011	0.050	0.012	0.010	0.009	0.006	0.007	0.004
Standard Deviation	0.211	0.210	0.210	0.032	0.030	0.044	0.048	0.214	0.049	0.041	0.038	0.024	0.029	0.016
Sample Variance	0.044	0.044	0.044	0.001	0.001	0.002	0.002	0.046	0.002	0.002	0.001	0.001	0.001	0.000
CV	4.446	4.328	4.267	4.233	4.181	6.615	7.705	11.937	5.360	6.694	5.587	6.614	7.316	3.887

***Pan troglodytes*, pooled sexes, humerus**

	hLEN1	*hLEN2*	*hLEN3*	*hPML*	*hPAP*	*hHEAP*	*hHEML*	*hLEN4*	*hDML*	*hDASML*	*hDHA*	*hTRPD*	*hTRML*	*hDAP*
Count	14	14	14	15	15	15	15	15	15	15	15	15	15	15
Range	0.569	0.614	0.633	0.090	0.071	0.064	0.114	0.437	0.147	0.067	0.073	0.122	0.082	0.061
Minimum	4.406	4.406	4.444	0.666	0.656	0.595	0.563	1.449	0.892	0.669	0.732	0.310	0.354	0.416
Maximum	4.976	5.020	5.077	0.757	0.727	0.658	0.677	1.887	1.039	0.736	0.805	0.432	0.437	0.477
Mean	4.725	4.767	4.816	0.700	0.685	0.632	0.602	1.645	0.970	0.699	0.778	0.361	0.379	0.440
Standard Error	0.040	0.045	0.049	0.007	0.005	0.005	0.007	0.037	0.010	0.004	0.005	0.009	0.005	0.005
Standard Deviation	0.152	0.167	0.182	0.027	0.021	0.020	0.028	0.142	0.040	0.017	0.021	0.035	0.019	0.019
Sample Variance	0.023	0.028	0.033	0.001	0.000	0.000	0.001	0.020	0.002	0.000	0.000	0.001	0.000	0.000
CV	3.207	3.506	3.772	3.924	3.060	3.222	4.704	8.601	4.111	2.441	2.667	9.773	5.078	4.232

Humeral Measures of Variance, Pooled Sexes, GM adjusted

***Papio hamadryas*, pooled sexes, humerus**

	hLEN1	*hLEN2*	*hLEN3*	*hPML*	*hPAP*	*hHEAP*	*hHEML*	*hLEN4*	*hDML*	*hDASML*	*hDHA*	*hTRPD*	*hTRML*	*hDAP*
Count	21	21	7	22	22	21	21	22	23	23	19	23	23	23
Range	0.789	0.859	0.378	0.091	0.099	0.191	0.111	0.584	0.166	0.119	0.336	0.141	0.152	0.099
Minimum	4.519	4.431	4.672	0.641	0.654	0.472	0.460	1.295	0.764	0.554	0.668	0.369	0.306	0.520
Maximum	5.308	5.290	5.050	0.732	0.752	0.662	0.571	1.879	0.930	0.672	1.004	0.510	0.458	0.619
Mean	4.873	4.827	4.821	0.694	0.698	0.588	0.541	1.520	0.863	0.627	0.761	0.445	0.355	0.562
Standard Error	0.045	0.046	0.050	0.005	0.006	0.010	0.005	0.028	0.008	0.006	0.017	0.007	0.009	0.005
Standard Deviation	0.206	0.209	0.132	0.023	0.027	0.045	0.024	0.131	0.037	0.030	0.076	0.035	0.045	0.023
Sample Variance	0.042	0.044	0.018	0.001	0.001	0.002	0.001	0.017	0.001	0.001	0.006	0.001	0.002	0.001
CV	4.227	4.323	2.745	3.278	3.836	7.606	4.411	8.628	4.323	4.714	9.961	7.947	12.669	4.025

***Theropithecus gelada*, pooled sexes, humerus**

	hLEN1	*hLEN2*	*hLEN3*	*hPML*	*hPAP*	*hHEAP*	*hHEML*	*hLEN4*	*hDML*	*hDASML*	*hDHA*	*hTRPD*	*hTRML*	*hDAP*
Count	13	13	4	12	13	9	9	13	13	13	10	13	13	13
Range	0.471	0.456	0.282	0.061	0.105	0.130	0.054	0.396	0.076	0.063	0.072	0.072	0.168	0.051
Minimum	4.665	4.637	4.748	0.646	0.700	0.586	0.517	1.237	0.814	0.567	0.694	0.411	0.292	0.541
Maximum	5.136	5.092	5.030	0.707	0.805	0.716	0.571	1.633	0.891	0.630	0.766	0.483	0.460	0.592
Mean	4.929	4.893	4.897	0.681	0.744	0.636	0.541	1.483	0.851	0.598	0.732	0.448	0.349	0.568
Standard Error	0.036	0.036	0.058	0.005	0.011	0.013	0.007	0.028	0.006	0.006	0.006	0.005	0.014	0.004
Standard Deviation	0.129	0.128	0.116	0.017	0.038	0.039	0.021	0.101	0.020	0.020	0.019	0.018	0.050	0.015
Sample Variance	0.017	0.016	0.014	0.000	0.001	0.002	0.000	0.010	0.000	0.000	0.000	0.000	0.003	0.000
CV	2.624	2.621	2.375	2.475	5.132	6.122	3.945	6.835	2.384	3.337	2.661	4.109	14.423	2.648

Humeral Measures of Variance, Pooled Sexes, GM adjusted

***Macaca fascicularis*, pooled sexes, humerus**

	hLEN1	*hLEN2*	*hLEN3*	*hPML*	*hPAP*	*hHEAP*	*hHEML*	*hLEN4*	*hDML*	*hDASML*	*hDHA*	*hTRPD*	*hTRML*	*hDAP*
Count	9	9	5	9	9	9	9	11	11	11	11	11	11	11
Range	1.293	1.291	1.304	0.060	0.074	0.069	0.084	0.656	0.152	0.122	0.241	0.085	0.097	0.078
Minimum	4.596	4.593	4.639	0.637	0.637	0.536	0.523	1.236	0.766	0.559	0.655	0.361	0.317	0.486
Maximum	5.889	5.884	5.944	0.697	0.711	0.605	0.607	1.892	0.918	0.681	0.897	0.447	0.414	0.564
Mean	5.099	5.110	5.147	0.667	0.680	0.577	0.554	1.619	0.866	0.625	0.750	0.413	0.364	0.515
Standard Error	0.123	0.124	0.233	0.007	0.008	0.009	0.010	0.062	0.011	0.012	0.018	0.008	0.009	0.007
Standard Deviation	0.369	0.372	0.520	0.022	0.025	0.026	0.030	0.206	0.037	0.041	0.060	0.025	0.029	0.025
Sample Variance	0.136	0.138	0.270	0.000	0.001	0.001	0.001	0.042	0.001	0.002	0.004	0.001	0.001	0.001
CV	7.233	7.271	10.102	3.305	3.673	4.531	5.340	12.690	4.307	6.502	7.954	6.129	8.052	4.823

***Macaca nemestrina*, pooled sexes, humerus**

	hLEN1	*hLEN2*	*hLEN3*	*hPML*	*hPAP*	*hHEAP*	*hHEML*	*hLEN4*	*hDML*	*hDASML*	*hDHA*	*hTRPD*	*hTRML*	*hDAP*
Count	3	3	2	3	3	3	3	3	3	3	3	3	3	3
Range	0.644	0.698	0.308	0.071	0.031	0.055	0.114	0.191	0.023	0.045	0.085	0.031	0.030	0.009
Minimum	4.709	4.626	4.740	0.657	0.656	0.566	0.527	1.375	0.861	0.605	0.683	0.414	0.347	0.544
Maximum	5.352	5.324	5.048	0.728	0.687	0.621	0.640	1.566	0.884	0.650	0.768	0.445	0.377	0.552
Mean	5.035	4.999	4.894	0.690	0.670	0.588	0.584	1.488	0.874	0.633	0.737	0.434	0.359	0.548
Standard Error	0.186	0.203	0.154	0.021	0.009	0.017	0.033	0.058	0.007	0.014	0.027	0.010	0.009	0.002
Standard Deviation	0.322	0.352	0.218	0.036	0.016	0.029	0.057	0.100	0.012	0.024	0.047	0.017	0.016	0.004
Sample Variance	0.104	0.124	0.047	0.001	0.000	0.001	0.003	0.010	0.000	0.001	0.002	0.000	0.000	0.000
CV	6.394	7.035	4.449	5.180	2.323	4.934	9.744	6.703	1.328	3.843	6.414	3.984	4.469	0.785

Humeral Measures of Variance, Split Sexes, GM adjusted

***Homo sapiens*, female only, humerus**

	hLEN1	*hLEN2*	*hLEN3*	*hPML*	*hPAP*	*hHEAP*	*hHEML*	*hLEN4*	*hDML*	*hDASML*	*hDHA*	*hTRPD*	*hTRML*	*hDAP*
Count	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Range	0.552	0.445	0.448	0.066	0.068	0.098	0.160	0.657	0.151	0.085	0.059	0.057	0.103	0.059
Minimum	4.602	4.750	4.798	0.722	0.676	0.612	0.516	1.394	0.829	0.561	0.624	0.323	0.354	0.377
Maximum	5.154	5.195	5.246	0.788	0.744	0.710	0.676	2.051	0.980	0.646	0.683	0.381	0.458	0.436
Mean	4.848	4.954	5.017	0.760	0.716	0.673	0.615	1.801	0.906	0.614	0.653	0.360	0.400	0.401
Standard Error	0.055	0.051	0.052	0.007	0.007	0.010	0.019	0.069	0.017	0.008	0.008	0.007	0.012	0.006
Standard Deviation	0.166	0.153	0.157	0.021	0.020	0.031	0.056	0.207	0.051	0.025	0.024	0.022	0.037	0.019
Sample Variance	0.028	0.023	0.025	0.000	0.000	0.001	0.003	0.043	0.003	0.001	0.001	0.000	0.001	0.000
CV	3.431	3.084	3.122	2.726	2.799	4.627	9.163	11.490	5.651	4.032	3.663	6.106	9.152	4.719

***Homo sapiens*, male only, humerus**

	hLEN1	*hLEN2*	*hLEN3*	*hPML*	*hPAP*	*hHEAP*	*hHEML*	*hLEN4*	*hDML*	*hDASML*	*hDHA*	*hTRPD*	*hTRML*	*hDAP*
Count	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Range	0.625	0.644	0.636	0.144	0.116	0.179	0.122	0.699	0.167	0.142	0.122	0.069	0.062	0.028
Minimum	4.345	4.456	4.521	0.701	0.671	0.518	0.568	1.432	0.854	0.565	0.644	0.317	0.369	0.399
Maximum	4.970	5.100	5.157	0.845	0.787	0.697	0.690	2.131	1.021	0.707	0.766	0.387	0.431	0.426
Mean	4.640	4.749	4.822	0.756	0.724	0.664	0.638	1.783	0.927	0.623	0.694	0.357	0.397	0.412
Standard Error	0.069	0.072	0.073	0.014	0.013	0.019	0.013	0.078	0.016	0.018	0.013	0.009	0.007	0.003
Standard Deviation	0.206	0.216	0.218	0.042	0.039	0.056	0.038	0.233	0.047	0.055	0.039	0.027	0.022	0.010
Sample Variance	0.043	0.047	0.048	0.002	0.001	0.003	0.001	0.054	0.002	0.003	0.001	0.001	0.000	0.000
CV	4.445	4.548	4.525	5.532	5.330	8.436	6.005	13.061	5.122	8.776	5.572	7.454	5.434	2.536

Humeral Measures of Variance, Split Sexes, GM adjusted

***Pan troglodytes*, female only, humerus**

	hLEN1	*hLEN2*	*hLEN3*	*hPML*	*hPAP*	*hHEAP*	*hHEML*	*hLEN4*	*hDML*	*hDASML*	*hDHA*	*hTRPD*	*hTRML*	*hDAP*
Count	8	8	8	9	9	9	9	9	9	9	9	9	9	9
Range	0.448	0.474	0.513	0.078	0.071	0.063	0.077	0.402	0.109	0.037	0.058	0.097	0.082	0.061
Minimum	4.528	4.546	4.564	0.666	0.656	0.595	0.563	1.485	0.892	0.675	0.747	0.310	0.354	0.416
Maximum	4.976	5.020	5.077	0.744	0.727	0.658	0.639	1.887	1.001	0.713	0.805	0.406	0.437	0.477
Mean	4.750	4.794	4.852	0.699	0.681	0.630	0.599	1.706	0.957	0.698	0.780	0.351	0.384	0.441
Standard Error	0.053	0.058	0.063	0.009	0.007	0.008	0.007	0.046	0.012	0.004	0.006	0.011	0.008	0.007
Standard Deviation	0.149	0.163	0.178	0.027	0.022	0.024	0.021	0.138	0.036	0.012	0.017	0.033	0.023	0.021
Sample Variance	0.022	0.027	0.032	0.001	0.000	0.001	0.000	0.019	0.001	0.000	0.000	0.001	0.001	0.000
CV	3.139	3.409	3.675	3.822	3.203	3.785	3.574	8.071	3.800	1.785	2.170	9.297	5.999	4.742

***Pan troglodytes*, male only, humerus**

	hLEN1	*hLEN2*	*hLEN3*	*hPML*	*hPAP*	*hHEAP*	*hHEML*	*hLEN4*	*hDML*	*hDASML*	*hDHA*	*hTRPD*	*hTRML*	*hDAP*
Count	6	6	6	6	6	6	6	6	6	6	6	6	6	6
Range	0.448	0.498	0.551	0.080	0.053	0.036	0.111	0.271	0.102	0.067	0.070	0.092	0.024	0.044
Minimum	4.406	4.406	4.444	0.676	0.660	0.622	0.566	1.449	0.936	0.669	0.732	0.340	0.362	0.418
Maximum	4.855	4.904	4.995	0.757	0.714	0.658	0.677	1.721	1.039	0.736	0.802	0.432	0.386	0.462
Mean	4.692	4.732	4.767	0.701	0.690	0.636	0.607	1.555	0.989	0.701	0.776	0.375	0.371	0.440
Standard Error	0.066	0.074	0.078	0.013	0.008	0.006	0.016	0.040	0.016	0.010	0.011	0.015	0.003	0.007
Standard Deviation	0.162	0.181	0.190	0.031	0.020	0.015	0.038	0.097	0.040	0.024	0.027	0.037	0.008	0.017
Sample Variance	0.026	0.033	0.036	0.001	0.000	0.000	0.001	0.009	0.002	0.001	0.001	0.001	0.000	0.000
CV	3.455	3.818	3.994	4.436	2.911	2.372	6.311	6.241	4.015	3.368	3.496	9.755	2.198	3.757

Humeral Measures of Variance, Split Sexes, GM adjusted

***Papio hamadryas*, female only, humerus**

	hLEN1	*hLEN2*	*hLEN3*	*hPML*	*hPAP*	*hHEAP*	*hHEML*	*hLEN4*	*hDML*	*hDASML*	*hDHA*	*hTRPD*	*hTRML*	*hDAP*
Count	7	7	2	8	8	8	8	8	8	8	7	8	8	8
Range	0.585	0.610	0.311	0.063	0.079	0.059	0.100	0.253	0.088	0.090	0.316	0.096	0.141	0.053
Minimum	4.688	4.609	4.739	0.649	0.654	0.558	0.460	1.342	0.821	0.557	0.688	0.373	0.317	0.520
Maximum	5.272	5.218	5.050	0.712	0.733	0.616	0.560	1.595	0.910	0.647	1.004	0.468	0.458	0.573
Mean	4.955	4.898	4.894	0.686	0.686	0.586	0.529	1.497	0.859	0.616	0.784	0.427	0.364	0.554
Standard Error	0.078	0.080	0.155	0.007	0.010	0.007	0.011	0.029	0.010	0.011	0.040	0.012	0.021	0.006
Standard Deviation	0.207	0.213	0.220	0.019	0.028	0.019	0.030	0.081	0.028	0.030	0.106	0.033	0.060	0.018
Sample Variance	0.043	0.045	0.048	0.000	0.001	0.000	0.001	0.007	0.001	0.001	0.011	0.001	0.004	0.000
CV	4.172	4.341	4.490	2.831	4.050	3.178	5.710	5.417	3.279	4.831	13.505	7.749	16.531	3.298

***Papio hamadryas*, male only, humerus**

	hLEN1	*hLEN2*	*hLEN3*	*hPML*	*hPAP*	*hHEAP*	*hHEML*	*hLEN4*	*hDML*	*hDASML*	*hDHA*	*hTRPD*	*hTRML*	*hDAP*
Count	14	14	5	14	14	13	13	14	15	15	12	15	15	15
Range	0.789	0.859	0.280	0.091	0.094	0.191	0.057	0.584	0.166	0.119	0.148	0.141	0.112	0.095
Minimum	4.519	4.431	4.672	0.641	0.658	0.472	0.515	1.295	0.764	0.554	0.668	0.369	0.306	0.524
Maximum	5.308	5.290	4.952	0.732	0.752	0.662	0.571	1.879	0.930	0.672	0.815	0.510	0.418	0.619
Mean	4.832	4.791	4.792	0.699	0.705	0.588	0.548	1.533	0.865	0.632	0.748	0.454	0.350	0.567
Standard Error	0.054	0.055	0.046	0.006	0.007	0.016	0.004	0.041	0.011	0.007	0.015	0.009	0.009	0.006
Standard Deviation	0.200	0.205	0.102	0.024	0.024	0.056	0.016	0.154	0.042	0.029	0.053	0.034	0.036	0.024
Sample Variance	0.040	0.042	0.010	0.001	0.001	0.003	0.000	0.024	0.002	0.001	0.003	0.001	0.001	0.001
CV	4.144	4.282	2.136	3.396	3.465	9.501	2.933	10.046	4.874	4.572	7.025	7.441	10.254	4.217

Humeral Measures of Variance, Split Sexes, GM adjusted

***Theropithecus gelada*, female only, humerus**

	hLEN1	*hLEN2*	*hLEN3*	*hPML*	*hPAP*	*hHEAP*	*hHEML*	*hLEN4*	*hDML*	*hDASML*	*hDHA*	*hTRPD*	*hTRML*	*hDAP*
Count	5	5	2	5	5	4	4	5	5	5	4	5	5	5
Range	0.471	0.456	0.141	0.014	0.052	0.049	0.030	0.301	0.054	0.057	0.025	0.027	0.149	0.051
Minimum	4.665	4.637	4.748	0.666	0.700	0.605	0.517	1.332	0.814	0.573	0.721	0.435	0.311	0.541
Maximum	5.136	5.092	4.889	0.679	0.752	0.654	0.547	1.633	0.868	0.630	0.746	0.462	0.460	0.592
Mean	4.887	4.866	4.819	0.673	0.719	0.631	0.534	1.513	0.846	0.601	0.734	0.449	0.369	0.564
Standard Error	0.080	0.078	0.070	0.002	0.009	0.010	0.006	0.050	0.011	0.010	0.005	0.005	0.027	0.009
Standard Deviation	0.180	0.174	0.100	0.006	0.020	0.020	0.012	0.112	0.025	0.021	0.010	0.011	0.060	0.021
Sample Variance	0.032	0.030	0.010	0.000	0.000	0.000	0.000	0.013	0.001	0.000	0.000	0.000	0.004	0.000
CV	3.678	3.571	2.068	0.817	2.717	3.213	2.295	7.411	2.975	3.532	1.392	2.418	16.382	3.717

***Theropithecus gelada*, male only, humerus**

	hLEN1	*hLEN2*	*hLEN3*	*hPML*	*hPAP*	*hHEAP*	*hHEML*	*hLEN4*	*hDML*	*hDASML*	*hDHA*	*hTRPD*	*hTRML*	*hDAP*
Count	8	8	2	7	8	5	5	8	8	8	6	8	8	8
Range	0.268	0.284	0.108	0.061	0.093	0.130	0.054	0.310	0.054	0.053	0.072	0.072	0.136	0.031
Minimum	4.818	4.784	4.922	0.646	0.711	0.586	0.517	1.237	0.837	0.567	0.694	0.411	0.292	0.554
Maximum	5.085	5.068	5.030	0.707	0.805	0.716	0.571	1.547	0.891	0.620	0.766	0.483	0.427	0.585
Mean	4.954	4.910	4.976	0.687	0.760	0.640	0.547	1.464	0.855	0.595	0.731	0.448	0.337	0.571
Standard Error	0.032	0.036	0.054	0.008	0.014	0.023	0.012	0.034	0.006	0.007	0.010	0.008	0.015	0.004
Standard Deviation	0.091	0.100	0.076	0.020	0.039	0.052	0.026	0.097	0.018	0.020	0.025	0.023	0.042	0.011
Sample Variance	0.008	0.010	0.006	0.000	0.002	0.003	0.001	0.009	0.000	0.000	0.001	0.001	0.002	0.000
CV	1.832	2.046	1.531	2.966	5.174	8.075	4.840	6.616	2.068	3.391	3.399	5.061	12.612	1.909

Humeral Measures of Variance, Split Sexes, GM adjusted

***Macaca fascicularis*, female only, humerus**

	hLEN1	*hLEN2*	*hLEN3*	*hPML*	*hPAP*	*hHEAP*	*hHEML*	*hLEN4*	*hDML*	*hDASML*	*hDHA*	*hTRPD*	*hTRML*	*hDAP*
Count	5	5	2	5	5	5	5	6	6	6	6	6	6	6
Range	0.853	0.833	0.589	0.057	0.060	0.069	0.060	0.656	0.119	0.122	0.108	0.063	0.052	0.063
Minimum	5.036	5.051	5.355	0.640	0.651	0.536	0.523	1.236	0.766	0.559	0.655	0.384	0.329	0.486
Maximum	5.889	5.884	5.944	0.697	0.711	0.605	0.584	1.892	0.885	0.681	0.763	0.447	0.381	0.549
Mean	5.322	5.344	5.649	0.666	0.676	0.577	0.545	1.655	0.849	0.621	0.722	0.410	0.357	0.506
Standard Error	0.150	0.144	0.294	0.010	0.010	0.015	0.013	0.107	0.017	0.018	0.017	0.009	0.008	0.010
Standard Deviation	0.336	0.321	0.416	0.023	0.022	0.034	0.028	0.262	0.042	0.044	0.042	0.021	0.019	0.023
Sample Variance	0.113	0.103	0.173	0.001	0.000	0.001	0.001	0.069	0.002	0.002	0.002	0.000	0.000	0.001
CV	6.313	6.007	7.371	3.379	3.256	5.821	5.218	15.833	4.946	7.124	5.810	5.136	5.337	4.610

***Macaca fascicularis*, male only, humerus**

	hLEN1	*hLEN2*	*hLEN3*	*hPML*	*hPAP*	*hHEAP*	*hHEML*	*hLEN4*	*hDML*	*hDASML*	*hDHA*	*hTRPD*	*hTRML*	*hDAP*
Count	4	4	3	4	4	4	4	5	5	5	5	5	5	5
Range	0.353	0.341	0.362	0.054	0.067	0.032	0.069	0.334	0.046	0.099	0.148	0.082	0.097	0.064
Minimum	4.596	4.593	4.639	0.637	0.637	0.561	0.538	1.408	0.872	0.569	0.748	0.361	0.317	0.499
Maximum	4.949	4.935	5.001	0.691	0.705	0.593	0.607	1.742	0.918	0.667	0.897	0.443	0.414	0.564
Mean	4.821	4.817	4.812	0.667	0.684	0.577	0.567	1.577	0.885	0.628	0.783	0.416	0.372	0.527
Standard Error	0.082	0.079	0.105	0.012	0.016	0.009	0.015	0.056	0.009	0.018	0.029	0.014	0.018	0.011
Standard Deviation	0.164	0.158	0.182	0.025	0.031	0.018	0.030	0.125	0.019	0.041	0.064	0.032	0.039	0.024
Sample Variance	0.027	0.025	0.033	0.001	0.001	0.000	0.001	0.016	0.000	0.002	0.004	0.001	0.002	0.001
CV	3.400	3.278	3.774	3.728	4.560	3.092	5.307	7.900	2.168	6.448	8.219	7.679	10.531	4.498

Humeral Measures of Variance, Split Sexes, GM adjusted

***Macaca nemestrina*, female only, humerus**

	hLEN1	*hLEN2*	*hLEN3*	*hPML*	*hPAP*	*hHEAP*	*hHEML*	*hLEN4*	*hDML*	*hDASML*	*hDHA*	*hTRPD*	*hTRML*	*hDAP*
Count	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Range	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Minimum	5.045	5.048	5.048	0.657	0.669	0.566	0.583	1.522	0.877	0.650	0.768	0.414	0.353	0.552
Maximum	5.045	5.048	5.048	0.657	0.669	0.566	0.583	1.522	0.877	0.650	0.768	0.414	0.353	0.552
Mean	5.045	5.048	5.048	0.657	0.669	0.566	0.583	1.522	0.877	0.650	0.768	0.414	0.353	0.552
Standard Error	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Standard Deviation	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Sample Variance	.	.	.	.	.	.	.	.	.	.	.	.	.	.
CV	.	.	.	.	.	.	.	.	.	.	.	.	.	.

***Macaca nemestrina*, male only, humerus**

	hLEN1	*hLEN2*	*hLEN3*	*hPML*	*hPAP*	*hHEAP*	*hHEML*	*hLEN4*	*hDML*	*hDASML*	*hDHA*	*hTRPD*	*hTRML*	*hDAP*
Count	2	2	1	2	2	2	2	2	2	2	2	2	2	2
Range	0.644	0.698	0.000	0.042	0.031	0.044	0.114	0.191	0.023	0.038	0.079	0.003	0.030	0.005
Minimum	4.709	4.626	4.740	0.686	0.656	0.577	0.527	1.375	0.861	0.605	0.683	0.442	0.347	0.544
Maximum	5.352	5.324	4.740	0.728	0.687	0.621	0.640	1.566	0.884	0.643	0.762	0.445	0.377	0.549
Mean	5.031	4.975	4.740	0.707	0.671	0.599	0.584	1.471	0.873	0.624	0.722	0.443	0.362	0.546
Standard Error	0.322	0.349	.	0.021	0.016	0.022	0.057	0.095	0.011	0.019	0.039	0.001	0.015	0.003
Standard Deviation	0.455	0.494	.	0.030	0.022	0.031	0.080	0.135	0.016	0.027	0.056	0.002	0.021	0.004
Sample Variance	0.207	0.244	.	0.001	0.000	0.001	0.006	0.018	0.000	0.001	0.003	0.000	0.000	0.000
CV	9.048	9.926	.	4.201	3.268	5.206	13.778	9.162	1.834	4.332	7.724	0.457	5.876	0.667

Radial Measures of Variance, Pooled Sexes, GM adjusted

***Homo sapiens*, pooled sexes, radius**

	rLEN1	*rLEN2*	*rPAP*	*rPML*	*rNE1*	*rNE2*	*rNE3*	*rTUB*	*rDML*	*rDAP*
Count	18	18	18	18	18	18	18	18	18	18
Range	1.203	1.220	0.175	0.136	0.220	0.206	0.137	0.192	0.448	0.356
Minimum	5.960	6.132	0.556	0.546	0.209	0.485	0.824	0.527	0.601	0.551
Maximum	7.163	7.352	0.730	0.682	0.429	0.691	0.961	0.720	1.049	0.907
Mean	6.384	6.557	0.609	0.582	0.370	0.631	0.893	0.623	0.867	0.620
Standard Error	0.081	0.080	0.009	0.007	0.012	0.010	0.008	0.011	0.021	0.019
Standard Deviation	0.342	0.340	0.038	0.031	0.050	0.044	0.034	0.046	0.091	0.079
Sample Variance	0.117	0.115	0.001	0.001	0.002	0.002	0.001	0.002	0.008	0.006
CV	5.351	5.180	6.304	5.314	13.392	6.987	3.800	7.397	10.464	12.677

***Pan troglodytes*, pooled sexes, radius**

	rLEN1	*rLEN2*	*rPAP*	*rPML*	*rNE1*	*rNE2*	*rNE3*	*rTUB*	*rDML*	*rDAP*
Count	15	15	15	15	15	15	15	15	15	15
Range	0.661	0.588	0.105	0.069	0.200	0.133	0.127	0.378	0.126	0.120
Minimum	6.056	6.143	0.514	0.517	0.393	0.689	0.880	0.426	0.679	0.465
Maximum	6.717	6.731	0.619	0.586	0.593	0.822	1.007	0.804	0.804	0.584
Mean	6.311	6.375	0.568	0.556	0.507	0.752	0.949	0.557	0.756	0.531
Standard Error	0.055	0.055	0.008	0.007	0.014	0.010	0.011	0.026	0.009	0.010
Standard Deviation	0.213	0.213	0.030	0.026	0.053	0.040	0.042	0.100	0.036	0.037
Sample Variance	0.045	0.045	0.001	0.001	0.003	0.002	0.002	0.010	0.001	0.001
CV	3.369	3.336	5.360	4.662	10.390	5.331	4.473	18.030	4.707	6.963

Radial Measures of Variance, Pooled Sexes, GM adjusted

***Papio hamadryas*, pooled sexes, radius**

	rLEN1	*rLEN2*	*rPAP*	*rPML*	*rNE1*	*rNE2*	*rNE3*	*rTUB*	*rDML*	*rDAP*
Count	7	18	33	33	18	7	18	7	23	23
Range	1.007	1.405	0.151	0.133	0.195	0.104	0.299	0.288	0.194	0.114
Minimum	6.929	6.747	0.520	0.501	0.201	0.532	0.656	0.675	0.641	0.550
Maximum	7.936	8.152	0.672	0.634	0.396	0.637	0.954	0.963	0.835	0.664
Mean	7.204	7.352	0.598	0.566	0.303	0.585	0.783	0.785	0.760	0.601
Standard Error	0.137	0.090	0.007	0.006	0.012	0.014	0.019	0.041	0.010	0.006
Standard Deviation	0.361	0.380	0.037	0.034	0.053	0.038	0.080	0.109	0.048	0.028
Sample Variance	0.131	0.144	0.001	0.001	0.003	0.001	0.006	0.012	0.002	0.001
CV	5.018	5.169	6.244	5.946	17.406	6.500	10.200	13.822	6.281	4.699

***Theropithecus gelada*, pooled sexes, radius**

	rLEN1	*rLEN2*	*rPAP*	*rPML*	*rNE1*	*rNE2*	*rNE3*	*rTUB*	*rDML*	*rDAP*
Count	4	11	12	12	11	4	11	4	10	10
Range	0.189	0.570	0.102	0.116	0.109	0.124	0.112	0.212	0.218	0.073
Minimum	7.598	7.819	0.548	0.556	0.222	0.446	0.650	0.881	0.592	0.579
Maximum	7.788	8.389	0.649	0.672	0.332	0.571	0.762	1.093	0.810	0.652
Mean	7.687	8.063	0.609	0.602	0.267	0.509	0.714	0.980	0.723	0.619
Standard Error	0.050	0.058	0.009	0.010	0.014	0.025	0.010	0.046	0.018	0.006
Standard Deviation	0.100	0.192	0.031	0.033	0.045	0.051	0.035	0.092	0.058	0.019
Sample Variance	0.010	0.037	0.001	0.001	0.002	0.003	0.001	0.008	0.003	0.000
CV	1.305	2.383	5.018	5.564	16.944	9.988	4.869	9.384	7.970	3.098

Radial Measures of Variance, Pooled Sexes, GM adjusted

***Macaca fascicularis*, pooled sexes, radius**										
	rLEN1	*rLEN2*	*rPAP*	*rPML*	*rNE1*	*rNE2*	*rNE3*	*rTUB*	*rDML*	*rDAP*
Count	5	5	12	12	5	5	5	5	12	12
Range	1.701	1.584	0.193	0.109	0.185	0.192	0.187	0.170	0.221	0.184
Minimum	6.260	6.530	0.476	0.501	0.308	0.613	0.813	0.660	0.632	0.489
Maximum	7.961	8.114	0.669	0.610	0.493	0.805	1.000	0.829	0.853	0.673
Mean	6.967	7.166	0.589	0.548	0.397	0.703	0.876	0.721	0.734	0.570
Standard Error	0.311	0.293	0.015	0.010	0.034	0.032	0.034	0.031	0.018	0.015
Standard Deviation	0.695	0.656	0.052	0.035	0.075	0.071	0.076	0.069	0.063	0.054
Sample Variance	0.483	0.430	0.003	0.001	0.006	0.005	0.006	0.005	0.004	0.003
CV	9.972	9.153	8.741	6.421	18.935	10.064	8.655	9.584	8.561	9.417

***Macaca nemestrina*, pooled sexes, radius**										
	rLEN1	*rLEN2*	*rPAP*	*rPML*	*rNE1*	*rNE2*	*rNE3*	*rTUB*	*rDML*	*rDAP*
Count	3	3	10	10	4	3	4	3	10	10
Range	0.888	0.910	0.178	0.178	0.161	0.078	0.045	0.128	0.183	0.165
Minimum	6.915	7.150	0.482	0.468	0.255	0.565	0.821	0.606	0.705	0.489
Maximum	7.803	8.061	0.660	0.647	0.416	0.643	0.866	0.734	0.888	0.654
Mean	7.311	7.538	0.592	0.575	0.361	0.603	0.834	0.685	0.793	0.595
Standard Error	0.261	0.271	0.016	0.018	0.036	0.023	0.011	0.040	0.019	0.016
Standard Deviation	0.452	0.470	0.051	0.058	0.072	0.039	0.021	0.069	0.059	0.049
Sample Variance	0.204	0.221	0.003	0.003	0.005	0.002	0.000	0.005	0.003	0.002
CV	6.178	6.232	8.691	10.034	20.049	6.497	2.557	10.059	7.396	8.275

Radial Measures of Variance, Split Sexes, GM adjusted

***Homo sapiens*, female only, radius**

	rLEN1	*rLEN2*	*rPAP*	*rPML*	*rNE1*	*rNE2*	*rNE3*	*rTUB*	*rDML*	*rDAP*
Count	9	9	9	9	9	9	9	9	9	9
Range	0.812	0.705	0.079	0.065	0.093	0.072	0.071	0.145	0.132	0.087
Minimum	5.998	6.266	0.584	0.561	0.336	0.602	0.860	0.575	0.787	0.551
Maximum	6.810	6.971	0.663	0.626	0.429	0.674	0.931	0.720	0.919	0.637
Mean	6.356	6.526	0.613	0.585	0.380	0.640	0.891	0.634	0.847	0.584
Standard Error	0.098	0.093	0.008	0.006	0.012	0.007	0.008	0.014	0.015	0.010
Standard Deviation	0.294	0.278	0.024	0.019	0.036	0.021	0.024	0.041	0.044	0.031
Sample Variance	0.086	0.077	0.001	0.000	0.001	0.000	0.001	0.002	0.002	0.001
CV	4.620	4.253	3.920	3.295	9.592	3.323	2.669	6.529	5.137	5.309

***Homo sapiens*, male only, radius**

	rLEN1	*rLEN2*	*rPAP*	*rPML*	*rNE1*	*rNE2*	*rNE3*	*rTUB*	*rDML*	*rDAP*
Count	9	9	9	9	9	9	9	9	9	9
Range	1.203	1.220	0.175	0.136	0.209	0.206	0.137	0.168	0.448	0.313
Minimum	5.960	6.132	0.556	0.546	0.209	0.485	0.824	0.527	0.601	0.594
Maximum	7.163	7.352	0.730	0.682	0.418	0.691	0.961	0.695	1.049	0.907
Mean	6.412	6.588	0.605	0.579	0.360	0.622	0.895	0.612	0.886	0.655
Standard Error	0.133	0.136	0.017	0.014	0.020	0.020	0.014	0.017	0.040	0.032
Standard Deviation	0.400	0.407	0.050	0.041	0.061	0.059	0.043	0.050	0.121	0.097
Sample Variance	0.160	0.166	0.003	0.002	0.004	0.003	0.002	0.003	0.015	0.009
CV	6.237	6.184	8.288	7.001	16.809	9.510	4.838	8.219	13.699	14.791

Radial Measures of Variance, Split Sexes, GM adjusted

***Pan troglodytes*, female only, radius**										
	rLEN1	*rLEN2*	*rPAP*	*rPML*	*rNE1*	*rNE2*	*rNE3*	*rTUB*	*rDML*	*rDAP*
Count	9	9	9	9	9	9	9	9	9	9
Range	0.646	0.578	0.061	0.062	0.183	0.133	0.108	0.378	0.079	0.091
Minimum	6.070	6.153	0.529	0.517	0.393	0.689	0.884	0.426	0.725	0.470
Maximum	6.717	6.731	0.590	0.580	0.576	0.822	0.992	0.804	0.804	0.561
Mean	6.334	6.397	0.564	0.550	0.509	0.757	0.953	0.553	0.760	0.532
Standard Error	0.080	0.078	0.008	0.008	0.017	0.012	0.013	0.041	0.009	0.010
Standard Deviation	0.239	0.233	0.023	0.025	0.052	0.037	0.038	0.122	0.028	0.029
Sample Variance	0.057	0.054	0.001	0.001	0.003	0.001	0.001	0.015	0.001	0.001
CV	3.774	3.637	4.062	4.469	10.175	4.887	3.959	22.077	3.672	5.357

***Pan troglodytes*, male only, radius**										
	rLEN1	*rLEN2*	*rPAP*	*rPML*	*rNE1*	*rNE2*	*rNE3*	*rTUB*	*rDML*	*rDAP*
Count	6	6	6	6	6	6	6	6	6	6
Range	0.451	0.454	0.105	0.065	0.178	0.116	0.127	0.178	0.125	0.120
Minimum	6.056	6.143	0.514	0.521	0.415	0.695	0.880	0.472	0.679	0.465
Maximum	6.506	6.597	0.619	0.586	0.593	0.811	1.007	0.650	0.804	0.584
Mean	6.276	6.343	0.575	0.564	0.504	0.744	0.944	0.564	0.750	0.530
Standard Error	0.074	0.080	0.017	0.011	0.024	0.019	0.021	0.027	0.019	0.021
Standard Deviation	0.181	0.195	0.041	0.028	0.059	0.047	0.052	0.066	0.047	0.050
Sample Variance	0.033	0.038	0.002	0.001	0.003	0.002	0.003	0.004	0.002	0.003
CV	2.887	3.071	7.117	4.941	11.676	6.262	5.521	11.697	6.280	9.488

Radial Measures of Variance, Split Sexes, GM adjusted

***Papio hamadryas*, female only, radius**

	rLEN1	*rLEN2*	*rPAP*	*rPML*	*rNE1*	*rNE2*	*rNE3*	*rTUB*	*rDML*	*rDAP*
Count	2	5	10	10	5	2	5	2	8	8
Range	0.597	0.909	0.117	0.093	0.126	0.016	0.104	0.079	0.096	0.074
Minimum	7.339	7.243	0.520	0.501	0.201	0.559	0.656	0.779	0.709	0.550
Maximum	7.936	8.152	0.637	0.594	0.327	0.575	0.759	0.858	0.805	0.624
Mean	7.637	7.734	0.579	0.552	0.284	0.567	0.725	0.819	0.751	0.583
Standard Error	0.298	0.155	0.013	0.010	0.022	0.008	0.020	0.039	0.013	0.008
Standard Deviation	0.422	0.347	0.041	0.032	0.050	0.011	0.045	0.056	0.036	0.022
Sample Variance	0.178	0.120	0.002	0.001	0.002	0.000	0.002	0.003	0.001	0.000
CV	5.525	4.481	7.144	5.820	17.522	2.001	6.211	6.799	4.765	3.697

***Papio hamadryas*, male only, radius**

	rLEN1	*rLEN2*	*rPAP*	*rPML*	*rNE1*	*rNE2*	*rNE3*	*rTUB*	*rDML*	*rDAP*
Count	5	13	23	23	13	5	13	5	15	15
Range	0.341	0.999	0.113	0.116	0.160	0.104	0.270	0.288	0.194	0.098
Minimum	6.929	6.747	0.558	0.519	0.236	0.532	0.685	0.675	0.641	0.566
Maximum	7.270	7.746	0.672	0.634	0.396	0.637	0.954	0.963	0.835	0.664
Mean	7.030	7.206	0.607	0.573	0.310	0.592	0.805	0.772	0.764	0.610
Standard Error	0.063	0.079	0.007	0.007	0.015	0.020	0.022	0.057	0.014	0.007
Standard Deviation	0.141	0.284	0.033	0.033	0.054	0.044	0.080	0.127	0.054	0.028
Sample Variance	0.020	0.081	0.001	0.001	0.003	0.002	0.006	0.016	0.003	0.001
CV	2.010	3.942	5.438	5.778	17.436	7.389	9.953	16.449	7.009	4.518

Radial Measures of Variance, Split Sexes, GM adjusted

***Theropithecus gelada*, female only, radius**										
	rLEN1	*rLEN2*	*rPAP*	*rPML*	*rNE1*	*rNE2*	*rNE3*	*rTUB*	*rDML*	*rDAP*
Count	2	5	5	5	5	2	5	2	4	4
Range	0.189	0.570	0.102	0.073	0.109	0.065	0.092	0.128	0.158	0.024
Minimum	7.598	7.819	0.548	0.556	0.222	0.506	0.650	0.881	0.592	0.608
Maximum	7.788	8.389	0.649	0.630	0.332	0.571	0.742	1.009	0.749	0.632
Mean	7.693	8.085	0.604	0.591	0.266	0.538	0.692	0.945	0.691	0.619
Standard Error	0.095	0.103	0.018	0.012	0.025	0.032	0.015	0.064	0.034	0.006
Standard Deviation	0.134	0.230	0.040	0.028	0.056	0.046	0.035	0.091	0.069	0.011
Sample Variance	0.018	0.053	0.002	0.001	0.003	0.002	0.001	0.008	0.005	0.000
CV	1.738	2.850	6.625	4.697	21.164	8.481	4.997	9.615	9.920	1.832

***Theropithecus gelada*, male only, radius**										
	rLEN1	*rLEN2*	*rPAP*	*rPML*	*rNE1*	*rNE2*	*rNE3*	*rTUB*	*rDML*	*rDAP*
Count	2	6	7	7	6	2	6	2	6	6
Range	0.156	0.448	0.074	0.107	0.094	0.065	0.062	0.157	0.102	0.073
Minimum	7.603	7.878	0.569	0.566	0.226	0.446	0.701	0.936	0.708	0.579
Maximum	7.759	8.327	0.643	0.672	0.319	0.512	0.762	1.093	0.810	0.652
Mean	7.681	8.044	0.613	0.609	0.267	0.479	0.732	1.014	0.744	0.619
Standard Error	0.078	0.071	0.009	0.014	0.016	0.033	0.010	0.078	0.017	0.010
Standard Deviation	0.110	0.174	0.025	0.037	0.039	0.046	0.025	0.111	0.042	0.024
Sample Variance	0.012	0.030	0.001	0.001	0.002	0.002	0.001	0.012	0.002	0.001
CV	1.435	2.168	4.023	6.113	14.714	9.631	3.401	10.926	5.708	3.907

Radial Measures of Variance, Split Sexes, GM adjusted

***Macaca fascicularis*, female only, radius**										
	rLEN1	*rLEN2*	*rPAP*	*rPML*	*rNE1*	*rNE2*	*rNE3*	*rTUB*	*rDML*	*rDAP*
Count	2	2	6	6	2	2	2	2	6	6
Range	0.775	0.728	0.121	0.067	0.072	0.110	0.014	0.170	0.148	0.124
Minimum	7.186	7.386	0.548	0.543	0.308	0.613	0.829	0.660	0.705	0.548
Maximum	7.961	8.114	0.669	0.610	0.380	0.722	0.843	0.829	0.853	0.673
Mean	7.574	7.750	0.611	0.575	0.344	0.667	0.836	0.745	0.774	0.592
Standard Error	0.388	0.364	0.020	0.012	0.036	0.055	0.007	0.085	0.023	0.024
Standard Deviation	0.548	0.515	0.050	0.028	0.051	0.078	0.010	0.120	0.055	0.058
Sample Variance	0.301	0.265	0.002	0.001	0.003	0.006	0.000	0.014	0.003	0.003
CV	7.240	6.640	8.145	4.903	14.887	11.619	1.164	16.143	7.156	9.821

***Macaca fascicularis*, male only, radius**										
	rLEN1	*rLEN2*	*rPAP*	*rPML*	*rNE1*	*rNE2*	*rNE3*	*rTUB*	*rDML*	*rDAP*
Count	3	3	6	6	3	3	3	3	6	6
Range	0.817	0.706	0.138	0.034	0.141	0.135	0.187	0.069	0.099	0.100
Minimum	6.260	6.530	0.476	0.501	0.352	0.670	0.813	0.678	0.632	0.489
Maximum	7.077	7.237	0.614	0.535	0.493	0.805	1.000	0.747	0.731	0.589
Mean	6.562	6.776	0.568	0.521	0.432	0.727	0.903	0.705	0.694	0.547
Standard Error	0.259	0.230	0.020	0.006	0.042	0.040	0.054	0.021	0.017	0.017
Standard Deviation	0.448	0.399	0.048	0.014	0.073	0.070	0.094	0.037	0.042	0.042
Sample Variance	0.201	0.159	0.002	0.000	0.005	0.005	0.009	0.001	0.002	0.002
CV	6.834	5.887	8.429	2.727	16.843	9.608	10.380	5.233	6.071	7.623

Radial Measures of Variance, Split Sexes, GM adjusted

***Macaca nemestrina*, female only, radius**

	rLEN1	*rLEN2*	*rPAP*	*rPML*	*rNE1*	*rNE2*	*rNE3*	*rTUB*	*rDML*	*rDAP*
Count	2	2	4	4	2	2	2	2	4	4
Range	0.888	0.910	0.038	0.144	0.142	0.041	0.045	0.020	0.100	0.015
Minimum	6.915	7.150	0.553	0.502	0.255	0.602	0.821	0.714	0.707	0.572
Maximum	7.803	8.061	0.590	0.647	0.398	0.643	0.866	0.734	0.807	0.587
Mean	7.359	7.605	0.570	0.570	0.327	0.623	0.844	0.724	0.770	0.580
Standard Error	0.444	0.455	0.008	0.031	0.071	0.020	0.023	0.010	0.023	0.003
Standard Deviation	0.628	0.644	0.017	0.061	0.101	0.029	0.032	0.014	0.046	0.007
Sample Variance	0.394	0.414	0.000	0.004	0.010	0.001	0.001	0.000	0.002	0.000
CV	8.530	8.462	2.949	10.739	30.843	4.631	3.797	1.965	6.029	1.204

***Macaca nemestrina*, male only, radius**

	rLEN1	*rLEN2*	*rPAP*	*rPML*	*rNE1*	*rNE2*	*rNE3*	*rTUB*	*rDML*	*rDAP*
Count	1	1	6	6	2	1	2	1	6	6
Range	0.000	0.000	0.178	0.176	0.042	0.000	0.002	0.000	0.183	0.165
Minimum	7.214	7.404	0.482	0.468	0.374	0.565	0.824	0.606	0.705	0.489
Maximum	7.214	7.404	0.660	0.644	0.416	0.565	0.826	0.606	0.888	0.654
Mean	7.214	7.404	0.607	0.578	0.395	0.565	0.825	0.606	0.808	0.605
Standard Error	.	.	0.026	0.025	0.021	.	0.001	.	0.026	0.026
Standard Deviation	.	.	0.063	0.061	0.030	.	0.002	.	0.065	0.063
Sample Variance	.	.	0.004	0.004	0.001	.	0.000	.	0.004	0.004
CV	.	.	10.375	10.544	7.539	.	0.189	.	7.995	10.494

Femoral Measures of Variance, Pooled Sexes, GM adjusted

***Homo sapiens*, pooled sexes, femur**																	
	fLEN1	*fLEN2*	*fPML*	*fMLLESS*	*fGT*	*fAPLESS*	*fHEPD*	*fHEML*	*fHEAP*	*fPSPD*	*fPSML*	*fDML*	*fDAP*	*fCPD*	*fCML*	*fICGPD*	*fICGML*
Count	18	18	18	18	18	18	18	18	18	18	18	18	18	18	18	18	18
Range	0.957	1.187	0.283	0.209	0.224	0.225	0.160	0.127	0.182	0.150	0.268	0.188	0.187	0.185	0.240	0.179	0.185
Minimum	7.716	8.027	1.598	0.570	0.078	0.551	0.789	0.698	0.777	0.593	0.731	1.414	1.116	0.667	1.281	0.416	0.294
Maximum	8.673	9.214	1.881	0.780	0.301	0.776	0.948	0.825	0.959	0.743	0.998	1.601	1.303	0.852	1.521	0.595	0.479
Mean	8.214	8.631	1.731	0.698	0.172	0.602	0.870	0.750	0.864	0.657	0.830	1.509	1.209	0.763	1.395	0.524	0.401
Standard Error	0.073	0.084	0.017	0.012	0.015	0.012	0.010	0.010	0.012	0.010	0.016	0.014	0.012	0.013	0.017	0.012	0.012
Standard Deviation	0.310	0.358	0.073	0.053	0.065	0.050	0.043	0.042	0.049	0.041	0.066	0.060	0.052	0.057	0.072	0.050	0.051
Sample Variance	0.096	0.128	0.005	0.003	0.004	0.003	0.002	0.002	0.002	0.002	0.004	0.004	0.003	0.003	0.005	0.003	0.003
CV	3.778	4.152	4.223	7.525	37.766	8.318	4.988	5.536	5.650	6.191	7.959	3.943	4.283	7.481	5.142	9.564	12.795

***Pan troglodytes*, pooled sexes, femur**																	
	fLEN1	*fLEN2*	*fPML*	*fMLLESS*	*fGT*	*fAPLESS*	*fHEPD*	*fHEML*	*fHEAP*	*fPSPD*	*fPSML*	*fDML*	*fDAP*	*fCPD*	*fCML*	*fICGPD*	*fICGML*
Count	13	13	15	15	15	15	15	15	15	14	14	14	14	14	14	14	14
Range	1.036	1.196	0.190	0.230	0.146	0.266	0.096	0.234	0.097	0.136	0.148	0.233	0.414	0.151	0.721	0.242	0.142
Minimum	6.545	6.579	1.456	0.681	0.254	0.569	0.769	0.596	0.769	0.608	0.718	1.373	0.930	0.647	0.732	0.311	0.347
Maximum	7.581	7.775	1.646	0.911	0.400	0.834	0.865	0.830	0.866	0.744	0.866	1.605	1.344	0.798	1.453	0.553	0.490
Mean	7.148	7.237	1.571	0.809	0.334	0.720	0.803	0.714	0.806	0.675	0.796	1.480	1.011	0.731	1.324	0.456	0.425
Standard Error	0.076	0.091	0.017	0.019	0.012	0.019	0.007	0.015	0.006	0.012	0.013	0.017	0.027	0.013	0.047	0.015	0.010
Standard Deviation	0.276	0.328	0.064	0.074	0.048	0.074	0.026	0.059	0.025	0.045	0.049	0.062	0.102	0.050	0.176	0.054	0.036
Sample Variance	0.076	0.108	0.004	0.005	0.002	0.005	0.001	0.003	0.001	0.002	0.002	0.004	0.010	0.003	0.031	0.003	0.001
CV	3.857	4.533	4.076	9.113	14.282	10.248	3.212	8.225	3.102	6.620	6.204	4.199	10.105	6.843	13.303	11.957	8.482

Femoral Measures of Variance, Pooled Sexes, GM adjusted

***Papio hamadryas*, pooled sexes, femur**

	fLEN1	*fLEN2*	*fPML*	*fMLLESS*	*fGT*	*fAPLESS*	*fHEPD*	*fHEML*	*fHEAP*	*fPSPD*	*fPSML*	*fDML*	*fDAP*	*fCPD*	*fCML*	*fICGPD*	*fICGML*
Count	19	19	19	7	17	7	19	19	19	19	7	19	19	19	7	7	7
Range	1.179	1.328	0.188	0.108	0.176	0.096	0.097	0.188	0.076	0.225	0.093	0.236	0.160	0.100	0.091	0.105	0.073
Minimum	7.752	7.418	1.512	0.683	0.408	0.597	0.719	0.591	0.739	0.544	0.687	1.145	0.967	0.657	1.153	0.401	0.328
Maximum	8.931	8.746	1.700	0.790	0.584	0.693	0.816	0.779	0.815	0.769	0.780	1.381	1.127	0.757	1.244	0.506	0.401
Mean	8.274	8.012	1.599	0.741	0.486	0.649	0.759	0.698	0.770	0.657	0.729	1.274	1.050	0.716	1.213	0.450	0.370
Standard Error	0.075	0.075	0.014	0.014	0.013	0.014	0.006	0.013	0.005	0.015	0.013	0.014	0.009	0.006	0.011	0.015	0.009
Standard Deviation	0.328	0.325	0.063	0.038	0.055	0.036	0.027	0.058	0.022	0.067	0.034	0.060	0.040	0.026	0.030	0.041	0.023
Sample Variance	0.108	0.106	0.004	0.001	0.003	0.001	0.001	0.003	0.001	0.004	0.001	0.004	0.002	0.001	0.001	0.002	0.001
CV	3.967	4.062	3.939	5.105	11.269	5.596	3.605	8.337	2.915	10.147	4.687	4.695	3.805	3.645	2.468	9.036	6.328

***Theropithecus gelada*, pooled sexes, femur**

	fLEN1	*fLEN2*	*fPML*	*fMLLESS*	*fGT*	*fAPLESS*	*fHEPD*	*fHEML*	*fHEAP*	*fPSPD*	*fPSML*	*fDML*	*fDAP*	*fCPD*	*fCML*	*fICGPD*	*fICGML*
Count	10	10	10	4	9	4	10	10	10	9	4	9	9	9	4	4	4
Range	0.524	0.515	0.209	0.074	0.150	0.229	0.079	0.152	0.081	0.176	0.098	0.086	0.086	0.131	0.058	0.037	0.050
Minimum	7.394	7.270	1.454	0.600	0.391	0.653	0.724	0.615	0.730	0.604	0.750	1.256	1.009	0.629	1.198	0.446	0.396
Maximum	7.917	7.785	1.663	0.674	0.540	0.882	0.804	0.767	0.811	0.780	0.848	1.342	1.095	0.760	1.256	0.484	0.446
Mean	7.666	7.446	1.525	0.640	0.461	0.796	0.757	0.690	0.765	0.662	0.786	1.307	1.041	0.696	1.237	0.463	0.423
Standard Error	0.052	0.060	0.017	0.017	0.016	0.055	0.008	0.019	0.008	0.018	0.022	0.009	0.010	0.013	0.013	0.009	0.010
Standard Deviation	0.165	0.191	0.055	0.035	0.047	0.110	0.024	0.060	0.026	0.055	0.044	0.028	0.029	0.038	0.026	0.018	0.021
Sample Variance	0.027	0.037	0.003	0.001	0.002	0.012	0.001	0.004	0.001	0.003	0.002	0.001	0.001	0.001	0.001	0.000	0.000
CV	2.148	2.568	3.605	5.407	10.165	13.766	3.224	8.704	3.409	8.376	5.627	2.119	2.755	5.422	2.114	3.980	4.907

Femoral Measures of Variance, Pooled Sexes, GM adjusted

***Macaca fascicularis*, pooled sexes, femur**

	fLEN1	*fLEN2*	*fPML*	*fMLLESS*	*fGT*	*fAPLESS*	*fHEPD*	*fHEML*	*fHEAP*	*fPSPD*	*fPSML*	*fDML*	*fDAP*	*fCPD*	*fCML*	*fICGPD*	*fICGML*
Count	10	10	11	5	11	5	11	11	11	10	5	10	10	10	5	5	5
Range	1.347	1.355	0.197	0.404	0.088	0.098	0.073	0.254	0.074	0.276	0.086	0.137	0.149	0.130	0.114	0.104	0.099
Minimum	8.144	7.965	1.432	0.587	0.382	0.624	0.723	0.626	0.739	0.582	0.585	1.199	0.975	0.692	1.197	0.435	0.342
Maximum	9.491	9.320	1.629	0.991	0.470	0.723	0.796	0.879	0.813	0.858	0.670	1.336	1.124	0.821	1.312	0.539	0.440
Mean	8.750	8.581	1.542	0.839	0.418	0.663	0.753	0.743	0.772	0.725	0.619	1.290	1.044	0.741	1.241	0.461	0.374
Standard Error	0.125	0.125	0.019	0.070	0.009	0.017	0.009	0.030	0.008	0.028	0.020	0.014	0.014	0.012	0.019	0.020	0.017
Standard Deviation	0.396	0.395	0.062	0.157	0.028	0.037	0.028	0.099	0.026	0.090	0.044	0.046	0.045	0.037	0.043	0.044	0.038
Sample Variance	0.157	0.156	0.004	0.025	0.001	0.001	0.001	0.010	0.001	0.008	0.002	0.002	0.002	0.001	0.002	0.002	0.001
CV	4.525	4.599	4.052	18.674	6.783	5.589	3.750	13.279	3.309	12.354	7.144	3.554	4.343	4.973	3.498	9.553	10.151

***Macaca nemestrina*, pooled sexes, femur**

	fLEN1	*fLEN2*	*fPML*	*fMLLESS*	*fGT*	*fAPLESS*	*fHEPD*	*fHEML*	*fHEAP*	*fPSPD*	*fPSML*	*fDML*	*fDAP*	*fCPD*	*fCML*	*fICGPD*	*fICGML*
Count	4	4	4	3	4	3	4	4	4	4	3	4	4	4	3	3	3
Range	1.259	1.298	0.146	0.136	0.124	0.146	0.117	0.098	0.097	0.082	0.185	0.105	0.067	0.136	0.035	0.153	0.035
Minimum	7.895	7.767	1.438	0.802	0.301	0.591	0.690	0.571	0.722	0.668	0.621	1.208	1.013	0.631	1.215	0.393	0.390
Maximum	9.154	9.065	1.583	0.937	0.425	0.738	0.807	0.669	0.819	0.750	0.805	1.313	1.080	0.767	1.251	0.546	0.426
Mean	8.682	8.593	1.490	0.880	0.360	0.658	0.743	0.639	0.751	0.718	0.700	1.257	1.054	0.702	1.229	0.491	0.413
Standard Error	0.287	0.298	0.032	0.041	0.026	0.043	0.025	0.023	0.023	0.019	0.055	0.025	0.014	0.031	0.011	0.049	0.011
Standard Deviation	0.574	0.596	0.065	0.070	0.052	0.074	0.050	0.045	0.046	0.038	0.095	0.049	0.029	0.062	0.019	0.085	0.019
Sample Variance	0.329	0.355	0.004	0.005	0.003	0.005	0.002	0.002	0.002	0.001	0.009	0.002	0.001	0.004	0.000	0.007	0.000
CV	6.610	6.933	4.332	7.981	14.403	11.232	6.689	7.122	6.126	5.284	13.574	3.900	2.734	8.795	1.535	17.332	4.681

Femoral Measures of Variance, Split Sexes, GM adjusted

***Homo sapiens*, female only, femur**

	fLEN1	*fLEN2*	*fPML*	*fMLLESS*	*fGT*	*fAPLESS*	*fHEPD*	*fHEML*	*fHEAP*	*fPSPD*	*fPSML*	*fDML*	*fDAP*	*fCPD*	*fCML*	*fICGPD*	*fICGML*
Count	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Range	0.957	1.064	0.220	0.207	0.189	0.075	0.095	0.094	0.083	0.114	0.113	0.139	0.187	0.144	0.163	0.165	0.185
Minimum	7.716	8.116	1.598	0.570	0.112	0.551	0.791	0.698	0.794	0.597	0.731	1.414	1.116	0.708	1.281	0.416	0.294
Maximum	8.673	9.180	1.818	0.778	0.301	0.626	0.886	0.792	0.878	0.711	0.844	1.553	1.303	0.852	1.444	0.581	0.479
Mean	8.177	8.611	1.710	0.687	0.205	0.582	0.848	0.728	0.841	0.665	0.807	1.480	1.206	0.786	1.353	0.516	0.398
Standard Error	0.119	0.119	0.025	0.021	0.019	0.009	0.011	0.011	0.010	0.012	0.011	0.017	0.017	0.017	0.020	0.018	0.021
Standard Deviation	0.357	0.358	0.075	0.062	0.056	0.026	0.032	0.033	0.030	0.036	0.033	0.050	0.052	0.052	0.059	0.055	0.062
Sample Variance	0.127	0.128	0.006	0.004	0.003	0.001	0.001	0.001	0.001	0.001	0.001	0.002	0.003	0.003	0.004	0.003	0.004
CV	4.363	4.153	4.413	8.983	27.611	4.505	3.777	4.581	3.598	5.458	4.079	3.370	4.318	6.611	4.399	10.745	15.573

***Homo sapiens*, male only, femur**

	fLEN1	*fLEN2*	*fPML*	*fMLLESS*	*fGT*	*fAPLESS*	*fHEPD*	*fHEML*	*fHEAP*	*fPSPD*	*fPSML*	*fDML*	*fDAP*	*fCPD*	*fCML*	*fICGPD*	*fICGML*
Count	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Range	0.747	1.187	0.210	0.137	0.187	0.193	0.160	0.118	0.182	0.150	0.246	0.181	0.161	0.174	0.154	0.158	0.148
Minimum	7.824	8.027	1.671	0.643	0.078	0.583	0.789	0.708	0.777	0.593	0.753	1.420	1.134	0.667	1.366	0.437	0.326
Maximum	8.571	9.214	1.881	0.780	0.264	0.776	0.948	0.825	0.959	0.743	0.998	1.601	1.294	0.841	1.521	0.595	0.475
Mean	8.251	8.650	1.751	0.709	0.139	0.623	0.891	0.771	0.887	0.649	0.852	1.538	1.212	0.741	1.438	0.533	0.403
Standard Error	0.091	0.127	0.023	0.014	0.019	0.020	0.015	0.013	0.018	0.015	0.028	0.019	0.018	0.018	0.019	0.015	0.014
Standard Deviation	0.273	0.380	0.069	0.042	0.058	0.061	0.044	0.039	0.054	0.045	0.084	0.056	0.054	0.055	0.057	0.046	0.042
Sample Variance	0.074	0.144	0.005	0.002	0.003	0.004	0.002	0.001	0.003	0.002	0.007	0.003	0.003	0.003	0.003	0.002	0.002
CV	3.306	4.389	3.920	5.953	41.662	9.792	4.947	4.996	6.095	6.987	9.851	3.659	4.491	7.462	3.986	8.646	10.305

Femoral Measures of Variance, Split Sexes, GM adjusted

***Pan troglodytes*, female only, femur**

	fLEN1	*fLEN2*	*fPML*	*fMLLESS*	*fGT*	*fAPLESS*	*fHEPD*	*fHEML*	*fHEAP*	*fPSPD*	*fPSML*	*fDML*	*fDAP*	*fCPD*	*fCML*	*fICGPD*	*fICGML*
Count	8	8	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Range	0.680	0.832	0.190	0.230	0.143	0.266	0.064	0.149	0.069	0.119	0.130	0.233	0.414	0.140	0.721	0.137	0.097
Minimum	6.901	6.942	1.456	0.681	0.254	0.569	0.770	0.603	0.769	0.608	0.736	1.373	0.930	0.656	0.732	0.416	0.378
Maximum	7.581	7.775	1.646	0.911	0.397	0.834	0.834	0.752	0.839	0.727	0.866	1.605	1.344	0.796	1.453	0.553	0.474
Mean	7.235	7.347	1.550	0.783	0.327	0.729	0.798	0.709	0.805	0.665	0.806	1.490	1.015	0.729	1.316	0.473	0.428
Standard Error	0.090	0.110	0.024	0.024	0.016	0.031	0.007	0.016	0.007	0.014	0.015	0.023	0.042	0.016	0.074	0.014	0.009
Standard Deviation	0.256	0.312	0.072	0.073	0.048	0.094	0.020	0.049	0.020	0.043	0.046	0.068	0.127	0.047	0.223	0.042	0.026
Sample Variance	0.065	0.098	0.005	0.005	0.002	0.009	0.000	0.002	0.000	0.002	0.002	0.005	0.016	0.002	0.050	0.002	0.001
CV	3.536	4.252	4.615	9.357	14.763	12.845	2.486	6.934	2.423	6.490	5.673	4.578	12.528	6.503	16.929	8.882	6.180

***Pan troglodytes*, male only, femur**

	fLEN1	*fLEN2*	*fPML*	*fMLLESS*	*fGT*	*fAPLESS*	*fHEPD*	*fHEML*	*fHEAP*	*fPSPD*	*fPSML*	*fDML*	*fDAP*	*fCPD*	*fCML*	*fICGPD*	*fICGML*
Count	5	5	6	6	6	6	6	6	6	5	5	5	5	5	5	5	5
Range	0.710	0.789	0.102	0.172	0.145	0.075	0.096	0.234	0.093	0.105	0.122	0.124	0.109	0.151	0.073	0.164	0.142
Minimum	6.545	6.579	1.541	0.737	0.255	0.676	0.769	0.596	0.774	0.639	0.718	1.388	0.954	0.647	1.295	0.311	0.347
Maximum	7.255	7.368	1.643	0.908	0.400	0.751	0.865	0.830	0.866	0.744	0.840	1.512	1.062	0.798	1.367	0.475	0.490
Mean	7.008	7.060	1.602	0.848	0.344	0.705	0.810	0.722	0.809	0.693	0.778	1.460	1.004	0.734	1.338	0.424	0.419
Standard Error	0.122	0.133	0.015	0.024	0.020	0.011	0.014	0.031	0.014	0.021	0.025	0.022	0.017	0.027	0.015	0.029	0.023
Standard Deviation	0.272	0.298	0.036	0.060	0.049	0.027	0.034	0.075	0.034	0.046	0.056	0.050	0.039	0.060	0.034	0.064	0.052
Sample Variance	0.074	0.089	0.001	0.004	0.002	0.001	0.001	0.006	0.001	0.002	0.003	0.003	0.002	0.004	0.001	0.004	0.003
CV	3.883	4.215	2.257	7.051	14.318	3.824	4.147	10.432	4.161	6.697	7.153	3.433	3.867	8.197	2.549	15.157	12.522

Femoral Measures of Variance, Split Sexes, GM adjusted

***Papio hamadryas*, female only, femur**

	fLEN1	*fLEN2*	*fPML*	*fMLLESS*	*fGT*	*fAPLESS*	*fHEPD*	*fHEML*	*fHEAP*	*fPSPD*	*fPSML*	*fDML*	*fDAP*	*fCPD*	*fCML*	*fICGPD*	*fICGML*
Count	6	6	6	2	4	2	6	6	6	6	2	6	6	6	2	2	2
Range	0.882	0.895	0.164	0.005	0.062	0.026	0.080	0.114	0.071	0.144	0.011	0.090	0.057	0.062	0.085	0.105	0.025
Minimum	7.964	7.696	1.512	0.735	0.408	0.664	0.734	0.647	0.743	0.594	0.702	1.205	0.994	0.657	1.153	0.401	0.376
Maximum	8.846	8.592	1.676	0.741	0.471	0.690	0.813	0.761	0.814	0.738	0.714	1.294	1.051	0.719	1.238	0.506	0.401
Mean	8.262	8.039	1.574	0.738	0.434	0.677	0.762	0.707	0.772	0.650	0.708	1.245	1.022	0.690	1.196	0.453	0.388
Standard Error	0.125	0.124	0.028	0.003	0.013	0.013	0.012	0.016	0.011	0.026	0.006	0.016	0.011	0.010	0.043	0.052	0.013
Standard Deviation	0.306	0.303	0.068	0.004	0.026	0.018	0.029	0.039	0.027	0.064	0.008	0.039	0.026	0.024	0.060	0.074	0.018
Sample Variance	0.094	0.092	0.005	0.000	0.001	0.000	0.001	0.002	0.001	0.004	0.000	0.002	0.001	0.001	0.004	0.005	0.000
CV	3.708	3.770	4.334	0.506	6.072	2.693	3.746	5.501	3.465	9.814	1.113	3.153	2.521	3.422	5.040	16.345	4.631

***Papio hamadryas*, male only, femur**

	fLEN1	*fLEN2*	*fPML*	*fMLLESS*	*fGT*	*fAPLESS*	*fHEPD*	*fHEML*	*fHEAP*	*fPSPD*	*fPSML*	*fDML*	*fDAP*	*fCPD*	*fCML*	*fICGPD*	*fICGML*
Count	13	13	13	5	13	5	13	13	13	13	5	13	13	13	5	5	5
Range	1.179	1.328	0.188	0.108	0.164	0.096	0.097	0.188	0.076	0.225	0.093	0.236	0.160	0.058	0.039	0.088	0.062
Minimum	7.752	7.418	1.512	0.683	0.420	0.597	0.719	0.591	0.739	0.544	0.687	1.145	0.967	0.699	1.205	0.403	0.328
Maximum	8.931	8.746	1.700	0.790	0.584	0.693	0.816	0.779	0.815	0.769	0.780	1.381	1.127	0.757	1.244	0.491	0.391
Mean	8.279	8.000	1.611	0.742	0.502	0.638	0.757	0.693	0.769	0.660	0.737	1.287	1.063	0.728	1.220	0.448	0.363
Standard Error	0.097	0.096	0.017	0.021	0.014	0.017	0.008	0.018	0.006	0.019	0.017	0.018	0.011	0.005	0.007	0.015	0.010
Standard Deviation	0.350	0.347	0.060	0.046	0.052	0.037	0.028	0.066	0.021	0.070	0.038	0.064	0.039	0.017	0.015	0.033	0.022
Sample Variance	0.122	0.120	0.004	0.002	0.003	0.001	0.001	0.004	0.000	0.005	0.001	0.004	0.002	0.000	0.000	0.001	0.001
CV	4.225	4.331	3.696	6.231	10.287	5.792	3.672	9.543	2.774	10.642	5.123	4.984	3.709	2.376	1.224	7.373	6.197

Femoral Measures of Variance, Split Sexes, GM adjusted

***Theropithecus gelada*, female only, femur**

	fLEN1	*fLEN2*	*fPML*	*fMLLESS*	*fGT*	*fAPLESS*	*fHEPD*	*fHEML*	*fHEAP*	*fPSPD*	*fPSML*	*fDML*	*fDAP*	*fCPD*	*fCML*	*fICGPD*	*fICGML*
Count	5	5	5	2	4	2	5	5	5	4	2	4	4	4	2	2	2
Range	0.524	0.515	0.158	0.040	0.056	0.116	0.079	0.136	0.059	0.077	0.026	0.081	0.016	0.099	0.048	0.026	0.023
Minimum	7.394	7.270	1.505	0.623	0.391	0.767	0.724	0.631	0.752	0.630	0.760	1.256	1.009	0.661	1.198	0.446	0.423
Maximum	7.917	7.785	1.663	0.663	0.447	0.882	0.804	0.767	0.811	0.707	0.785	1.337	1.024	0.760	1.246	0.472	0.446
Mean	7.667	7.510	1.551	0.643	0.421	0.824	0.763	0.694	0.777	0.655	0.773	1.305	1.016	0.705	1.222	0.459	0.434
Standard Error	0.093	0.096	0.029	0.020	0.012	0.058	0.014	0.028	0.012	0.018	0.013	0.018	0.004	0.021	0.024	0.013	0.012
Standard Deviation	0.208	0.214	0.066	0.028	0.024	0.082	0.031	0.062	0.028	0.036	0.018	0.035	0.007	0.042	0.034	0.019	0.016
Sample Variance	0.043	0.046	0.004	0.001	0.001	0.007	0.001	0.004	0.001	0.001	0.000	0.001	0.000	0.002	0.001	0.000	0.000
CV	2.707	2.851	4.245	4.398	5.780	9.911	4.008	8.884	3.587	5.424	2.334	2.692	0.697	6.013	2.769	4.039	3.759

***Theropithecus gelada*, male only, femur**

	fLEN1	*fLEN2*	*fPML*	*fMLLESS*	*fGT*	*fAPLESS*	*fHEPD*	*fHEML*	*fHEAP*	*fPSPD*	*fPSML*	*fDML*	*fDAP*	*fCPD*	*fCML*	*fICGPD*	*fICGML*
Count	5	5	5	2	5	2	5	5	5	5	2	5	5	5	2	2	2
Range	0.328	0.394	0.073	0.074	0.087	0.228	0.042	0.150	0.050	0.176	0.098	0.058	0.058	0.089	0.009	0.036	0.032
Minimum	7.562	7.276	1.454	0.600	0.453	0.653	0.728	0.615	0.730	0.604	0.750	1.285	1.037	0.629	1.248	0.448	0.396
Maximum	7.890	7.670	1.527	0.674	0.540	0.881	0.770	0.765	0.780	0.780	0.848	1.342	1.095	0.719	1.256	0.484	0.427
Mean	7.665	7.382	1.499	0.637	0.492	0.767	0.752	0.687	0.754	0.668	0.799	1.309	1.060	0.688	1.252	0.466	0.411
Standard Error	0.060	0.073	0.012	0.037	0.015	0.114	0.008	0.029	0.009	0.032	0.049	0.011	0.010	0.016	0.004	0.018	0.016
Standard Deviation	0.134	0.162	0.028	0.053	0.034	0.161	0.018	0.065	0.020	0.071	0.070	0.024	0.023	0.037	0.006	0.025	0.022
Sample Variance	0.018	0.026	0.001	0.003	0.001	0.026	0.000	0.004	0.000	0.005	0.005	0.001	0.001	0.001	0.000	0.001	0.001
CV	1.748	2.197	1.849	8.250	6.971	21.026	2.423	9.533	2.717	10.698	8.714	1.869	2.184	5.323	0.488	5.397	5.448

Femoral Measures of Variance, Split Sexes, GM adjusted

***Macaca fascicularis*, female only, femur**

	fLEN1	*fLEN2*	*fPML*	*fMLLESS*	*fGT*	*fAPLESS*	*fHEPD*	*fHEML*	*fHEAP*	*fPSPD*	*fPSML*	*fDML*	*fDAP*	*fCPD*	*fCML*	*fICGPD*	*fICGML*
Count	6	6	6	2	6	2	6	6	6	6	2	6	6	6	2	2	2
Range	1.029	0.880	0.152	0.319	0.088	0.024	0.060	0.254	0.046	0.172	0.078	0.075	0.117	0.078	0.047	0.094	0.074
Minimum	8.462	8.439	1.477	0.587	0.382	0.644	0.736	0.626	0.757	0.627	0.586	1.254	0.975	0.743	1.197	0.445	0.366
Maximum	9.491	9.320	1.629	0.907	0.470	0.669	0.796	0.879	0.803	0.799	0.664	1.329	1.092	0.821	1.244	0.539	0.440
Mean	8.950	8.812	1.536	0.747	0.413	0.656	0.770	0.776	0.781	0.702	0.625	1.306	1.035	0.762	1.221	0.492	0.403
Standard Error	0.144	0.126	0.026	0.160	0.015	0.012	0.010	0.045	0.008	0.025	0.039	0.011	0.016	0.012	0.023	0.047	0.037
Standard Deviation	0.353	0.308	0.063	0.226	0.037	0.017	0.023	0.111	0.019	0.062	0.055	0.027	0.039	0.030	0.033	0.066	0.052
Sample Variance	0.124	0.095	0.004	0.051	0.001	0.000	0.001	0.012	0.000	0.004	0.003	0.001	0.002	0.001	0.001	0.004	0.003
CV	3.940	3.499	4.123	30.232	8.877	2.636	3.026	14.281	2.377	8.831	8.774	2.038	3.769	3.950	2.699	13.498	13.009

***Macaca fascicularis*, male only, femur**

	fLEN1	*fLEN2*	*fPML*	*fMLLESS*	*fGT*	*fAPLESS*	*fHEPD*	*fHEML*	*fHEAP*	*fPSPD*	*fPSML*	*fDML*	*fDAP*	*fCPD*	*fCML*	*fICGPD*	*fICGML*
Count	4	4	5	3	5	3	5	5	5	4	3	4	4	4	3	3	3
Range	0.608	0.497	0.171	0.193	0.037	0.098	0.042	0.178	0.074	0.276	0.086	0.137	0.134	0.045	0.096	0.010	0.023
Minimum	8.144	7.965	1.432	0.798	0.402	0.624	0.723	0.629	0.739	0.582	0.585	1.199	0.990	0.692	1.216	0.435	0.342
Maximum	8.752	8.462	1.603	0.991	0.438	0.723	0.766	0.808	0.813	0.858	0.670	1.336	1.124	0.737	1.312	0.445	0.364
Mean	8.449	8.234	1.549	0.901	0.423	0.668	0.733	0.703	0.763	0.758	0.615	1.266	1.058	0.710	1.255	0.440	0.355
Standard Error	0.124	0.102	0.030	0.056	0.007	0.029	0.008	0.033	0.014	0.062	0.028	0.031	0.028	0.010	0.029	0.003	0.007
Standard Deviation	0.248	0.204	0.068	0.097	0.016	0.050	0.018	0.074	0.031	0.123	0.048	0.062	0.057	0.019	0.050	0.005	0.012
Sample Variance	0.062	0.042	0.005	0.009	0.000	0.003	0.000	0.005	0.001	0.015	0.002	0.004	0.003	0.000	0.003	0.000	0.000
CV	2.940	2.481	4.394	10.785	3.800	7.510	2.524	10.473	4.123	16.249	7.866	4.893	5.360	2.747	4.011	1.110	3.392

Femoral Measures of Variance, Split Sexes, GM adjusted

***Macaca nemestrina*, female only, femur**

	fLEN1	*fLEN2*	*fPML*	*fMLLESS*	*fGT*	*fAPLESS*	*fHEPD*	*fHEML*	*fHEAP*	*fPSPD*	*fPSML*	*fDML*	*fDAP*	*fCPD*	*fCML*	*fICGPD*	*fICGML*
Count	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
Range	0.440	0.514	0.100	0.136	0.042	0.146	0.054	0.011	0.094	0.077	0.053	0.031	0.014	0.028	0.035	0.141	0.004
Minimum	8.619	8.551	1.483	0.802	0.301	0.591	0.752	0.658	0.724	0.668	0.621	1.282	1.066	0.739	1.215	0.393	0.422
Maximum	9.060	9.065	1.583	0.937	0.343	0.738	0.807	0.669	0.819	0.745	0.674	1.313	1.080	0.767	1.251	0.534	0.426
Mean	8.839	8.808	1.533	0.870	0.322	0.664	0.780	0.664	0.772	0.707	0.647	1.297	1.073	0.753	1.233	0.464	0.424
Standard Error	0.220	0.257	0.050	0.068	0.021	0.073	0.027	0.005	0.047	0.038	0.027	0.015	0.007	0.014	0.018	0.071	0.002
Standard Deviation	0.311	0.363	0.071	0.096	0.030	0.103	0.038	0.008	0.067	0.054	0.038	0.022	0.010	0.020	0.025	0.100	0.003
Sample Variance	0.097	0.132	0.005	0.009	0.001	0.011	0.001	0.000	0.004	0.003	0.001	0.000	0.000	0.000	0.001	0.010	0.000
CV	3.524	4.125	4.607	11.040	9.258	15.562	4.919	1.148	8.644	7.662	5.801	1.668	0.946	2.638	2.030	21.537	0.691

***Macaca nemestrina*, male only, femur**

	fLEN1	*fLEN2*	*fPML*	*fMLLESS*	*fGT*	*fAPLESS*	*fHEPD*	*fHEML*	*fHEAP*	*fPSPD*	*fPSML*	*fDML*	*fDAP*	*fCPD*	*fCML*	*fICGPD*	*fICGML*
Count	2	2	2	1	2	1	2	2	2	2	1	2	2	2	1	1	1
Range	1.259	1.223	0.020	0.000	0.055	0.000	0.033	0.086	0.016	0.042	0.000	0.017	0.046	0.041	0.000	0.000	0.000
Minimum	7.895	7.767	1.438	0.901	0.370	0.646	0.690	0.571	0.722	0.708	0.805	1.208	1.013	0.631	1.222	0.546	0.390
Maximum	9.154	8.990	1.458	0.901	0.425	0.646	0.723	0.657	0.738	0.750	0.805	1.225	1.059	0.672	1.222	0.546	0.390
Mean	8.525	8.378	1.448	0.901	0.397	0.646	0.706	0.614	0.730	0.729	0.805	1.216	1.036	0.652	1.222	0.546	0.390
Standard Error	0.629	0.612	0.010	.	0.028	.	0.017	0.043	0.008	0.021	.	0.009	0.023	0.020	.	.	.
Standard Deviation	0.890	0.865	0.014	.	0.039	.	0.023	0.061	0.011	0.030	.	0.012	0.032	0.029	.	.	.
Sample Variance	0.792	0.748	0.000	.	0.002	.	0.001	0.004	0.000	0.001	.	0.000	0.001	0.001	.	.	.
CV	10.441	10.323	0.990	.	9.813	.	3.310	9.883	1.541	4.104	.	1.010	3.109	4.419	.	.	.

Tibial Measures of Variance, Pooled Sexes, GM adjusted

***Homo sapiens*, pooled sexes, tibia**												
	tLEN1	*tLEN2*	*tPML*	*tPAP*	*tLFAP*	*tMFAP*	*tLFML*	*tMFML*	*tDAP*	*tDML*	*tMMPD*	*tDASML*
Count	17	17	17	17	17	17	17	17	17	17	17	17
Range	1.007	1.319	0.100	0.135	0.137	0.118	0.130	0.107	0.138	0.149	0.160	0.166
Minimum	6.580	6.122	1.357	0.901	0.654	0.787	0.470	0.490	0.675	0.803	0.188	0.444
Maximum	7.587	7.441	1.457	1.035	0.792	0.905	0.601	0.597	0.813	0.952	0.348	0.610
Mean	7.089	6.925	1.407	0.967	0.725	0.846	0.539	0.540	0.733	0.873	0.261	0.515
Standard Error	0.075	0.084	0.007	0.009	0.010	0.009	0.009	0.007	0.009	0.010	0.009	0.011
Standard Deviation	0.307	0.346	0.029	0.036	0.040	0.039	0.035	0.028	0.038	0.040	0.038	0.045
Sample Variance	0.094	0.120	0.001	0.001	0.002	0.002	0.001	0.001	0.001	0.002	0.001	0.002
CV	4.333	4.999	2.044	3.710	5.464	4.628	6.528	5.164	5.210	4.638	14.630	8.721

***Pan troglodytes*, pooled sexes, tibia**												
	tLEN1	*tLEN2*	*tPML*	*tPAP*	*tLFAP*	*tMFAP*	*tLFML*	*tMFML*	*tDAP*	*tDML*	*tMMPD*	*tDASML*
Count	15	14	15	15	15	15	15	15	15	15	15	15
Range	1.042	1.030	0.106	0.074	0.206	0.192	0.118	0.077	0.227	0.122	0.091	0.196
Minimum	5.531	5.298	1.341	0.877	0.626	0.662	0.540	0.557	0.597	0.809	0.294	0.501
Maximum	6.573	6.328	1.448	0.951	0.832	0.853	0.658	0.634	0.824	0.932	0.385	0.696
Mean	6.069	5.842	1.401	0.919	0.729	0.788	0.594	0.594	0.641	0.871	0.334	0.593
Standard Error	0.094	0.099	0.009	0.005	0.014	0.015	0.008	0.007	0.015	0.010	0.006	0.014
Standard Deviation	0.364	0.370	0.035	0.020	0.054	0.058	0.033	0.025	0.057	0.039	0.024	0.055
Sample Variance	0.133	0.137	0.001	0.000	0.003	0.003	0.001	0.001	0.003	0.002	0.001	0.003
CV	6.001	6.331	2.499	2.135	7.448	7.400	5.481	4.281	8.877	4.488	7.205	9.358

Tibial Measures of Variance, Pooled Sexes, GM adjusted

***Papio hamadryas*, pooled sexes, tibia**

	tLEN1	*tLEN2*	*tPML*	*tPAP*	*tLFAP*	*tMFAP*	*tLFML*	*tMFML*	*tDAP*	*tDML*	*tMMPD*	*tDASML*
Count	20	20	35	35	35	35	23	23	20	35	23	23
Range	1.371	1.349	0.170	0.219	0.198	0.189	0.115	0.090	0.082	0.148	0.149	0.124
Minimum	6.657	6.320	1.212	0.873	0.664	0.723	0.521	0.498	0.641	0.734	0.222	0.452
Maximum	8.028	7.668	1.382	1.092	0.862	0.912	0.636	0.589	0.723	0.882	0.371	0.576
Mean	7.076	6.780	1.295	0.985	0.749	0.823	0.577	0.543	0.681	0.820	0.280	0.531
Standard Error	0.082	0.083	0.006	0.010	0.007	0.007	0.006	0.004	0.005	0.006	0.009	0.008
Standard Deviation	0.365	0.373	0.037	0.058	0.040	0.040	0.028	0.020	0.023	0.035	0.045	0.040
Sample Variance	0.133	0.139	0.001	0.003	0.002	0.002	0.001	0.000	0.001	0.001	0.002	0.002
CV	5.159	5.495	2.842	5.842	5.311	4.827	4.774	3.644	3.449	4.277	16.100	7.602

***Theropithecus gelada*, pooled sexes, tibia**

	tLEN1	*tLEN2*	*tPML*	*tPAP*	*tLFAP*	*tMFAP*	*tLFML*	*tMFML*	*tDAP*	*tDML*	*tMMPD*	*tDASML*
Count	11	11	12	12	12	12	10	10	11	12	10	10
Range	0.763	0.758	0.114	0.175	0.123	0.162	0.141	0.070	0.042	0.119	0.148	0.104
Minimum	7.028	6.704	1.284	0.887	0.667	0.732	0.463	0.496	0.657	0.756	0.231	0.493
Maximum	7.791	7.462	1.398	1.062	0.789	0.895	0.605	0.566	0.699	0.875	0.379	0.598
Mean	7.367	7.000	1.326	0.984	0.735	0.805	0.547	0.543	0.669	0.831	0.286	0.554
Standard Error	0.060	0.065	0.009	0.018	0.010	0.016	0.015	0.007	0.004	0.010	0.018	0.012
Standard Deviation	0.200	0.214	0.030	0.062	0.035	0.054	0.048	0.023	0.014	0.035	0.058	0.039
Sample Variance	0.040	0.046	0.001	0.004	0.001	0.003	0.002	0.001	0.000	0.001	0.003	0.002
CV	2.713	3.059	2.226	6.265	4.732	6.678	8.684	4.147	2.140	4.263	20.358	7.064

Tibial Measures of Variance, Pooled Sexes, GM adjusted

***Macaca fascicularis*, pooled sexes, tibia**

	tLEN1	*tLEN2*	*tPML*	*tPAP*	*tLFAP*	*tMFAP*	*tLFML*	*tMFML*	*tDAP*	*tDML*	*tMMPD*	*tDASML*
Count	5	5	12	12	12	12	12	12	5	12	12	12
Range	1.176	1.141	0.125	0.128	0.157	0.241	0.158	0.082	0.014	0.152	0.135	0.189
Minimum	7.193	6.958	1.211	0.883	0.711	0.712	0.463	0.495	0.642	0.736	0.212	0.451
Maximum	8.370	8.099	1.336	1.011	0.867	0.953	0.620	0.577	0.656	0.887	0.347	0.640
Mean	7.799	7.522	1.277	0.941	0.796	0.804	0.576	0.529	0.648	0.811	0.273	0.545
Standard Error	0.224	0.219	0.013	0.013	0.013	0.020	0.012	0.009	0.003	0.014	0.013	0.013
Standard Deviation	0.501	0.490	0.045	0.046	0.044	0.069	0.043	0.031	0.006	0.049	0.046	0.046
Sample Variance	0.251	0.240	0.002	0.002	0.002	0.005	0.002	0.001	0.000	0.002	0.002	0.002
CV	6.422	6.508	3.547	4.918	5.528	8.564	7.474	5.916	0.874	6.010	16.923	8.446

***Macaca nemestrina*, pooled sexes, tibia**

	tLEN1	*tLEN2*	*tPML*	*tPAP*	*tLFAP*	*tMFAP*	*tLFML*	*tMFML*	*tDAP*	*tDML*	*tMMPD*	*tDASML*
Count	4	4	9	9	9	9	8	8	4	9	8	8
Range	1.187	1.202	0.194	0.294	0.134	0.066	0.265	0.107	0.035	0.107	0.104	0.167
Minimum	7.123	6.748	1.222	0.863	0.674	0.740	0.429	0.479	0.635	0.761	0.230	0.427
Maximum	8.310	7.951	1.416	1.157	0.808	0.807	0.694	0.586	0.670	0.868	0.334	0.594
Mean	7.808	7.467	1.311	0.940	0.749	0.778	0.578	0.539	0.659	0.807	0.271	0.506
Standard Error	0.292	0.293	0.022	0.031	0.013	0.009	0.027	0.012	0.008	0.012	0.016	0.019
Standard Deviation	0.583	0.587	0.065	0.092	0.039	0.026	0.076	0.035	0.016	0.037	0.046	0.054
Sample Variance	0.340	0.344	0.004	0.009	0.002	0.001	0.006	0.001	0.000	0.001	0.002	0.003
CV	7.471	7.859	4.965	9.832	5.209	3.280	13.111	6.520	2.423	4.645	16.859	10.627

Tibial Measures of Variance, Split Sexes, GM adjusted

***Homo sapiens*, female only, tibia**

	tLEN1	*tLEN2*	*tPML*	*tPAP*	*tLFAP*	*tMFAP*	*tLFML*	*tMFML*	*tDAP*	*tDML*	*tMMPD*	*tDASML*
Count	9	9	9	9	9	9	9	9	9	9	9	9
Range	1.007	1.002	0.078	0.121	0.137	0.118	0.106	0.065	0.138	0.149	0.134	0.122
Minimum	6.580	6.440	1.357	0.901	0.654	0.787	0.495	0.505	0.675	0.803	0.188	0.474
Maximum	7.587	7.441	1.435	1.022	0.792	0.905	0.601	0.570	0.813	0.952	0.322	0.597
Mean	7.167	7.012	1.409	0.964	0.729	0.836	0.543	0.536	0.730	0.868	0.259	0.516
Standard Error	0.114	0.114	0.009	0.012	0.015	0.012	0.013	0.007	0.014	0.017	0.014	0.013
Standard Deviation	0.341	0.342	0.027	0.035	0.044	0.037	0.038	0.021	0.043	0.050	0.041	0.039
Sample Variance	0.117	0.117	0.001	0.001	0.002	0.001	0.001	0.000	0.002	0.002	0.002	0.002
CV	4.764	4.877	1.900	3.627	6.019	4.482	6.915	3.908	5.913	5.716	15.864	7.579

***Homo sapiens*, male only, tibia**

	tLEN1	*tLEN2*	*tPML*	*tPAP*	*tLFAP*	*tMFAP*	*tLFML*	*tMFML*	*tDAP*	*tDML*	*tMMPD*	*tDASML*
Count	9	9	9	9	9	9	9	9	9	9	9	9
Range	0.811	1.179	0.095	0.111	0.120	0.106	0.100	0.119	0.119	0.096	0.119	0.166
Minimum	6.586	6.122	1.362	0.925	0.661	0.791	0.470	0.478	0.681	0.849	0.229	0.444
Maximum	7.397	7.301	1.457	1.035	0.781	0.897	0.570	0.597	0.801	0.944	0.348	0.610
Mean	7.007	6.829	1.403	0.976	0.722	0.855	0.535	0.536	0.736	0.878	0.266	0.512
Standard Error	0.080	0.108	0.011	0.014	0.012	0.013	0.011	0.013	0.011	0.009	0.012	0.017
Standard Deviation	0.241	0.324	0.033	0.041	0.035	0.038	0.032	0.040	0.032	0.028	0.036	0.050
Sample Variance	0.058	0.105	0.001	0.002	0.001	0.001	0.001	0.002	0.001	0.001	0.001	0.003
CV	3.437	4.739	2.319	4.189	4.793	4.501	5.977	7.384	4.373	3.153	13.641	9.808

Tibial Measures of Variance, Split Sexes, GM adjusted

***Pan troglodytes*, female only, tibia**

	tLEN1	*tLEN2*	*tPML*	*tPAP*	*tLFAP*	*tMFAP*	*tLFML*	*tMFML*	*tDAP*	*tDML*	*tMMPD*	*tDASML*
Count	9	8	9	9	9	9	9	9	9	9	9	9
Range	0.984	0.924	0.106	0.074	0.143	0.139	0.118	0.060	0.225	0.098	0.085	0.139
Minimum	5.589	5.340	1.341	0.877	0.678	0.715	0.540	0.566	0.600	0.809	0.300	0.501
Maximum	6.573	6.264	1.448	0.951	0.820	0.853	0.658	0.626	0.824	0.907	0.385	0.639
Mean	6.098	5.830	1.405	0.918	0.737	0.787	0.605	0.589	0.649	0.857	0.336	0.576
Standard Error	0.114	0.128	0.012	0.008	0.014	0.018	0.010	0.007	0.023	0.011	0.008	0.015
Standard Deviation	0.343	0.363	0.035	0.025	0.042	0.055	0.031	0.020	0.070	0.033	0.025	0.046
Sample Variance	0.117	0.132	0.001	0.001	0.002	0.003	0.001	0.000	0.005	0.001	0.001	0.002
CV	5.618	6.222	2.494	2.712	5.724	6.953	5.125	3.330	10.754	3.842	7.468	7.909

***Pan troglodytes*, male only, tibia**

	tLEN1	*tLEN2*	*tPML*	*tPAP*	*tLFAP*	*tMFAP*	*tLFML*	*tMFML*	*tDAP*	*tDML*	*tMMPD*	*tDASML*
Count	6	6	6	6	6	6	6	6	6	6	6	6
Range	1.028	1.030	0.098	0.025	0.206	0.192	0.087	0.077	0.074	0.098	0.071	0.153
Minimum	5.531	5.298	1.347	0.910	0.626	0.662	0.546	0.557	0.597	0.834	0.294	0.543
Maximum	6.559	6.328	1.445	0.935	0.832	0.853	0.633	0.634	0.671	0.932	0.365	0.696
Mean	6.025	5.859	1.395	0.920	0.718	0.789	0.578	0.602	0.628	0.891	0.332	0.618
Standard Error	0.173	0.169	0.015	0.004	0.029	0.028	0.012	0.013	0.012	0.017	0.010	0.026
Standard Deviation	0.424	0.413	0.037	0.009	0.072	0.069	0.030	0.033	0.030	0.042	0.025	0.063
Sample Variance	0.180	0.171	0.001	0.000	0.005	0.005	0.001	0.001	0.001	0.002	0.001	0.004
CV	7.035	7.057	2.678	0.985	9.999	8.709	5.188	5.479	4.846	4.664	7.413	10.205

Tibial Measures of Variance, Split Sexes, GM adjusted

***Papio hamadryas*, female only, tibia**

	tLEN1	*tLEN2*	*tPML*	*tPAP*	*tLFAP*	*tMFAP*	*tLFML*	*tMFML*	*tDAP*	*tDML*	*tMMPD*	*tDASML*
Count	6	6	11	11	11	11	8	8	6	11	8	8
Range	1.148	1.150	0.104	0.151	0.161	0.119	0.069	0.090	0.046	0.121	0.140	0.112
Minimum	6.880	6.518	1.244	0.903	0.701	0.746	0.531	0.498	0.664	0.742	0.222	0.456
Maximum	8.028	7.668	1.348	1.054	0.862	0.865	0.600	0.589	0.709	0.863	0.362	0.568
Mean	7.293	6.946	1.279	0.977	0.743	0.816	0.569	0.537	0.685	0.818	0.274	0.526
Standard Error	0.194	0.196	0.009	0.015	0.013	0.010	0.008	0.010	0.007	0.011	0.016	0.016
Standard Deviation	0.475	0.481	0.031	0.050	0.044	0.033	0.022	0.028	0.016	0.035	0.046	0.046
Sample Variance	0.225	0.232	0.001	0.002	0.002	0.001	0.000	0.001	0.000	0.001	0.002	0.002
CV	6.508	6.927	2.406	5.080	5.976	4.008	3.799	5.250	2.342	4.281	16.848	8.689

***Papio hamadryas*, male only, tibia**

	tLEN1	*tLEN2*	*tPML*	*tPAP*	*tLFAP*	*tMFAP*	*tLFML*	*tMFML*	*tDAP*	*tDML*	*tMMPD*	*tDASML*
Count	14	14	24	24	24	24	15	15	14	24	15	15
Range	0.924	0.918	0.170	0.219	0.146	0.189	0.115	0.044	0.082	0.148	0.139	0.124
Minimum	6.657	6.320	1.212	0.873	0.664	0.723	0.521	0.526	0.641	0.734	0.232	0.452
Maximum	7.581	7.238	1.382	1.092	0.810	0.912	0.636	0.571	0.723	0.882	0.371	0.576
Mean	6.983	6.709	1.302	0.989	0.753	0.827	0.582	0.547	0.680	0.821	0.283	0.533
Standard Error	0.074	0.083	0.008	0.013	0.008	0.009	0.008	0.004	0.007	0.007	0.012	0.010
Standard Deviation	0.278	0.309	0.038	0.062	0.038	0.043	0.030	0.014	0.026	0.036	0.046	0.039
Sample Variance	0.077	0.096	0.001	0.004	0.001	0.002	0.001	0.000	0.001	0.001	0.002	0.001
CV	3.975	4.609	2.896	6.222	5.066	5.175	5.166	2.481	3.886	4.362	16.181	7.256

Tibial Measures of Variance, Split Sexes, GM adjusted

***Theropithecus gelada*, female only, tibia**												
	tLEN1	*tLEN2*	*tPML*	*tPAP*	*tLFAP*	*tMFAP*	*tLFML*	*tMFML*	*tDAP*	*tDML*	*tMMPD*	*tDASML*
Count	5	5	5	5	5	5	4	4	5	5	4	4
Range	0.180	0.187	0.041	0.147	0.038	0.105	0.052	0.028	0.042	0.066	0.106	0.070
Minimum	7.180	6.851	1.284	0.887	0.727	0.732	0.515	0.534	0.657	0.790	0.240	0.503
Maximum	7.361	7.038	1.325	1.034	0.765	0.837	0.567	0.562	0.699	0.856	0.346	0.572
Mean	7.291	6.922	1.308	0.969	0.746	0.805	0.547	0.552	0.677	0.823	0.292	0.540
Standard Error	0.033	0.036	0.007	0.029	0.006	0.019	0.012	0.006	0.008	0.013	0.026	0.019
Standard Deviation	0.075	0.081	0.017	0.066	0.014	0.042	0.024	0.013	0.018	0.029	0.053	0.037
Sample Variance	0.006	0.007	0.000	0.004	0.000	0.002	0.001	0.000	0.000	0.001	0.003	0.001
CV	1.023	1.167	1.276	6.802	1.887	5.239	4.385	2.328	2.611	3.471	18.090	6.858

***Theropithecus gelada,* male only, tibia**												
	tLEN1	*tLEN2*	*tPML*	*tPAP*	*tLFAP*	*tMFAP*	*tLFML*	*tMFML*	*tDAP*	*tDML*	*tMMPD*	*tDASML*
Count	6	6	7	7	7	7	6	6	6	7	6	6
Range	0.763	0.758	0.096	0.164	0.123	0.154	0.141	0.070	0.011	0.119	0.148	0.104
Minimum	7.028	6.704	1.303	0.898	0.667	0.741	0.463	0.496	0.657	0.756	0.231	0.493
Maximum	7.791	7.462	1.398	1.062	0.789	0.895	0.605	0.566	0.668	0.875	0.379	0.598
Mean	7.430	7.065	1.339	0.995	0.726	0.805	0.548	0.536	0.661	0.836	0.281	0.563
Standard Error	0.104	0.112	0.012	0.023	0.016	0.024	0.025	0.011	0.002	0.015	0.027	0.017
Standard Deviation	0.255	0.274	0.031	0.061	0.044	0.064	0.061	0.026	0.004	0.041	0.066	0.041
Sample Variance	0.065	0.075	0.001	0.004	0.002	0.004	0.004	0.001	0.000	0.002	0.004	0.002
CV	3.427	3.885	2.301	6.138	5.999	7.967	11.139	4.866	0.677	4.895	23.456	7.269

Tibial Measures of Variance, Split Sexes, GM adjusted

***Macaca fascicularis*, female only, tibia**

	tLEN1	*tLEN2*	*tPML*	*tPAP*	*tLFAP*	*tMFAP*	*tLFML*	*tMFML*	*tDAP*	*tDML*	*tMMPD*	*tDASML*
Count	2	2	6	6	6	6	6	6	2	6	6	6
Range	0.180	0.218	0.117	0.128	0.096	0.220	0.158	0.039	0.002	0.114	0.115	0.189
Minimum	8.190	7.882	1.219	0.883	0.772	0.733	0.463	0.495	0.642	0.773	0.232	0.451
Maximum	8.370	8.099	1.336	1.011	0.867	0.953	0.620	0.534	0.644	0.887	0.347	0.640
Mean	8.280	7.990	1.290	0.950	0.816	0.813	0.572	0.509	0.643	0.821	0.274	0.553
Standard Error	0.090	0.109	0.018	0.022	0.015	0.036	0.024	0.006	0.001	0.020	0.018	0.025
Standard Deviation	0.127	0.154	0.045	0.055	0.038	0.087	0.059	0.015	0.002	0.048	0.043	0.061
Sample Variance	0.016	0.024	0.002	0.003	0.001	0.008	0.003	0.000	0.000	0.002	0.002	0.004
CV	1.537	1.927	3.514	5.761	4.630	10.700	10.248	2.933	0.252	5.883	15.844	10.986

***Macaca fascicularis*, male only, tibia**

	tLEN1	*tLEN2*	*tPML*	*tPAP*	*tLFAP*	*tMFAP*	*tLFML*	*tMFML*	*tDAP*	*tDML*	*tMMPD*	*tDASML*
Count	3	3	6	6	6	6	6	6	3	6	6	6
Range	0.645	0.611	0.118	0.093	0.102	0.136	0.069	0.081	0.010	0.128	0.129	0.076
Minimum	7.193	6.958	1.211	0.892	0.711	0.712	0.550	0.496	0.647	0.736	0.212	0.499
Maximum	7.839	7.569	1.329	0.985	0.813	0.848	0.619	0.577	0.656	0.863	0.341	0.575
Mean	7.478	7.210	1.264	0.932	0.776	0.795	0.580	0.549	0.651	0.800	0.272	0.536
Standard Error	0.190	0.184	0.019	0.016	0.018	0.021	0.010	0.013	0.003	0.021	0.022	0.011
Standard Deviation	0.329	0.319	0.046	0.039	0.043	0.052	0.025	0.031	0.005	0.051	0.053	0.028
Sample Variance	0.108	0.102	0.002	0.002	0.002	0.003	0.001	0.001	0.000	0.003	0.003	0.001
CV	4.401	4.427	3.610	4.190	5.561	6.489	4.237	5.719	0.753	6.406	19.484	5.188

Tibial Measures of Variance, Split Sexes, GM adjusted

***Macaca nemestrina*, female only, tibia**

	tLEN1	*tLEN2*	*tPML*	*tPAP*	*tLFAP*	*tMFAP*	*tLFML*	*tMFML*	*tDAP*	*tDML*	*tMMPD*	*tDASML*
Count	2	2	4	4	4	4	4	4	2	4	4	4
Range	0.753	0.714	0.062	0.055	0.082	0.055	0.063	0.062	0.032	0.107	0.102	0.118
Minimum	7.522	7.227	1.255	0.863	0.674	0.747	0.551	0.524	0.635	0.761	0.232	0.475
Maximum	8.275	7.941	1.317	0.918	0.756	0.801	0.614	0.586	0.668	0.868	0.334	0.594
Mean	7.899	7.584	1.279	0.884	0.723	0.781	0.585	0.543	0.652	0.813	0.284	0.535
Standard Error	0.376	0.357	0.013	0.013	0.017	0.012	0.013	0.015	0.016	0.022	0.027	0.025
Standard Deviation	0.532	0.505	0.027	0.025	0.035	0.024	0.026	0.029	0.023	0.045	0.055	0.049
Sample Variance	0.283	0.255	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.002	0.003	0.002
CV	6.739	6.659	2.090	2.840	4.790	3.050	4.460	5.393	3.515	5.486	19.205	9.243

***Macaca nemestrina*, male only, tibia**

	tLEN1	*tLEN2*	*tPML*	*tPAP*	*tLFAP*	*tMFAP*	*tLFML*	*tMFML*	*tDAP*	*tDML*	*tMMPD*	*tDASML*
Count	2	2	5	5	5	5	4	4	2	5	4	4
Range	1.187	1.202	0.194	0.262	0.077	0.066	0.265	0.100	0.009	0.081	0.083	0.108
Minimum	7.123	6.748	1.222	0.895	0.731	0.740	0.429	0.479	0.661	0.762	0.230	0.427
Maximum	8.310	7.951	1.416	1.157	0.808	0.807	0.694	0.579	0.670	0.843	0.313	0.534
Mean	7.717	7.349	1.336	0.985	0.769	0.775	0.572	0.536	0.666	0.802	0.257	0.477
Standard Error	0.593	0.601	0.035	0.047	0.014	0.013	0.056	0.022	0.005	0.016	0.019	0.023
Standard Deviation	0.839	0.850	0.078	0.105	0.031	0.029	0.112	0.045	0.007	0.035	0.038	0.045
Sample Variance	0.704	0.723	0.006	0.011	0.001	0.001	0.013	0.002	0.000	0.001	0.001	0.002
CV	10.875	11.569	5.852	10.641	3.992	3.777	19.647	8.345	0.985	4.400	14.596	9.512

APPENDIX F

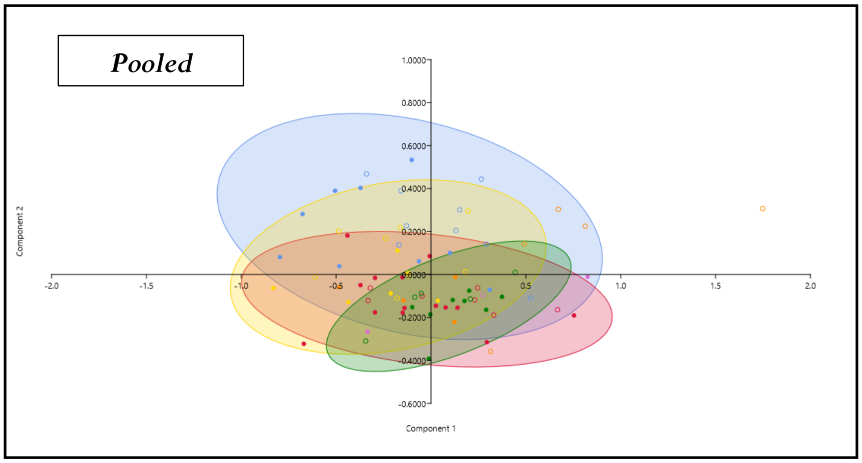
PRINCIPAL COMPONENT ANALYSES, SCATTER PLOTS AND EIGENVALUES

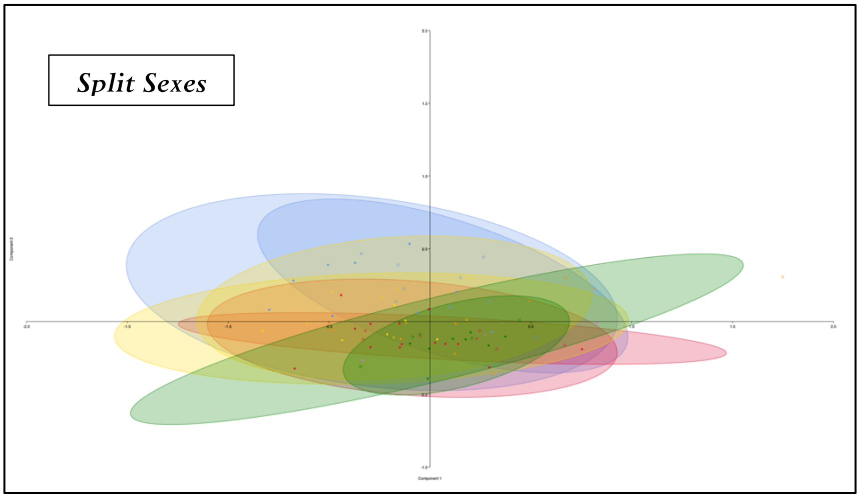
This appendix contains all principal components analyses which were performed in Chapter 2. For each bony element, a principal components analysis was performed in order to assess variation within the samples. Results from these analyses are described using scatter plots of all six study species, including confidence ellipses, with both pooled sexes and split-sex groups depicted. Additionally, the associated Eigenvalues and their percent variance are also included in their entirety for each bony element. Note that pooled sexes and split-sex scatter plots differ only in confidence ellipses, and thus their visual aspects, due to differences in variable labeling; Eigenvalues of these samples remain the same.

Humerus

PC	Eigenvalue	% variance
1	0.1716	72.783
2	0.0424795	18.017
3	0.00836758	3.5491
4	0.00468002	1.985
5	0.00261534	1.1093
6	0.00134251	0.56942
7	0.00105775	0.44864
8	0.000962657	0.4083
9	0.000742309	0.31485
10	0.000666595	0.28273
11	0.000493722	0.20941
12	0.00037792	0.16029
13	0.000291976	0.12384
14	9.17355E-05	0.038909

Scatter Plot Key		
Taxon	**Color**	**N=78**
Homo sapiens	Blue	18
Pan troglodytes	Yellow	14
Papio hamadryas	Red	21
Theropithecus gelada	Green	13
Macaca fascicularis	Orange	9
Macaca nemestrina	Purple	3

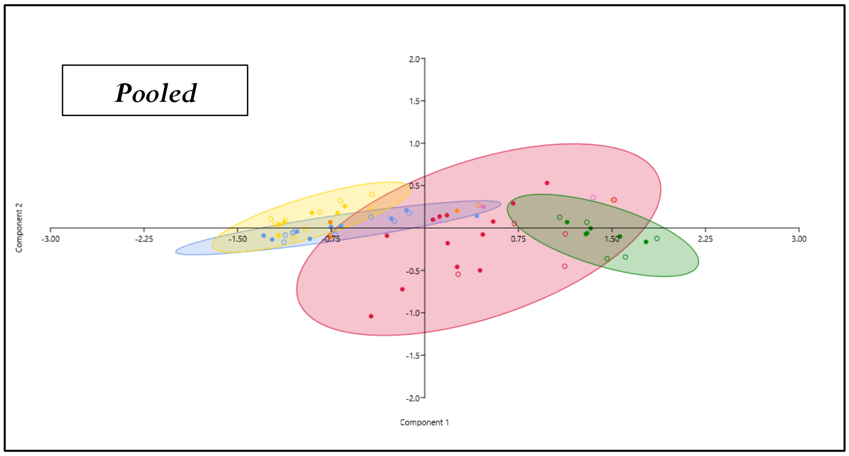

Pooled

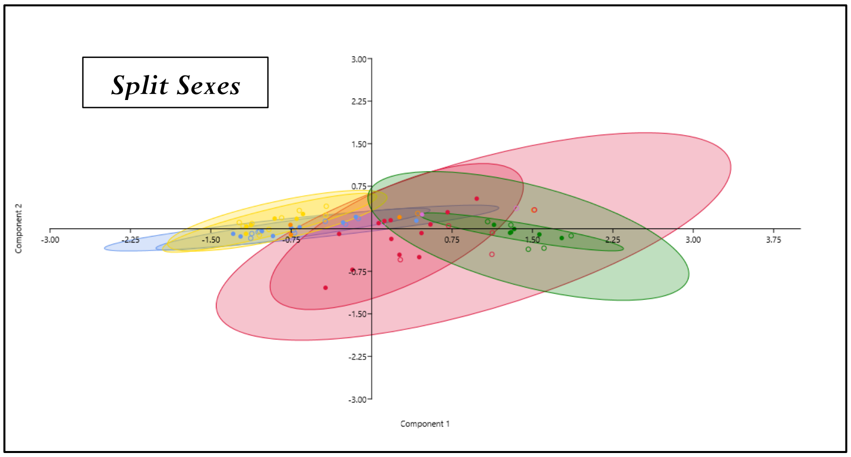

Split Sexes

Radius

PC	Eigenvalue	% variance
1	0.90889	91.269
2	0.0679089	6.8193
3	0.00991483	0.99563
4	0.0033872	0.34014
5	0.00169435	0.17014
6	0.00155052	0.1557
7	0.000988257	0.099239
8	0.000830276	0.083375
9	0.00048528	0.048731
10	0.000182926	0.018369

Scatter Plot Key		
Taxon	**Color**	**N=70**
Homo sapiens	Blue	18
Pan troglodytes	Yellow	15
Papio hamadryas	Red	18
Theropithecus gelada	Green	11
Macaca fascicularis	Orange	5
Macaca nemestrina	Purple	3

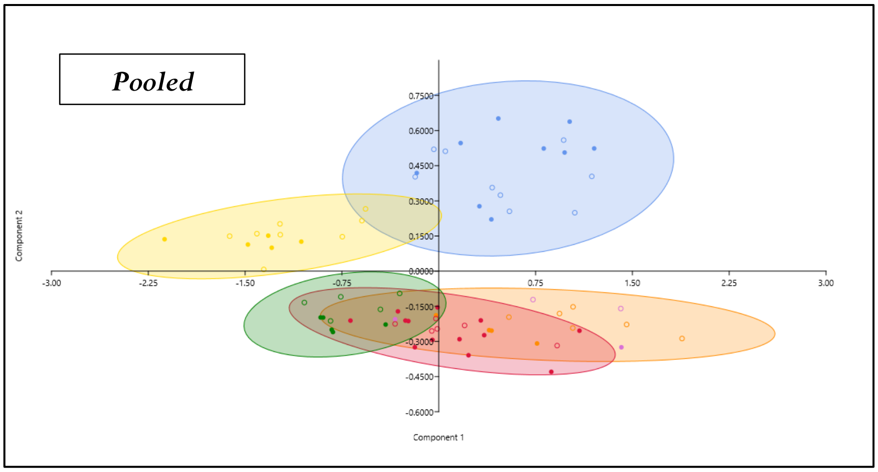


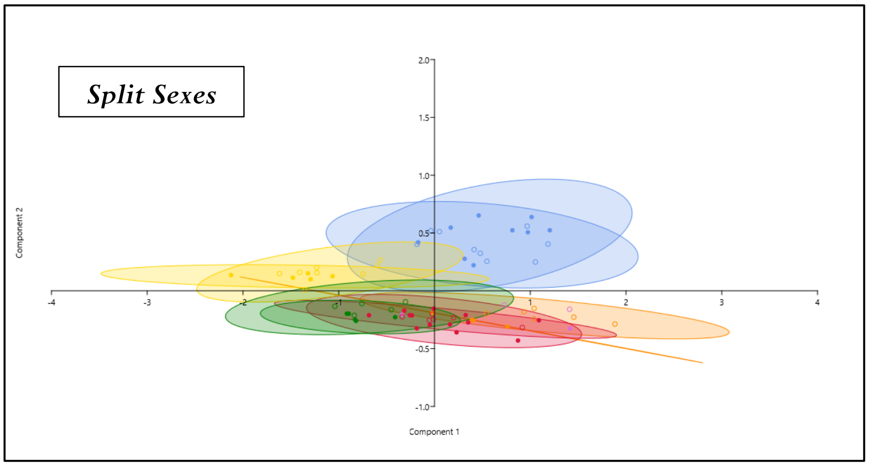


Femur

PC	Eigenvalue	% variance
1	0.75491	84.866
2	0.0895821	10.071
3	0.00834635	0.93829
4	0.00699067	0.78588
5	0.00587392	0.66034
6	0.00549499	0.61774
7	0.00442741	0.49772
8	0.00321913	0.36189
9	0.00244207	0.27454
10	0.0018523	0.20823
11	0.00164163	0.18455
12	0.00139037	0.1563
13	0.00102823	0.11559
14	0.000877164	0.09861
15	0.000814995	0.091621
16	0.00051042	0.057381
17	0.000128962	0.014498

Scatter Plot Key		
Taxon	**Color**	**N=74**
Homo sapiens	Blue	18
Pan troglodytes	Yellow	13
Papio hamadryas	Red	19
Theropithecus gelada	Green	10
Macaca fascicularis	Orange	10
Macaca nemestrina	Purple	4


Pooled

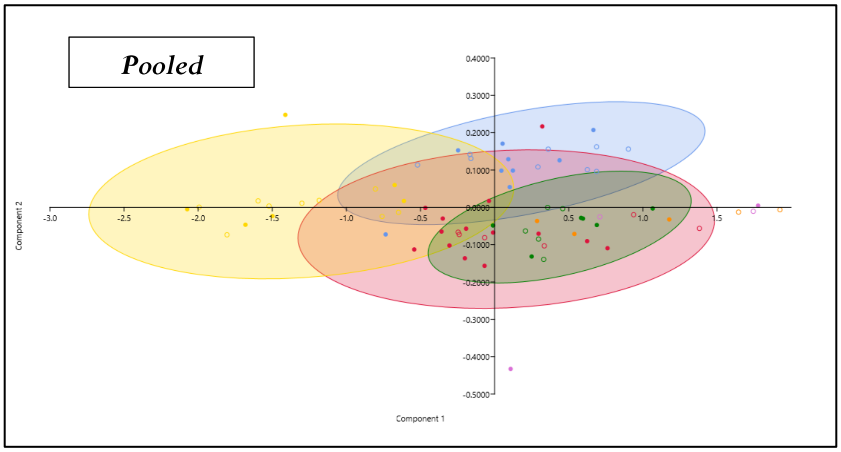

Split Sexes

Tibia

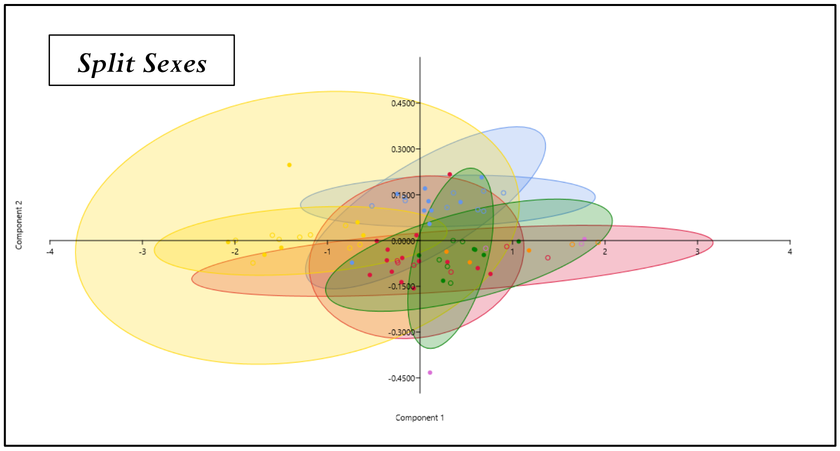
PC	Eigenvalue	% variance
1	0.777344	96.025
2	0.0114036	1.4087
3	0.00586926	0.72503
4	0.00486841	0.60139
5	0.00263299	0.32525
6	0.00202432	0.25006
7	0.00170458	0.21057
8	0.00125982	0.15563
9	0.00097727	0.12072
10	0.000762791	0.094227
11	0.000463509	0.057257
12	0.000209597	0.025891

Scatter Plot Key

Taxon	**Color**	**N=73**
Homo sapiens	Blue	18
Pan troglodytes	Yellow	15
Papio hamadryas	Red	20
Theropithecus gelada	Green	11
Macaca fascicularis	Orange	5
Macaca nemestrina	Purple	4



Pooled



Split Sexes

APPENDIX G

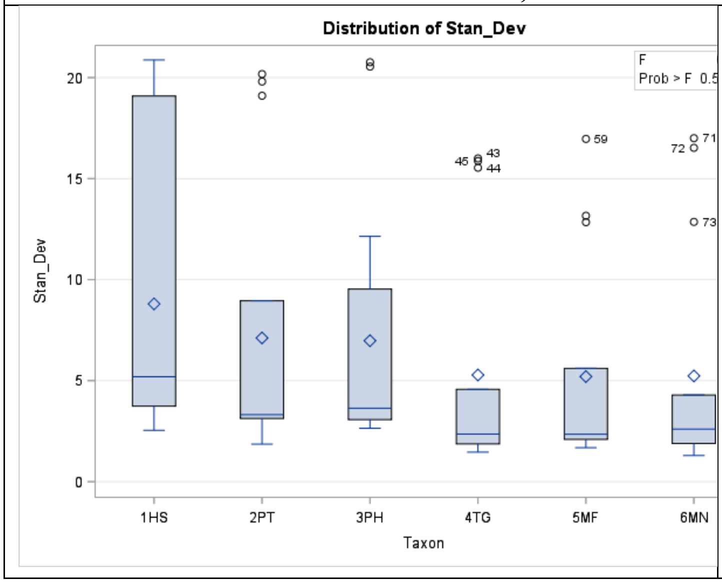
POSTCRANIAL ANALYSES OF VARIANCE

This appendix contains results derived from analyses of variance, including boxplots and p-values reported from ANOVAs to discern significant variation among species. All six sample species were described using three measures of variance: standard deviation, sample variance, and coefficient of variation. Each of these statistics were used to compare patterns of variation within each bony element (Humerus, Radius, Femur, Tibia), and also across the limbs using variable sets (Skeletal, Total; Skeletal, Length; Skeletal, Width). Further, each measure of variance was performed on raw data, and also performed on data which has been adjusted by the geometric mean to reduce the effects of body size. Thus, each bony element measurement set, and each variable set, are reported here as the results of six ANOVAs per set. A summary of results from these analyses is provided below. Complete methodologies for these analyses are described in Chapter 2. For each ANOVA performed, corrected alpha levels were applied to determine true significance in variation differences, given the number of groups tested. Where statistical significance was achieved in ANOVAs, p-values are bolded (see **Results Summary**); where significance was also achieved using corrected alpha levels, p-values are marked with an asterisk.

Results Summary

	Stan Dev	*Adj SD*	*Samp Var*	*Adj SV*	*Coef Var*	*Adj CV*
Humerus	0.5882	0.4522	0.6265	0.1277	**<.0001***	0.1475
Radius	0.9768	0.5725	0.9535	0.3124	**<.0001***	0.4795
Femur	0.6617	0.7469	0.7101	0.4972	**<.0001***	0.3362
Tibia	0.9246	0.8750	0.8774	0.6163	**<.0001***	0.7775
Skeletal, Total	0.4586	0.1417	0.4123	**0.0169**	**<.0001***	0.2922
Skeletal, Length	**0.0001***	**<.0001***	**0.0002***	**<.0001***	**<.0001***	**<.0001***
Skeletal, Width	**<.0001***	0.5905	**<.0001***	0.7507	**<.0001***	0.9112

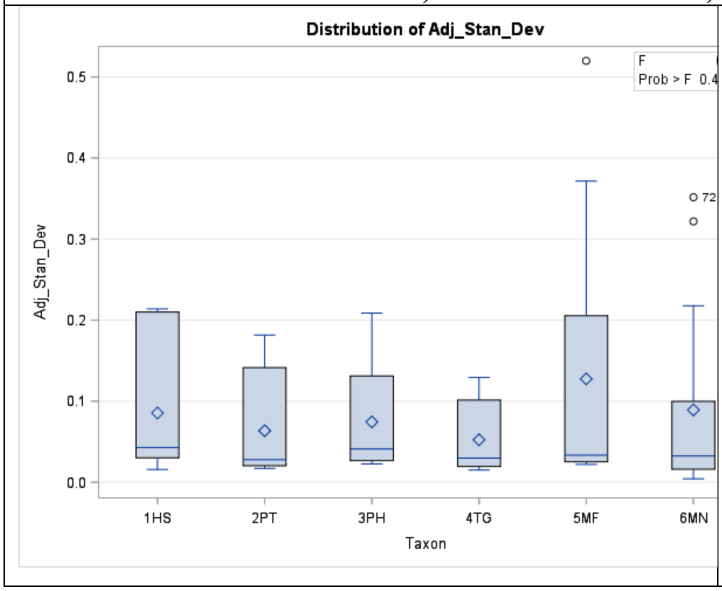
HUMERUS, Standard Deviation



Means with the same letter
are not significantly different.

Bon Grouping	Mean	N	Taxon
A	8.799	14	HS
A	7.112	14	PT
A	6.975	14	PH
A	5.280	14	TG
A	5.234	14	MN
A	5.201	14	MF

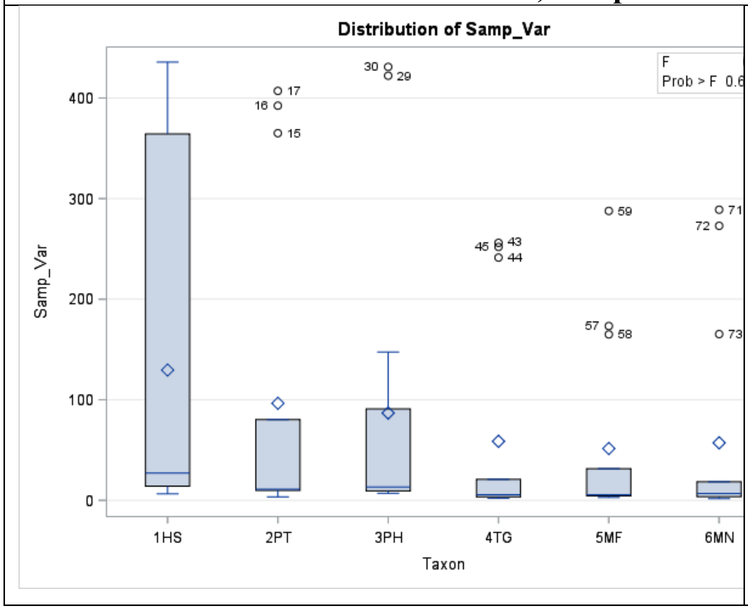
HUMERUS, Standard Deviation, GM adjusted



Means with the same letter
are not significantly different.

Bon Grouping	Mean	N	Taxon
A	0.12753	14	MF
A	0.08922	14	MN
A	0.08544	14	HS
A	0.07442	14	PH
A	0.06355	14	PT
A	0.05244	14	TG

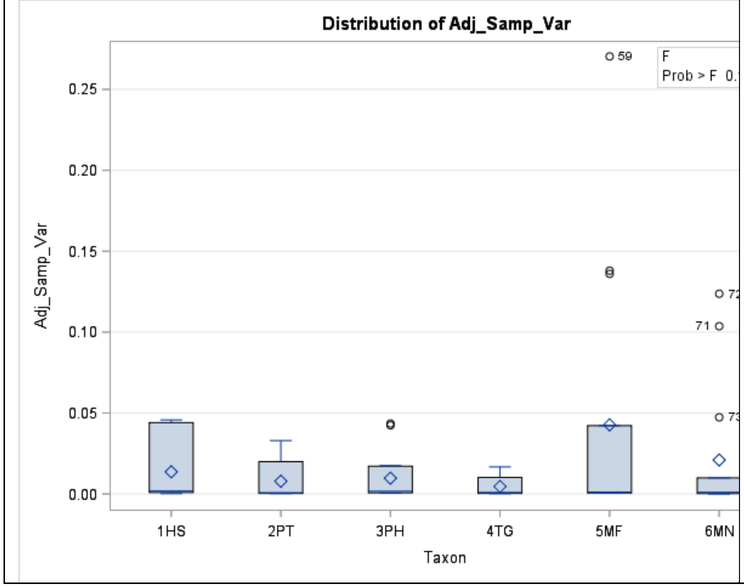
HUMERUS, Sample Variance



Means with the same letter
are not significantly different.

Bon Grouping	Mean	N	Taxon
A	129.51	14	HS
A	96.51	14	PT
A	86.79	14	PH
A	58.63	14	TG
A	57.16	14	MN
A	51.48	14	MF

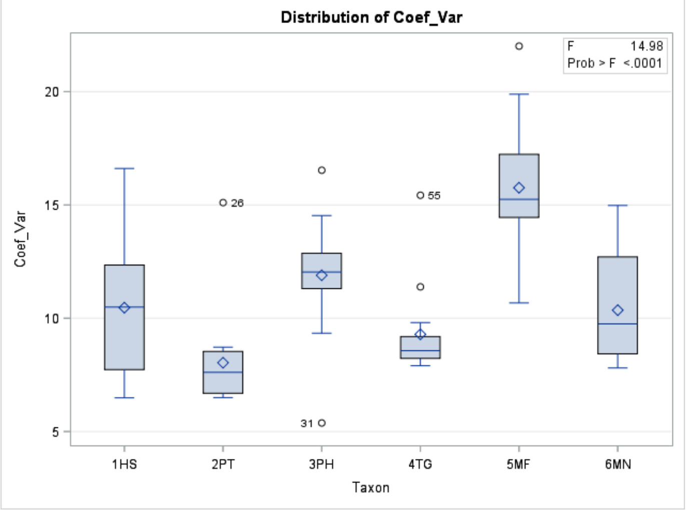
HUMERUS, Sample Variance, GM adjusted



Means with the same letter
are not significantly different.

Bon Grouping	Mean	N	Taxon
A	0.04271	14	MF
A	0.02099	14	MN
A	0.01370	14	HS
A	0.00973	14	PH
A	0.00790	14	PT
A	0.00464	14	TG

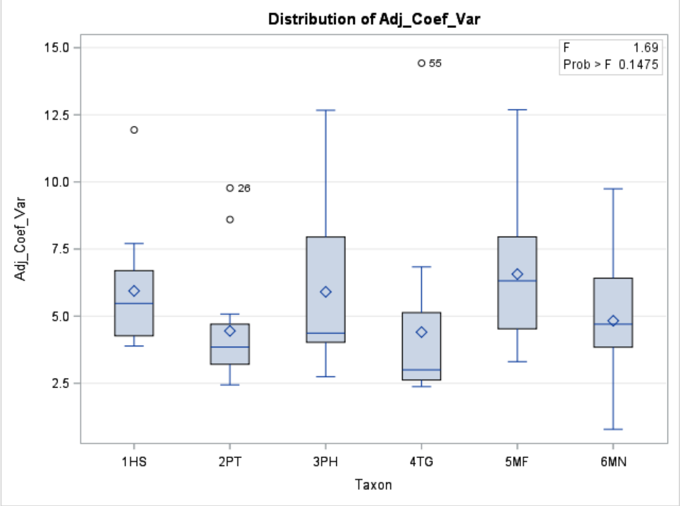
HUMERUS, Coefficient of Variation*



Means with the same letter
are not significantly different.

Bon Grouping		Mean	N	Taxon
	A	15.7584	14	MF
	B	11.8968	14	PH
C	B	10.4636	14	HS
C	B	10.3559	14	MN
C	B	9.2919	14	TG
C		8.0374	14	PT

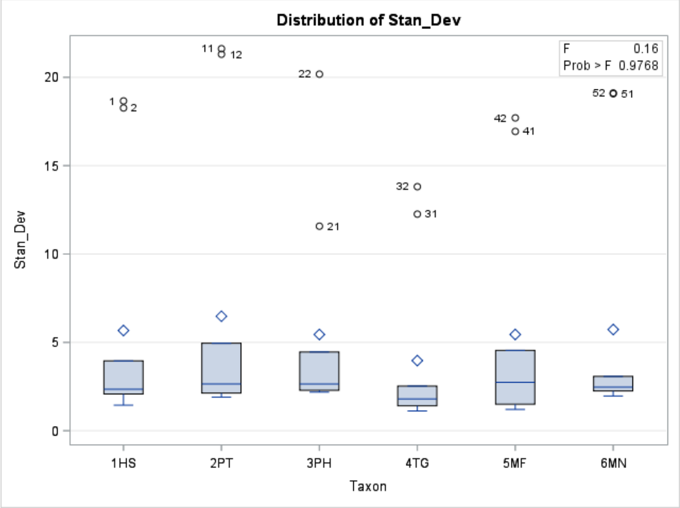
HUMERUS, Coefficient of Variation, GM adjusted



Means with the same letter
are not significantly different.

Bon Grouping	Mean	N	Taxon
A	6.5652	14	MF
A	5.9407	14	HS
A	5.9066	14	PH
A	4.8275	14	MN
A	4.4499	14	PT
A	4.4066	14	TG

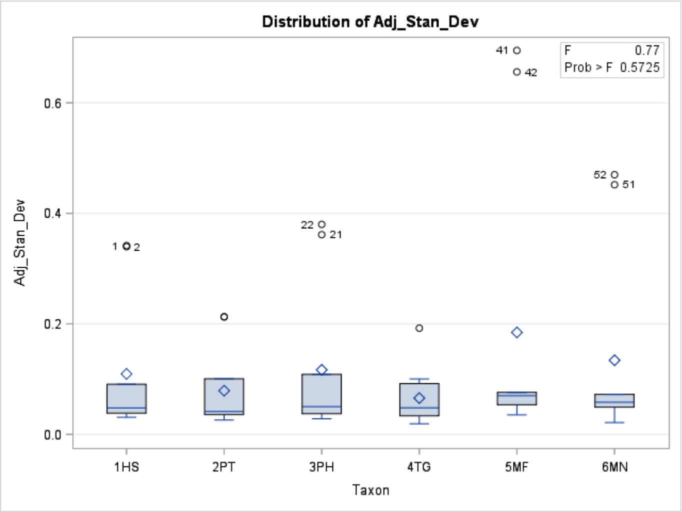
RADIUS, Standard Deviation



Means with the same letter
are not significantly different.

Bon Grouping	Mean	N	Taxon
A	6.477	10	PT
A	5.728	10	MN
A	5.669	10	HS
A	5.446	10	MF
A	5.445	10	PH
A	3.968	10	TG

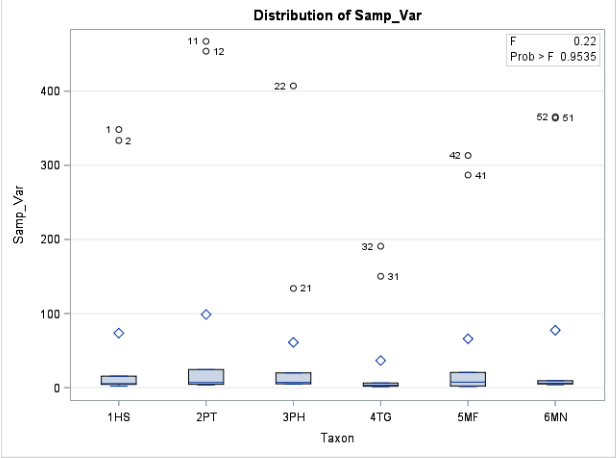
RADIUS, Standard Deviation, GM adjusted



Means with the same letter
are not significantly different.

Bon Grouping	Mean	N	Taxon
A	0.18447	10	MF
A	0.13402	10	MN
A	0.11676	10	PH
A	0.10935	10	HS
A	0.07900	10	PT
A	0.06560	10	TG

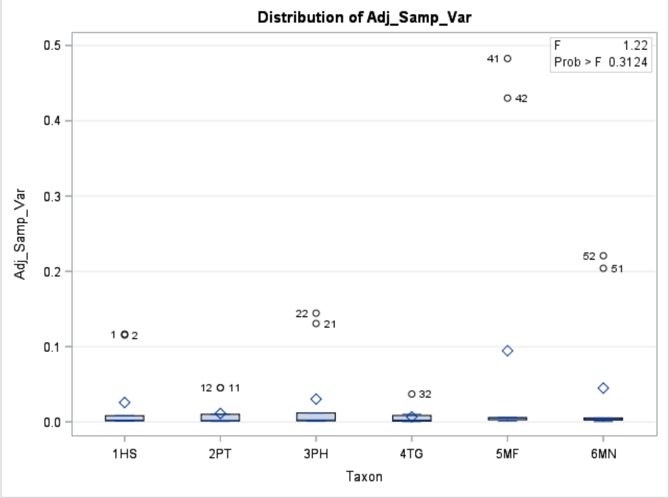
RADIUS, Sample Variance



Means with the same letter
are not significantly different.

Bon Grouping	Mean	N	Taxon
A	98.77	10	PT
A	77.54	10	MN
A	73.62	10	HS
A	65.95	10	MF
A	61.08	10	PH
A	36.60	10	TG

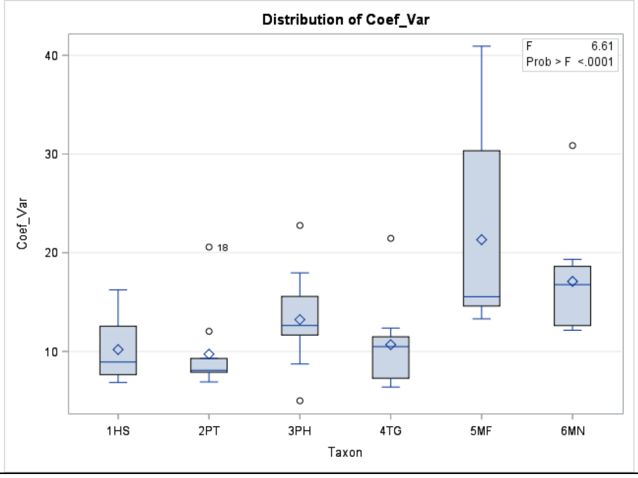
RADIUS, Sample Variance, GM adjusted



Means with the same letter
are not significantly different.

Bon Grouping	Mean	N	Taxon
A	0.09447	10	MF
A	0.04485	10	MN
A	0.03031	10	PH
A	0.02565	10	HS
A	0.01110	10	PT
A	0.00670	10	TG

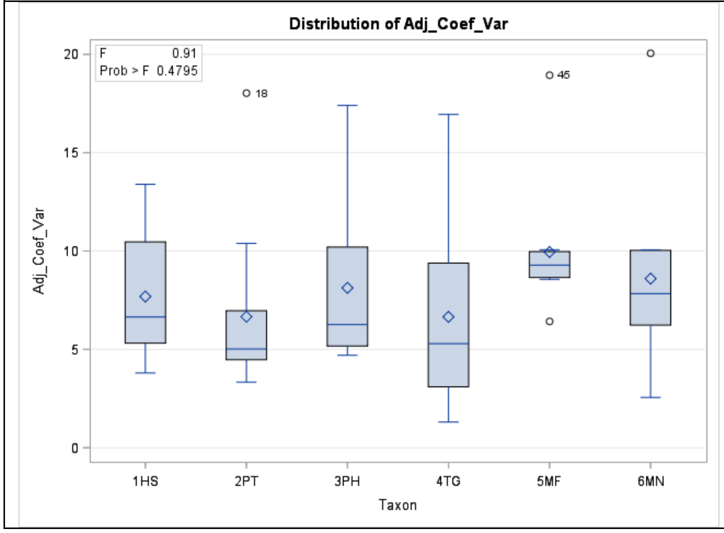
RADIUS, Coefficient of Variation*



Means with the same letter
are not significantly different.

Bon Grouping		Mean	N	Taxon
	A	21.319	10	MF
B	A	17.098	10	MN
B		13.224	10	PH
B		10.688	10	TG
B		10.187	10	HS
B		9.729	10	PT

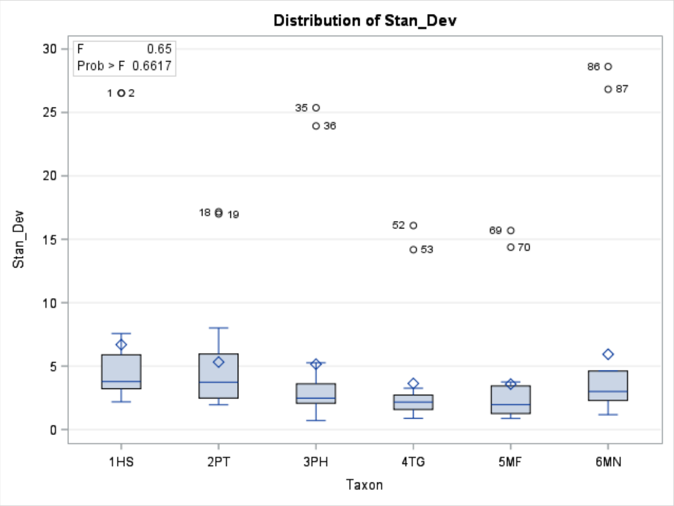
RADIUS, Coefficient of Variation, GM adjusted



Means with the same letter
are not significantly different.

Bon Grouping	Mean	N	Taxon
A	9.950	10	MF
A	8.597	10	MN
A	8.128	10	PH
A	7.687	10	HS
A	6.662	10	PT
A	6.652	10	TG

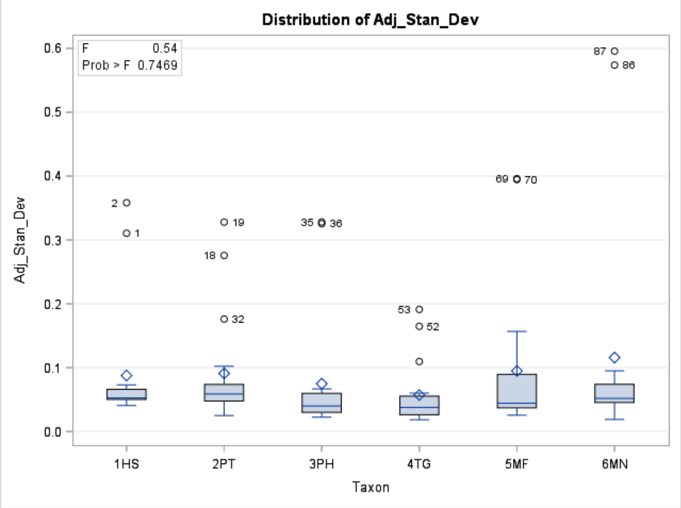
FEMUR, Standard Deviation



Means with the same letter
are not significantly different.

Bon Grouping	Mean	N	Taxon
A	6.694	17	HS
A	5.932	17	MN
A	5.324	17	PT
A	5.153	17	PH
A	3.632	17	TG
A	3.581	17	MF

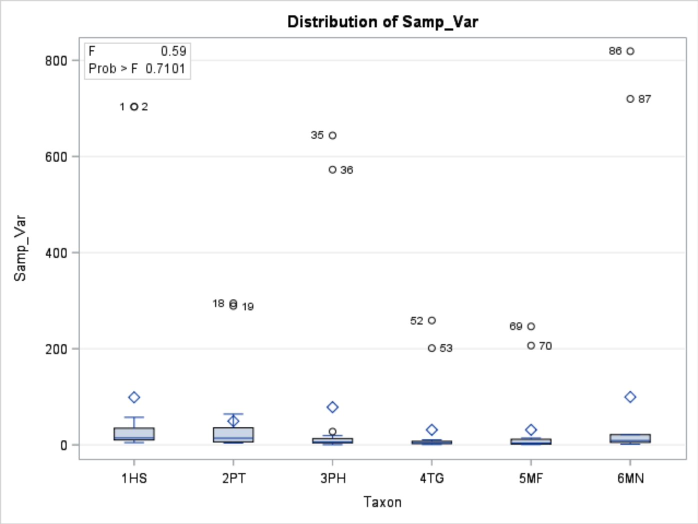
FEMUR, Standard Deviation, GM adjusted



Means with the same letter
are not significantly different.

Bon Grouping	Mean	N	Taxon
A	0.11572	17	MN
A	0.09499	17	MF
A	0.09102	17	PT
A	0.08772	17	HS
A	0.07495	17	PH
A	0.05715	17	TG

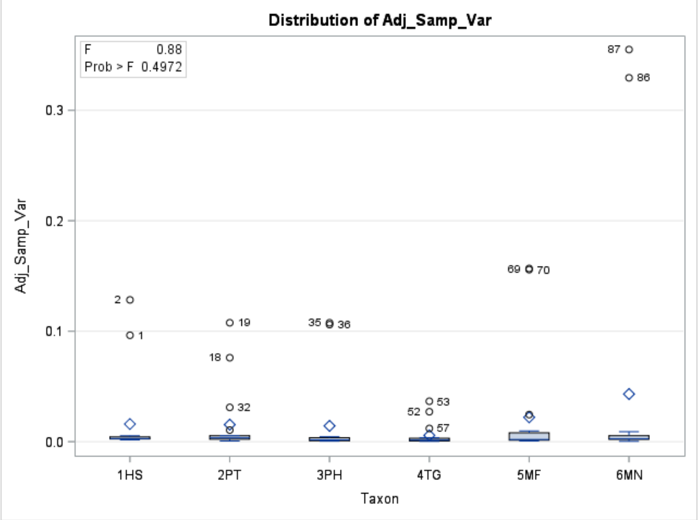
FEMUR, Sample Variance



Means with the same letter
are not significantly different.

Bon Grouping	Mean	N	Taxon
A	99.65	17	MN
A	98.98	17	HS
A	78.44	17	PH
A	49.56	17	PT
A	31.32	17	TG
A	31.20	17	MF

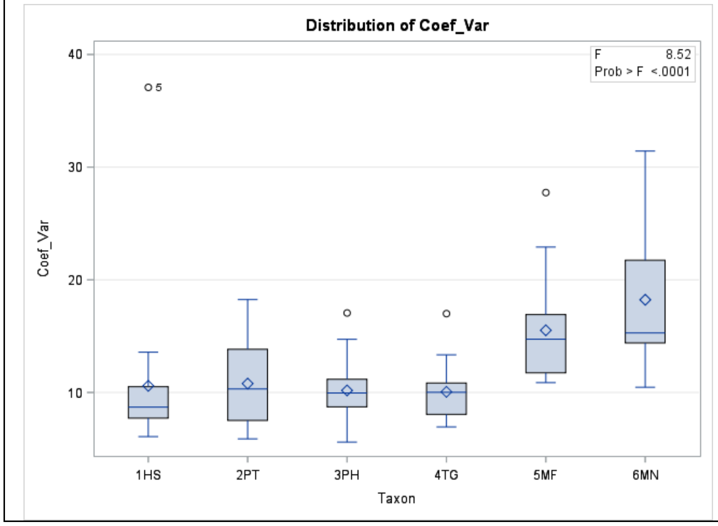
FEMUR, Sample Variance, GM adjusted



Means with the same letter
are not significantly different.

Bon Grouping	Mean	N	Taxon
A	0.04316	17	MN
A	0.02206	17	MF
A	0.01596	17	HS
A	0.01542	17	PT
A	0.01427	17	PH
A	0.00568	17	TG

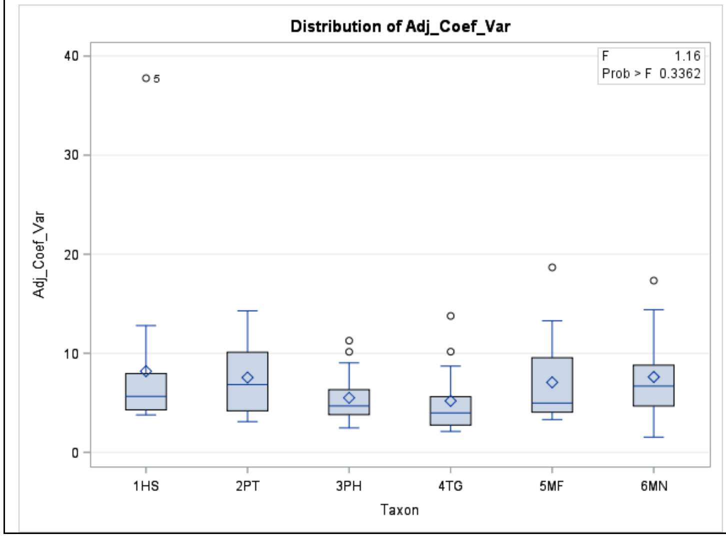
FEMUR, Coefficient of Variation*



Means with the same letter
are not significantly different.

Bon Grouping		Mean	N	Taxon
	A	18.225	17	MN
B	A	15.520	17	MF
B	C	10.788	17	PT
B	C	10.585	17	HS
	C	10.177	17	PH
	C	10.056	17	TG

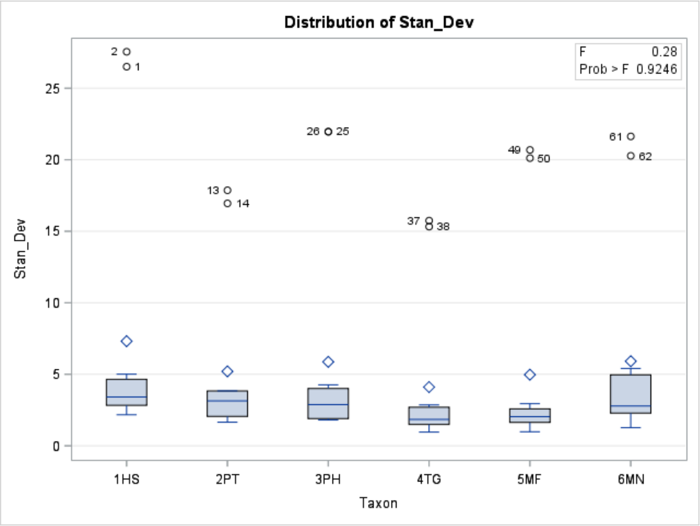
FEMUR, Coefficient of Variation, GM adjusted



Means with the same letter
are not significantly different.

Bon Grouping	Mean	N	Taxon
A	8.194	17	HS
A	7.604	17	MN
A	7.551	17	PT
A	7.066	17	MF
A	5.506	17	PH
A	5.194	17	TG

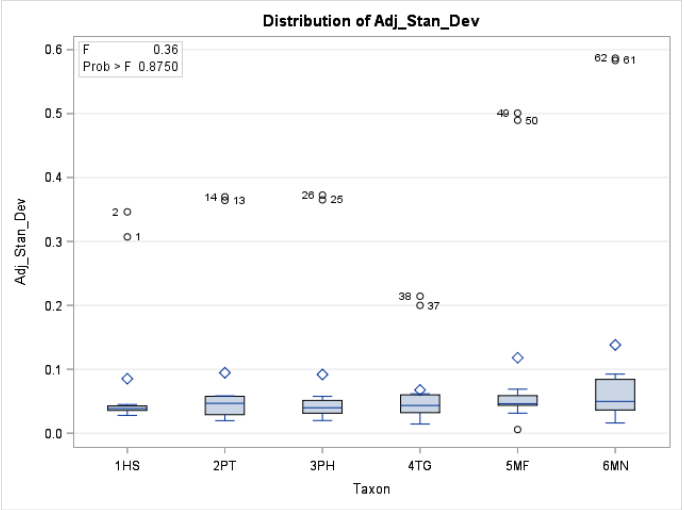
TIBIA, Standard Deviation



Means with the same letter
are not significantly different.

Bon Grouping	Mean	N	Taxon
A	7.317	12	HS
A	5.913	12	MN
A	5.868	12	PH
A	5.202	12	PT
A	4.971	12	MF
A	4.106	12	TG

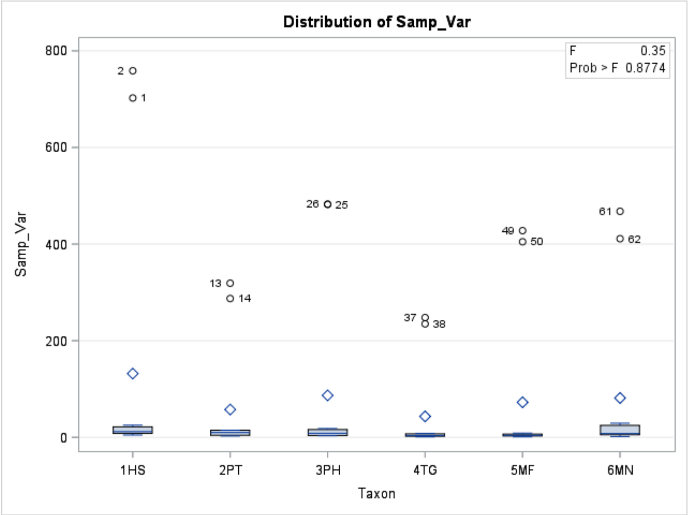
TIBIA, Standard Deviation, GM adjusted



Means with the same letter
are not significantly different.

Bon Grouping	Mean	N	Taxon
A	0.13800	12	MN
A	0.11798	12	MF
A	0.09457	12	PT
A	0.09190	12	PH
A	0.08513	12	HS
A	0.06757	12	TG

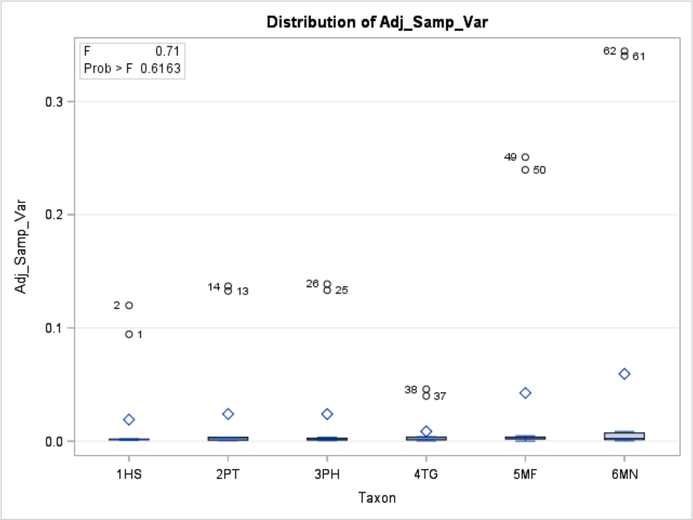
TIBIA, Sample Variance



Means with the same letter
are not significantly different.

Bon Grouping	Mean	N	Taxon
A	131.82	12	HS
A	86.82	12	PH
A	81.40	12	MN
A	72.56	12	MF
A	57.45	12	PT
A	43.25	12	TG

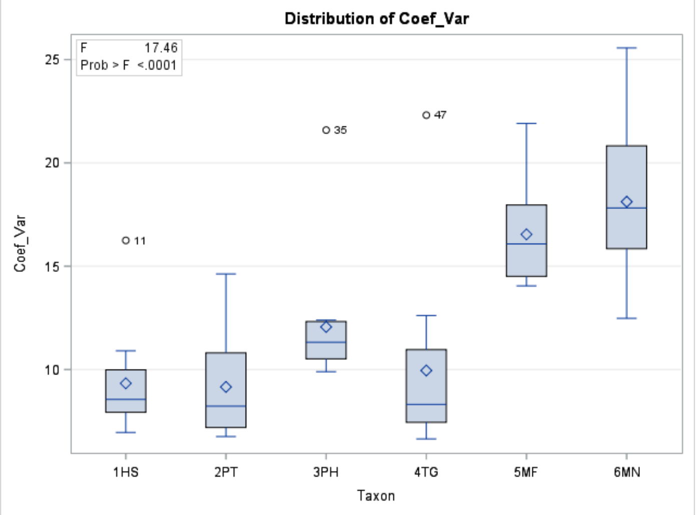
TIBIA, Sample Variance, GM adjusted



Means with the same letter
are not significantly different.

Bon Grouping	Mean	N	Taxon
A	0.05943	12	MN
A	0.04257	12	MF
A	0.02396	12	PT
A	0.02387	12	PH
A	0.01900	12	HS
A	0.00864	12	TG

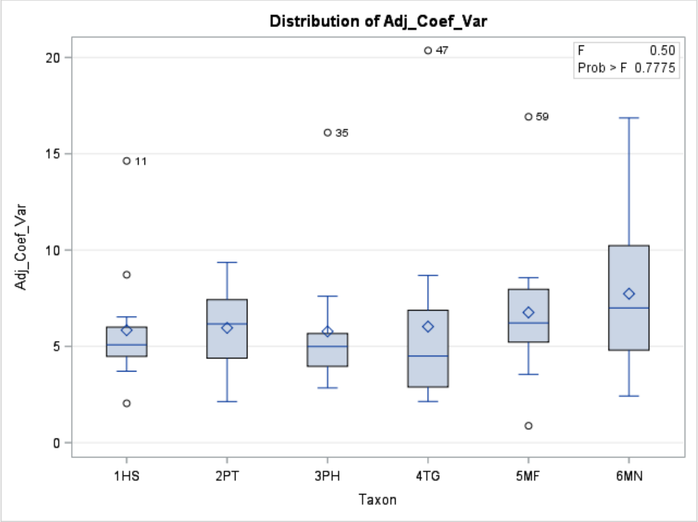
TIBIA, Coefficient of Variation*



Means with the same letter
are not significantly different.

Bon Grouping	Mean	N	Taxon
A	18.121	12	MN
A	16.541	12	MF
B	12.062	12	PH
B	9.953	12	TG
B	9.332	12	HS
B	9.156	12	PT

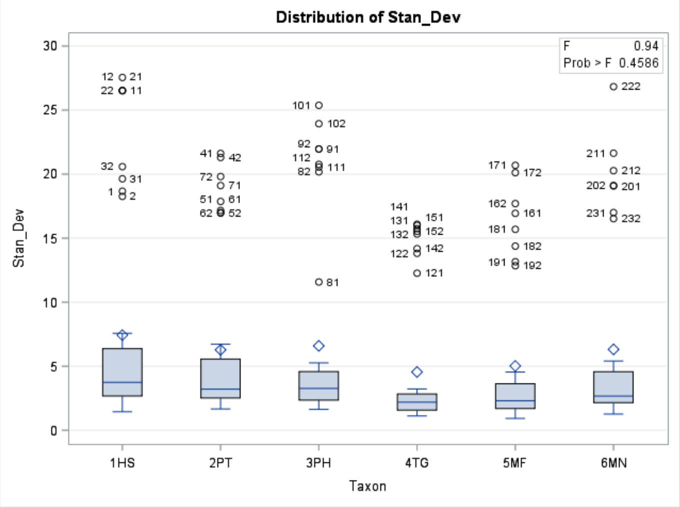
TIBIA, Coefficient of Variation, GM adjusted



Means with the same letter
are not significantly different.

Bon Grouping	Mean	N	Taxon
A	7.733	12	MN
A	6.761	12	MF
A	6.028	12	TG
A	5.959	12	PT
A	5.839	12	HS
A	5.777	12	PH

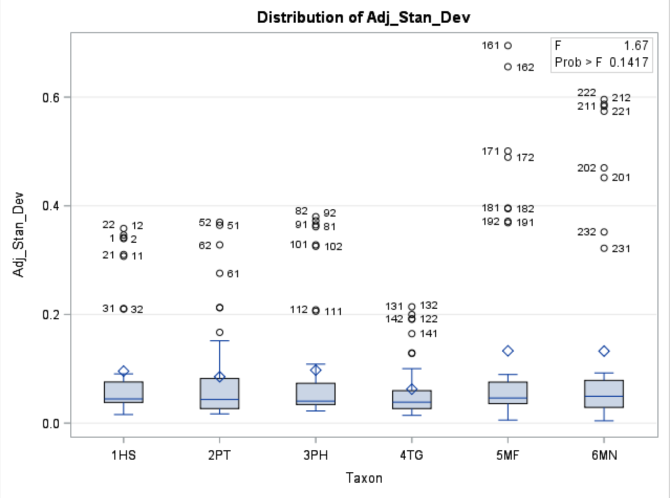
SKELETAL TOTAL, Standard Deviation



Means with the same letter
are not significantly different.

Bon Grouping	Mean	N	Taxon
A	7.429	40	HS
A	6.594	40	PH
A	6.316	40	MN
A	6.281	40	PT
A	5.022	40	MF
A	4.551	40	TG

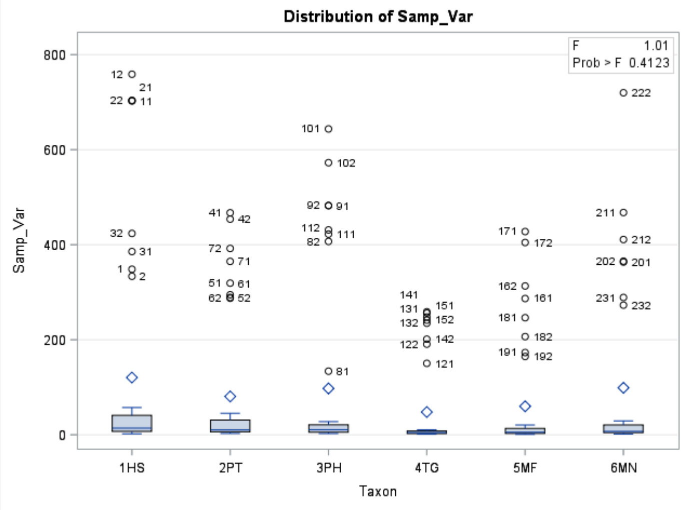
SKELETAL TOTAL, Standard Deviation, GM adjusted



Means with the same letter
are not significantly different.

Bon Grouping	Mean	N	Taxon
A	0.13313	40	MF
A	0.13263	40	MN
A	0.09753	40	PH
A	0.09579	40	HS
A	0.08541	40	PT
A	0.06254	40	TG

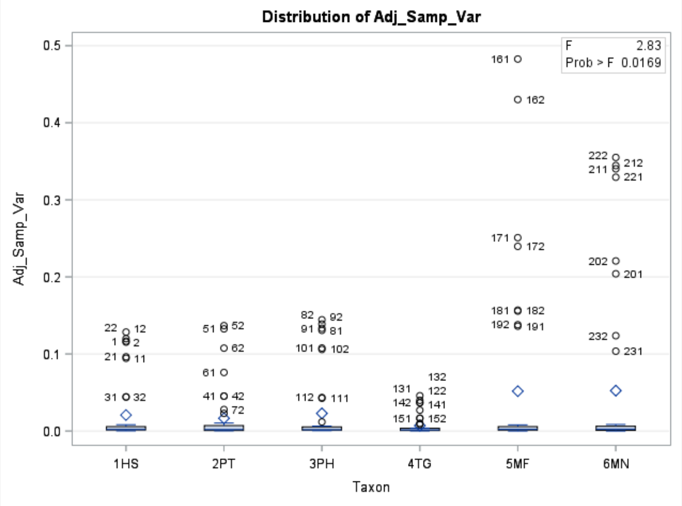
SKELETAL TOTAL, Sample Variance



Means with the same letter
are not significantly different.

Bon Grouping	Mean	N	Taxon
A	120.45	40	HS
A	98.84	40	MN
A	97.47	40	PH
A	80.70	40	PT
A	59.90	40	MF
A	47.90	40	TG

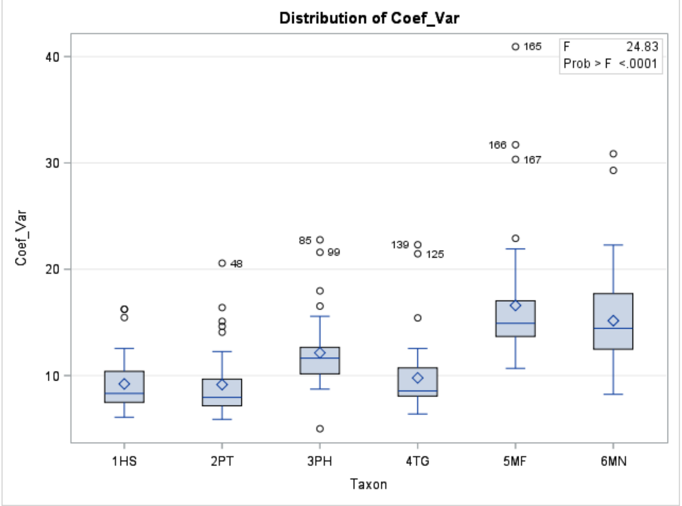
SKELETAL TOTAL, Sample Variance, GM adjusted



Means with the same letter
are not significantly different.

Bon Grouping	Mean	N	Taxon
A	0.05236	40	MN
A	0.05168	40	MF
A	0.02286	40	PH
A	0.02072	40	HS
A	0.01660	40	PT
A	0.00707	40	TG

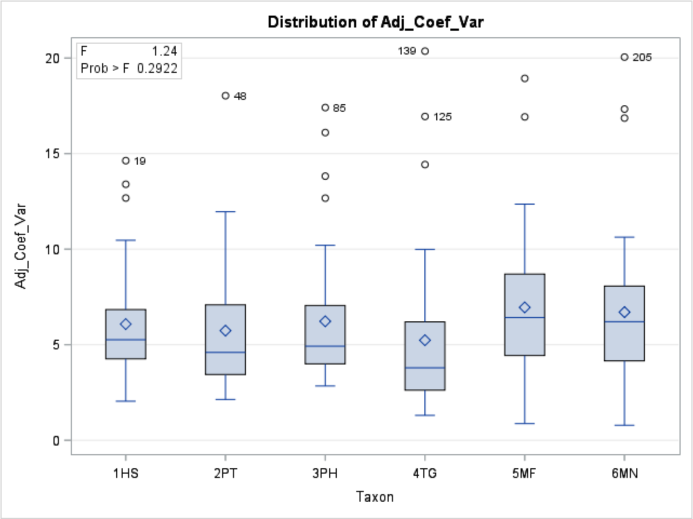
SKELETAL TOTAL, Coefficient of Variation*



Means with the same letter
are not significantly different.

Bon Grouping		Mean	N	Taxon
	A	16.5992	40	MF
	A	15.1584	40	MN
	B	12.1372	40	PH
C	B	9.7837	40	TG
C		9.2124	40	HS
C		9.1498	40	PT

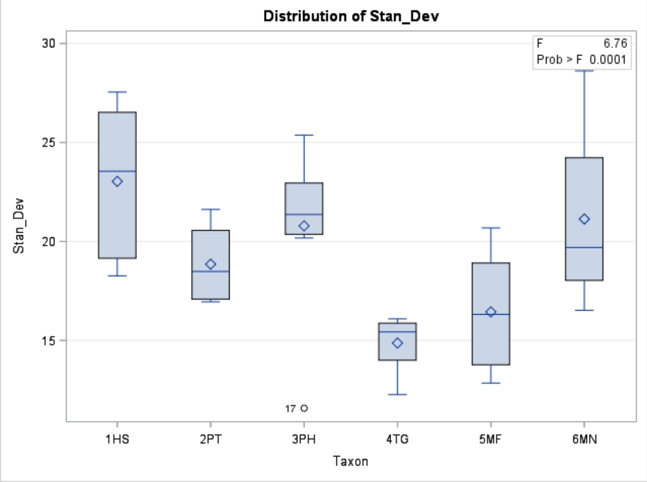
SKELETAL TOTAL, Coefficient of Variation, GM Adjusted



Means with the same letter
are not significantly different.

Bon Grouping	Mean	N	Taxon
A	6.9521	40	MF
A	6.7037	40	MN
A	6.2237	40	PH
A	6.0792	40	HS
A	5.7355	40	PT
A	5.2376	40	TG

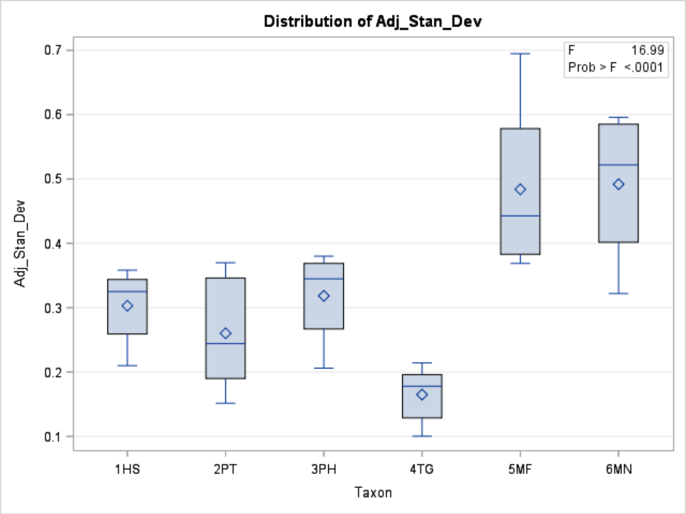
SKELETAL LENGTH, Coefficient of Variation*



Means with the same letter
are not significantly different.

Bon Grouping			**Mean**	**N**	**Taxon**
	A		23.031	8	HS
B	A		21.132	8	MN
B	A		20.786	8	PH
B	A	C	18.852	8	PT
B		C	16.439	8	MF
		C	14.869	8	TG

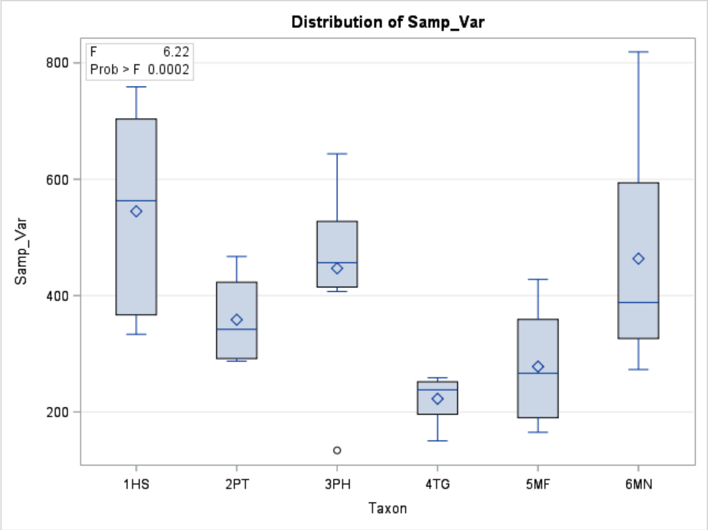
SKELETAL LENGTH, Coefficient of Variation, GM adjusted*



Means with the same letter
are not significantly different.

Bon Grouping		**Mean**	**N**	**Taxon**
	A	0.49187	8	MN
	A	0.48399	8	MF
	B	0.31843	8	PH
	B	0.30302	8	HS
C	B	0.26022	8	PT
C		0.16500	8	TG

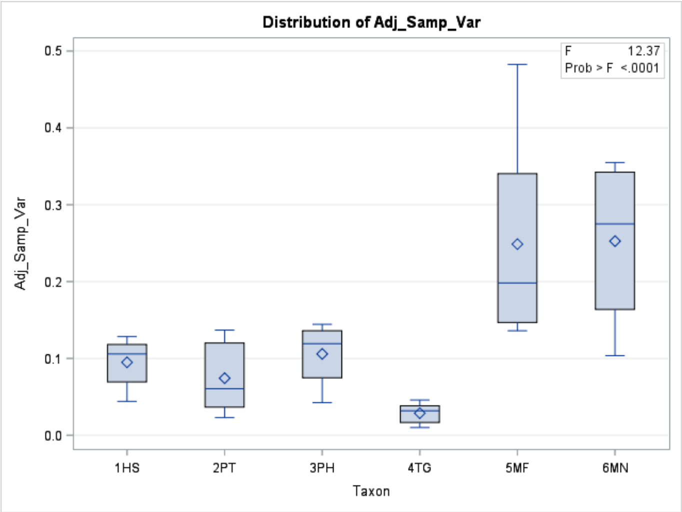
SKELETAL LENGTH, Sample Variance*



Means with the same letter
are not significantly different.

Bon Grouping			Mean	N	Taxon
	A		544.94	8	HS
B	A		463.57	8	MN
B	A		446.92	8	PH
B	A	C	358.57	8	PT
B		C	277.97	8	MF
		C	222.65	8	TG

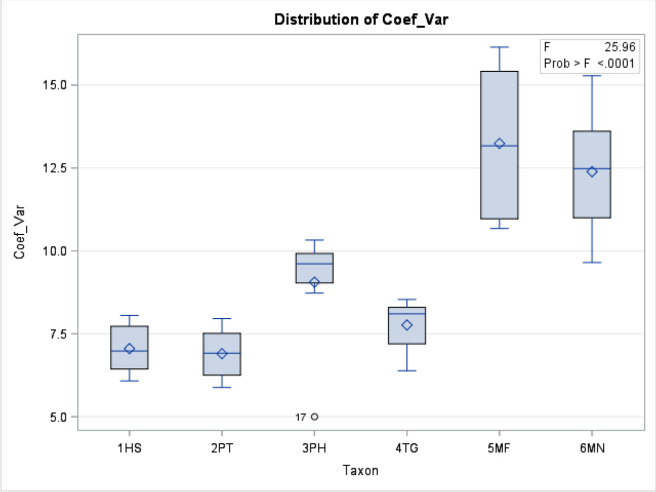
SKELETAL LENGTH, Sample Variance, GM Adjusted*



Means with the same letter
are not significantly different.

Bon Grouping	Mean	N	Taxon
A	0.25263	8	MN
A	0.24873	8	MF
B	0.10584	8	PH
B	0.09494	8	HS
B	0.07430	8	PT
B	0.02871	8	TG

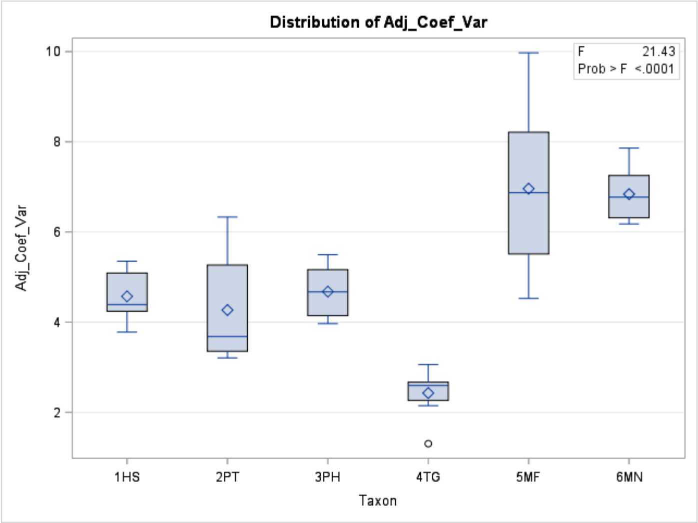
SKELETAL LENGTH, Coefficient of Variation*



Means with the same letter
are not significantly different.

Bon Grouping	Mean	N	Taxon
A	13.2410	8	MF
A	12.3889	8	MN
B	9.0586	8	PH
B	7.7651	8	TG
B	7.0534	8	HS
B	6.9011	8	PT

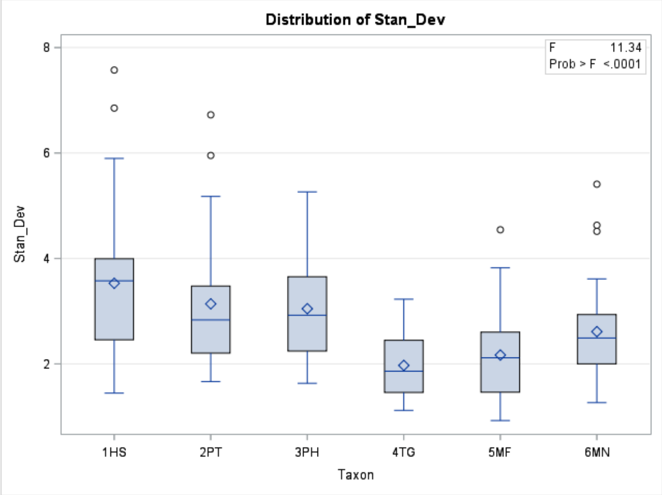
SKELETAL LENGTH, Coefficient of Variation, GM Adjusted*



Means with the same letter
are not significantly different.

Bon Grouping	Mean	N	Taxon
A	6.9603	8	MF
A	6.8391	8	MN
B	4.6775	8	PH
B	4.5709	8	HS
B	4.2675	8	PT
C	2.4278	8	TG

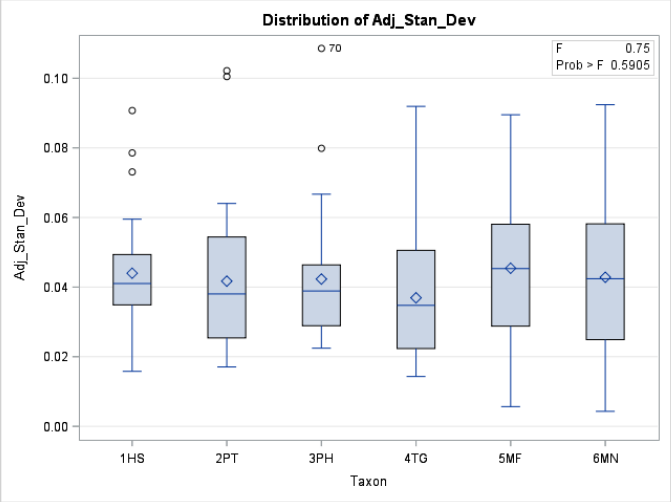
SKELETAL WIDTH, Standard Deviation*



Means with the same letter
are not significantly different.

Bon Grouping		Mean	N	Taxon
	A	3.5290	32	HS
B	A	3.1388	32	PT
B	A	3.0462	32	PH
B	C	2.6119	32	MN
	C	2.1680	32	MF
	C	1.9719	32	TG

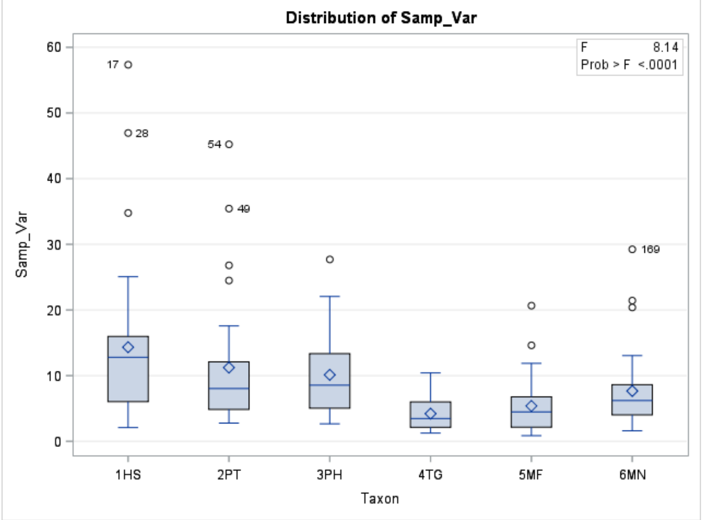
SKELETAL WIDTH, Standard Deviation, GM adjusted



Means with the same letter
are not significantly different.

Bon Grouping	Mean	N	Taxon
A	0.045419	32	5MF
A	0.043982	32	1HS
A	0.042821	32	6MN
A	0.042307	32	3PH
A	0.041705	32	2PT
A	0.036928	32	4TG

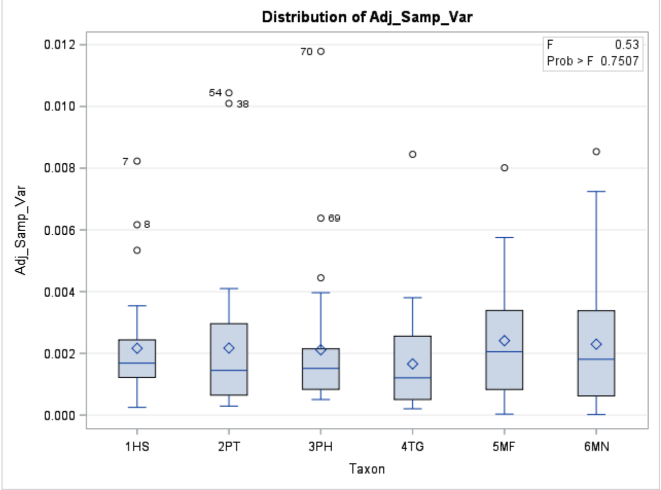
SKELETAL WIDTH, Sample Variance*



Means with the same letter
are not significantly different.

Bon Grouping			Mean	N	Taxon
	A		14.328	32	HS
B	A		11.228	32	PT
B	A	C	10.114	32	PH
B	D	C	7.662	32	MN
	D	C	5.387	32	MF
	D		4.212	32	TG

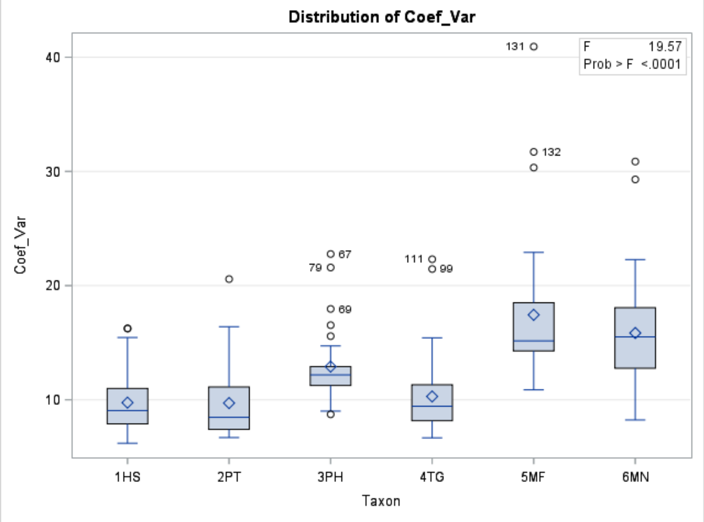
SKELETAL WIDTH, Sample Variance, GM adjusted



Means with the same letter
are not significantly different.

Bon Grouping	Mean	N	Taxon
A	0.002413	32	MF
A	0.002298	32	MN
A	0.002172	32	PT
A	0.002163	32	HS
A	0.002116	32	PH
A	0.001658	32	TG

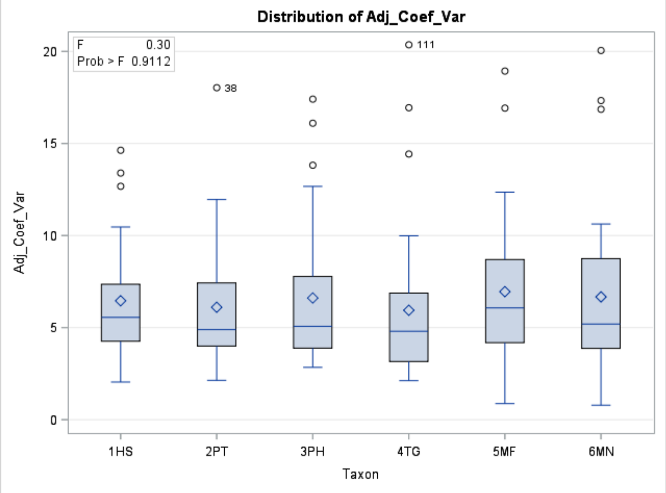
SKELETAL WIDTH, Coefficient of Variation*



Means with the same letter are not significantly different.

Bon Grouping		Mean	N	Taxon
	A	17.439	32	MF
B	A	15.851	32	MN
B	C	12.907	32	PH
D	C	10.288	32	TG
D	C	9.752	32	HS
D		9.712	32	PT

SKELETAL WIDTH, Coefficient of Variation, GM adjusted



Means with the same letter are not significantly different.

Bon Grouping	Mean	N	Taxon
A	6.9500	32	MF
A	6.6699	32	MN
A	6.6103	32	PH
A	6.4563	32	HS
A	6.1025	32	PT
A	5.9401	32	TG

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